Metazoa: Platyzoa

Abreviated Dendrogram

```
BILATERIA
|--Chaetognatha
|--Deuterostomia
`--+--Spiralia
   |  |--Mollusca
   |  |--Annelida
   |  |--Brachiopoda
   |  `--Platyzoa
   `--Ecdysozoa
```

Contents

Overview

The free-living flatworm *Dugesia gonocephala*
Photo by Biopix, via Encyclopaedia of Life - Platyhelminthes, Creative Commons Attribution Non-Commercial

The Platyzoa are one of the many new taxa proposed in the 1990s. It was proposed by Thomas Cavalier-Smith in 1998 as an infrakingdom for the Platyhelminthes or flatworms and several phyla of microscopic animals, and since then supported (or not) by some molecular phylogenists. It is quite likely that Platyzoa is not a clade but a paraphyletic or polyphyletic assemblage of Spiralia ("Lophotrochozoan") phyla, the members of which have undergone minaturisation and/or simplification of body plans, and hence acquired characteristics. Despite appearing to be something of a wastebasket taxon for non-ecdysozoan acoelomate or pseudocoelomate animals, some of these phyla may still constitute a monophyletic group. MAK120423

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Brachiopoda

```
LOPHOTROCHOZOA
|--Bryozoa
`--"Halkieriida"
   |--MOLLUSCA
   `--+--Annelida
      `--+--Tommotiida
         `--BRACHIOPODA
            |--Linguliformea
            `--+--Craniiformea
               `--Rhynchonelliformea
```

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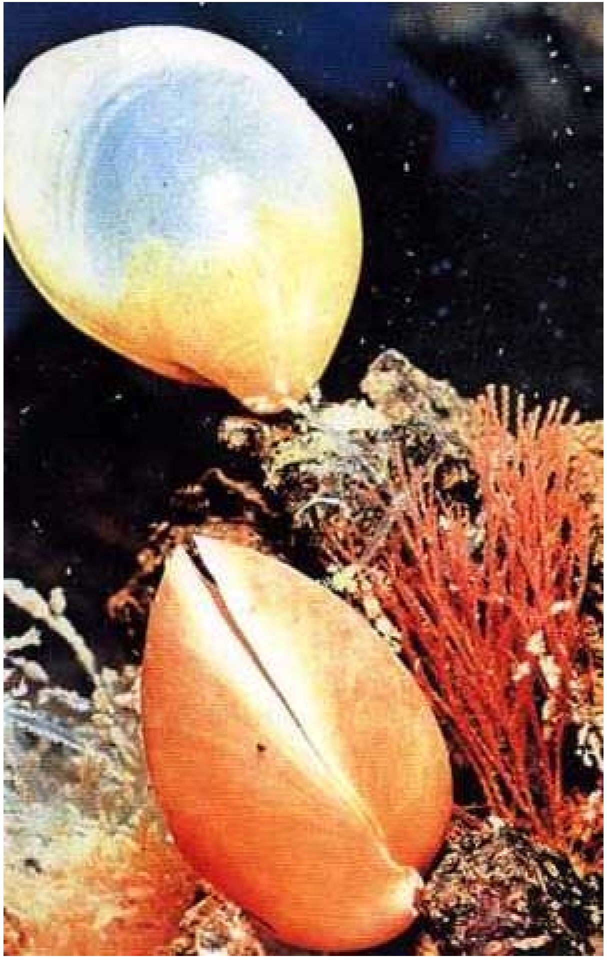
The Brachiopods



Apart perhaps from the trilobite, no other organism typifies the Age of Invertebrates more than the brachiopod. They were the first animals to loose their mobility and encase their bodies in a solid external shell. Despite a superficially similar appearance to clams, they are actually completely different in their anatomy, belonging to the group known as the *Lophophorata*, which use a fringe of tentacles known as the *lophophore* to sweep food particles into their mouths. Brachiopods are rare today, but during the Paleozoic era (especially from the Middle Ordovician period onwards) they absolutely dominated every benthic (bottom-living) marine ecology, their shells accumulating in countless billions. Today their petrified remains are the most common of all fossils.

Brachiopods

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Brachiopoda

```
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|--Bryozoa
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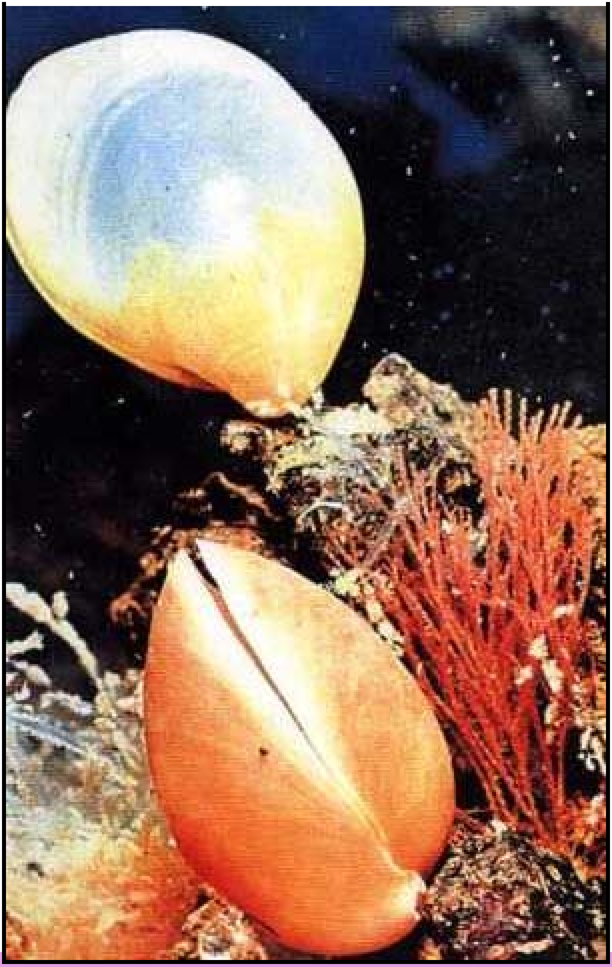
Introduction

Apart perhaps from the trilobite, no other organism typifies the Age of Invertebrates more than the brachiopod. They were the first bilaterian animals to lose their mobility and encase their bodies in a solid external shell. Despite a superficially similar appearance to clams, they are actually completely different in their anatomy, belonging to the group known as the *Lophophorata*, which use a fringe of tentacles known as the *lophophore* to sweep food particles into their mouths. Brachiopods are rare today, but during the Paleozoic era (especially from the Middle Ordovician period onwards) they absolutely dominated every benthic (bottom-living) marine ecology, their shells accumulating in countless billions. Today their petrified remains are the most common of all fossils.

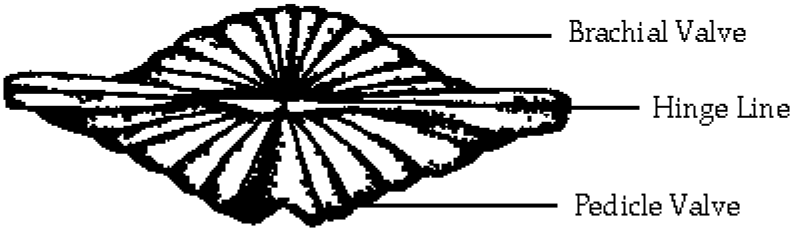
Brachiopods are marine shelled invertebrates that look superficially very much like clams. They are actually quite different from clams in their anatomy, and they are not closely related to mollusks at all. In fact they belong to a (possibly polyphyletic) group known as the *Lophophorata*, because they feed by using a fringe of tentacles known as the *lophophore*. These tentacles sweep microscopic food particles in the water into the creature's mouth. Most species of brachiopods are attached to the substrate by a muscular stalk, known as the *pedicle*. There is however still a free-floating larval stage.

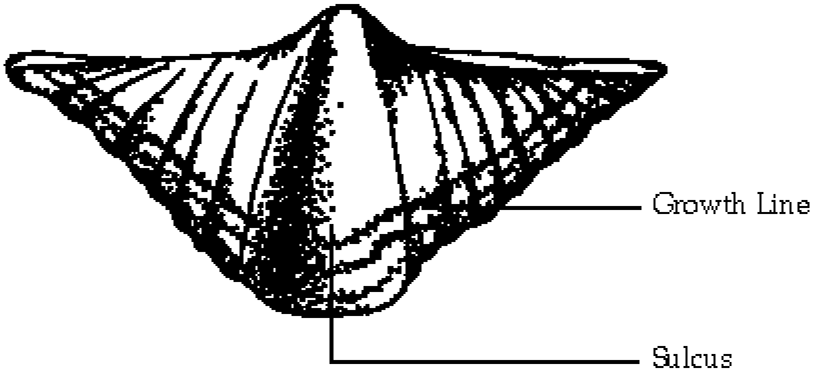
Sixteen hundred genera and many more species of Brachiopoda are known altogether, the vast majority being fossil (extinct) forms.



The Brachiopod Shell

Brachiopods superficially resemble bivalve mollusks in that the animal secretes a bivalved (two-part) shell of calcium carbonate or a combination of calcium phosphate and chitinous organic substance. However, Bivalve mollusks generally have shells that are equal in size and shape (although mirror images of each other), whereas the two shells of brachiopods are of unequal size (the technical term is *inequalvalved*). The *valve* (shell) that has the attachment for the pedicle is the *pedicle valve* which is usually the lower and larger valve. This valve includes the pedicle opening.





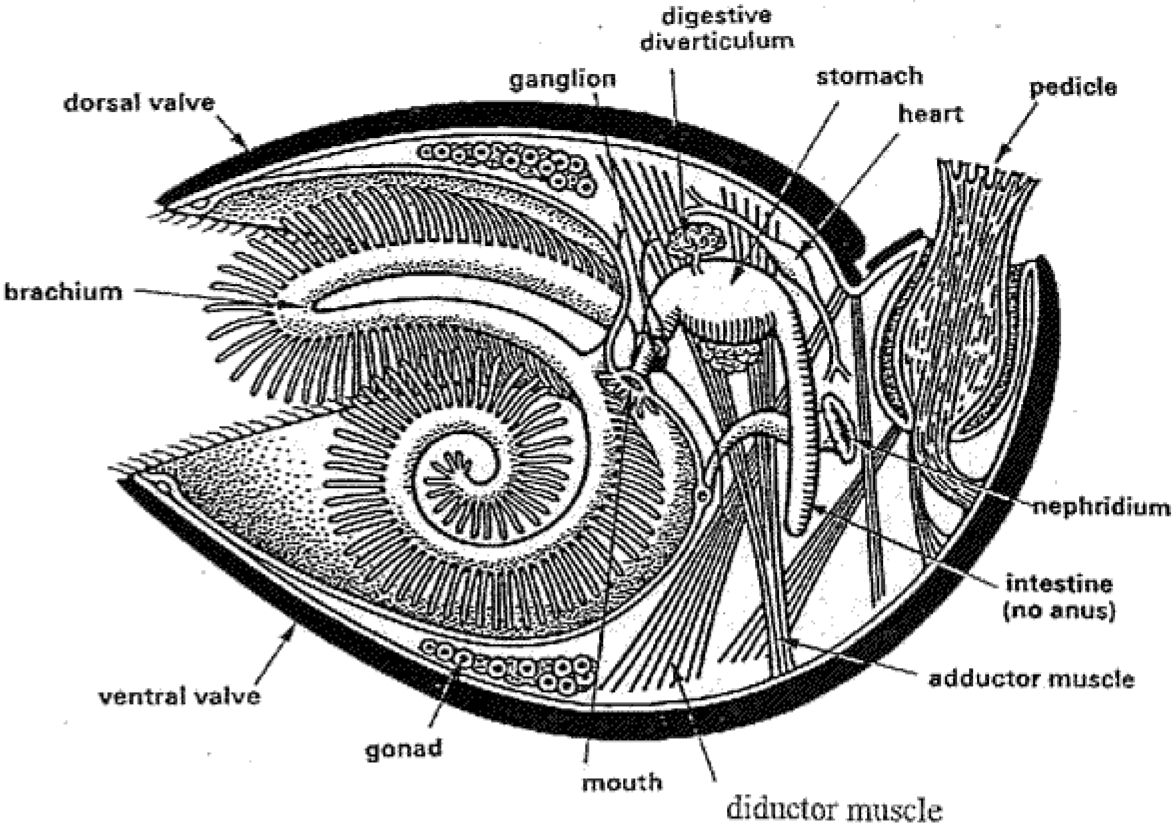
The valve that holds the a feeding tentacles - the lophophore or *brachia* - is called, naturally enough, the *brachial valve*. The *brachidium*, a long ribbon or loop-shaped calcified support for the lophophore, is attached to this shell. The brachial valve is usually, but not always, on the dorsal ("top") side of the organism.

Usually on the pedicle valve there is a raised area called the *fold* with a complimentary depression, the *sulcus*, on the brachial valve.

The area where the two valves are in permanent contact is the *hinge*. The hinge may extend across the entire posterior of both valves, in which case the shell is called *Strophic*. In *Non-Strophic* brachiopods the hinge axis passes through teeth and sockets and these serve as a fulcrum for the opening and closing of the shell.

The brachiopods have traditionally been divided into two classes, the Inarticulata and the Articulata. This classification is now no longer considered valid by many workers in this field. Nevertheless it is still useful as a functional analysis. In articulate brachiopods the hinge axis is lined with a set of interlocking teeth and sockets. Inarticulate brachiopods, as their name indicates, lack these teeth and sockets by which to articulate.

Anatomy



The interior of the shell is lined with a *mantle*, a membranous duplication of the body wall, through which respiration may occur and which secretes the shells. The shell is closed and opened by *adductor* and *diductor* muscles respectively. The scars of these muscles may be seen on the inside of the valves. The body of the animal occupies only about one-third of the interior of the shell. The rest is taken up by the *lophophore*, which is supported by a two-limbed, calcareous structure, the *brachidium*. The brachidium is variable in shape consisting in its simplest form of the *loop* of two short or moderately long, curved structures, and in its more complex form of two thin, spirally coiled ribbons or *spires*. The shape of the brachidium is very important in determining the classification of brachiopod types. The brachidium supports the *brachia*, the fleshy arm-like part of the lophophore which bear the tentacles or *cirri* that sweep food particles into the mouth.

Ecology

Unlike their cousins the bryozoans, brachiopods are solitary, and never form colonies. They are limited to marine environments, although some inarticulate brachiopods like *Lingula* tolerate brackish water. During the early to mid Paleozoic Lingulids lived in association with armoured jawless fish (Ostracoderms) in marginal marine environments.

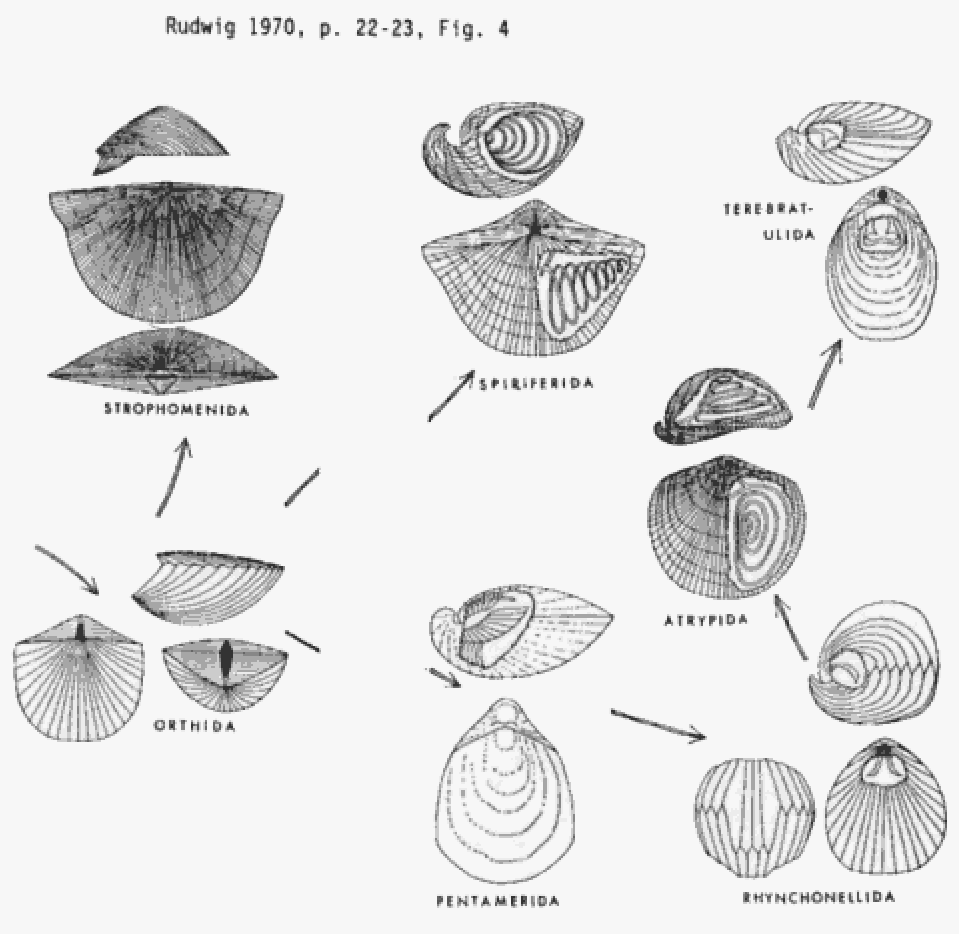
Brachiopods are sessile (attached to a substrate), benthic (bottom-living) suspension-feeders, feeding on micro-organisms or organic particles dissolved in the water. Most brachiopods were or are epifaunal, living on the surface of the sea-bottom, but a few, like the very primitive and ancient inarticulate genus *Lingula* is infaunal, burrowing in the sediment. Some articulate species also apparently lived partially buried in the sediment, but these were exceptional. Generally brachiopods differed from bivalves in that bivalves have explored and taken over the *infaunal* (buried) zone, something the articulate brachiopods were (with a few exceptions) unable to do.

Recent species attached to a surface by the pedicle. Some species have pedicles that are fibrous and muscular and can elevate and rotate the shell directly, while in others the pedicles are inert anchors. Some extinct brachiopods either have no pedicle openings or have a tiny opening for a pedicle that served a tethering function, but did not support the shell. These species were free lying. These did not attach to the substrate but simply grew in piles. Some of these species had a functional pedicle in the juvenile stage, but became free-lying as adults. Going to the other extreme some recent inarticulates and some fossil articulates, cemented their shells to the substrate.

Brachiopods have evolved to use very little energy or oxygen. Consequently they are found in marginal environments such as deep-water, dysaerobic and brackish settings. In the past brachiopods were often a dominant organism in their ecosystem. Usually several species are found together.

Benthic assemblages of brachiopods are correlated with increasing depth. The determining factors were temperature, water pressure, water turbulence, salinity, substrate and food supply.

Evolutionary History


Rudwig 1970, p. 22-23, Fig. 4

Despite their unassuming character, the brachiopods constitute one of the most important and abundant groups of Paleozoic marine organisms. They diversified into a number of different morphologies and even participated in the build-up of ancient reefs. Certainly in terms of numbers of fossil remains they are the most numerous of any paleozoic organism. Fossil brachiopods are a favourite subject for paleontologists because of their abundance, diversity, and usefulness in stratigraphic correlation. They are much less important in neontological zoology, and most of the knowledge of modern species is based upon old studies.

Brachiopods first appear at the very beginning of the Cambrian Period. During this time they were almost entirely (apart from a few rare types) Inarticulates. There were a number of lineages of Inarticulate type. These developed either or both the strophic (wide) hinge and the calcitic shell that typify the articulate condition. The first true articulates, the strophic order Orthida also appear at this time. The syntrophidiine (strophic hinged) pentamerids appeared a little later, during the Middle Cambrian. Some of the small Inarticulate orders died out about this time.

The Articulate Brachiopods (see above diagram for representative types) expanded greatly in numbers and diversity during the Ordovician. It was during this period that they attained a pre-eminence that they would hold until the end of the Paleozoic era. 200 genera are known from the Late Ordovician alone, but this is probably only a tiny fraction of the real number of types alive then.

The Early Ordovician saw not only a great increase in the Orthids and Pentamerids, but also the origin of two important orders, the strophomenids and the rhynchonellids. The latter represented the first truly non-strophic (narrow hinge) shells with a purely internal articulation (teeth-sockets); a configuration more like that of bivalves. The rhynchonellids in their turn seem to have given rise to the atrypids and athyrids spire-bearers. It is now believed that these types evolved a spiral or coiled lophophore independently of true spirifids, which appeared during the Late Ordovician-.

The Ordovician represented the heyday for the Orthids, which outnumbered every other order of brachiopod. The Inarticulates also seem to have reached their peak around this time, although they were rather rarer than the Articulates.

The terminal Ordovician extinction hit the Orthids badly. By the start of the Silurian they were no more diverse than the other Brachiopod lineages. The Silurian in general seems to have been a rather uneventful time for brachiopod evolution. At this time the Inarticulate types had become quite rare, and they were never again to retain their Cambrian status.

During the Devonian period the articulate brachiopods underwent another great evolutionary radiation, like that of the Ordovician. This period represented the peak of diversity for the Spiriferida. So abundant were these brachiopods that the Devonian period can well be called the "age of spiriferids". At the same time important new groups like the strophomenids and the terebratulids appeared. Conversely there was a general decline and widespread extinction of pentamerids and atrypid spiriferids.

The Carboniferous period saw the Spiriferids supplanted by the strophomenids, especially the productids, which were to remain the most important brachiopod group until the end of the Permian. During this time the other orders of brachiopods declined slightly (e.g.Spiriferids, Orthids), or remained at the same stage of diversity as they had attained during the Devonian.

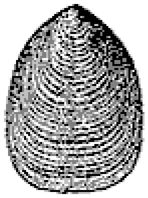
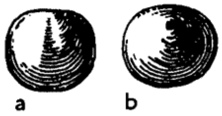
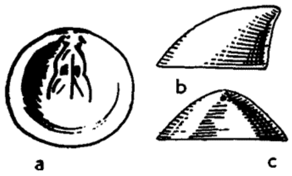
The Brachiopods were much reduced by the terminal Permian extinction, with the Orthids being wiped out entirely. The spiriferids and strophomenids made it into the Triassic in reduced numbers, the strophomenids being now very rare. Most of the remaining Spiriferids were knocked out by the Triassic terminal extinction, with only a few stragglers making it through to the Jurassic.

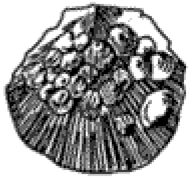
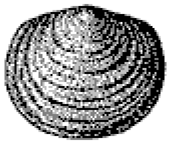
The Terebratulids and Rhynchonellids staged a mild resurgence during the Jurassic, while during the same period the spiriferids and strophomenids died out completely.

By the Cretaceous period only the Terebratulids and Rhynchonellids remained in any number. They were accompanied by two surviving orders of Inarticulates and the enigmatic Thecideida.

The Brachiopods now make up a relatively insignificant element in most marine faunas. Most surviving forms are found in parts of the Pacific Ocean, mostly in very cold water, either in polar regions or at great depths in the ocean. There are seventy surviving genera and about 300 living species of brachiopods.

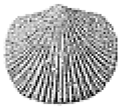
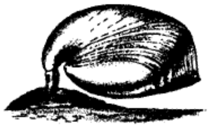
Inarticulate brachiopods

				
Lingulida	**Discinida**	**Acrotretida**	**Siphonotretida**	**Paterinida**

	**no image available yet**		

Craniida	**Chileata**	**Obolellida**	**Kutorginida**

Articulate brachiopods

no image available yet			
		Unidentified spiriferidines from Invertebrate Paleontology Tutorial (SUNY Cortland)	*Sellithyris* from Asociación "Amigos de la paleontología de Morella"
Strophomenida	**Orthida**	**Spiriferida**	**Terebratulida**
			
Ripidiorhynchus, adapted from Sokiran (2002)			
Rhynchonellida	**Atrypida**	**Athyridida**	**Pentamerida**

Links

Links

Introduction to the Brachiopoda

Brachio-Philes - a good up to date intro to the Brachiopods

The Centre for Recent Brachiopod Taxonomy

BrachNet - this European Web site includes up-to-date information on Brachiopoda, references, systematics, diagnoses...) a directory of specialists working on brachiopods (Brachiopodologists - yes, there is such a term!).

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Linguliformea

(Early Cambrian to Recent)

```
BRACHIOPODA
|-Linguliformea
|  |--Paterinida
|  `--Lingulata
|     |--Lingulida
|     `--Acrotretida
|        |--Discinida
|        `--Acrotretoidea
`--+--Craniiformea
   `--Rhynchonelliformea
```

Lingula anatina, from Open Cage.

Editor's note: Palaeos is a huge project, and hence updating it is beyond the scope of one person. For tis reason, and pending more original material, I have decided to cheat by copying (with minor editing, from Wikipedia MAK120107

In the revised classification of Brachiopods used in the current edition of the *Treatise*, Linguliformea is one of the three subphyla and major clades of brachiopods. Like the other two groups, they range from the Cambrian to Recent. These inarticulate brachiopods diversified and flourished during the Cambrian and Ordovician, but declined thereafter, with only a single order, the extant Lingulida, making it into the late Paleozoic.

Linguliforms have adductor and oblique muscles, but no diductor muscles. The anus is located at the side of the body. The pedicle is a hollow extension of the ventral body wall. Posterior body wall separates dorsal and ventral mantles. Their shells are usually made up of apatite (calcium phosphate), however rare cases have calcite or aragonite shells.

Characters (from Williams & Holmer 2002): Shell laminar, organophosphatic, attached by a pedicel developing as an outgrowth of the posterior body wall; gut U-shaped with both mouth and anus opening into mantle cavity.

There are two classes: Lingulata and Paterinata

Dendrogram

(only a few of the many genera and species are shown)

```
Linguliformea [Lingulata]
   |  i. s.: Oepikites
   |         Discinida
   |         Siphonotretida
   |--+--Schizambon
   |  |--Paterinidae [Paterinata, Paterinida]
   |  |    |--Paterina
   |  |    `--Micromitra Meek 1873
   |  |         |--*M. sculptilis Meek 1873
   |  |         `--M. modesta Lochman 1940
   |  `--+--Acrothele
   |     `--Linguloidea [Lingulida]
   |          |--Lingula
   |          |     |--L. anatina
   |          |     |--L. lingua
   |          |     |--L. subparallela
   |          |     `--L. yunnanensis
   |          |--Lingulellotreta Koneva in Gorjansky & Koneva 1983 [Lingulellotretidae]
   |          |        `--L. malongensis Rong 1974 [=Lingulepis malongensis]
   |          |--Obolus apollinis
   |          `--Lingulella chengjiangensis
   `--Acrotretida
        |  i. s.: Prototreta
        `--Acrotretidae
             |--Acrotretinae
             |    |--Angulotreta Palmer 1954
             |    |    `--*A. triangularis Palmer 1954
             |    `--Linnarssonella Walcott 1902
             |         |--*L. girtyi Walcott 1902
             |         |--L. elongata Bell 1941
             |         `--L. tubicula Robson, Nowlan & Pratt 2003
             |--Neotretinae
             |    |--Neotreta Sobolev 1976
             |    |    |--*N. tumida Sobolev 1976
             |    |    `--N. davidi Popov, Berg-Madsen & Holmer 1994
             |    `--Rhondellina Rowell 1986
             |         |--*R. dorei Rowell 1986
             |         |--R. albertensis Robson, Nowlan & Pratt 2003
             |         `--R. karatauensis Koneva 1992
             `--Linnarssoniinae
                  |--Opisthotreta Palmer 1954
                  |    `--*O. depressa Palmer 1954
                  |--Stilpnotreta Henderson & MacKinnon 1981
                  |    `--*S. magna Henderson & MacKinnon 1981
                  `--Picnotreta Henderson & MacKinnon 1981
                       |--*P. debilis Henderson & MacKinnon 1981
                       |--P. karakichiensis Holmer et al. 2001
                       |--P. lophocracenta Robson & Pratt 2001
                       `--P. robusta Holmer, Popov & Lehnert 1999
```

* Type species of genus indicated

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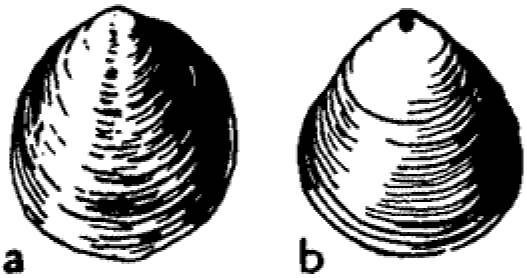
Siphonotretida

(Furongian-Ordovician)



Siphonotreta tertis (Walcott)
a, brachial and **b** pedicle valves
length about 5 mm
Furongian, Alberta.
image from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.224

The siphonotretids are another one of the many small early lineages of inarticulate brachiopods. Both valves typically have obtuse-angle interareas and marginal apices. The pedicle opening is apical or in front of the apex of the pedicle valve (see above, right)

Characters: "Primitive thick-walled calcareous or chitinous shells with the pedicle emerging through a ventral sheath. The pedicle opening is circular, tends to be axial, and is not modified by a listrium. It may be posterior or anterior to the protegulum and may be elongate if it has migrated through the protegulum." - Twenhofel, W. H., and Shrock, R. R., *Invertebrate Paleontology,* 1935. McGraw- Hill Book Co., N. Y. p.287 (copyright expired)

Life posture of Schizambon. The pedicle opening is located between the apex of the pedicle valve and the shell margin.

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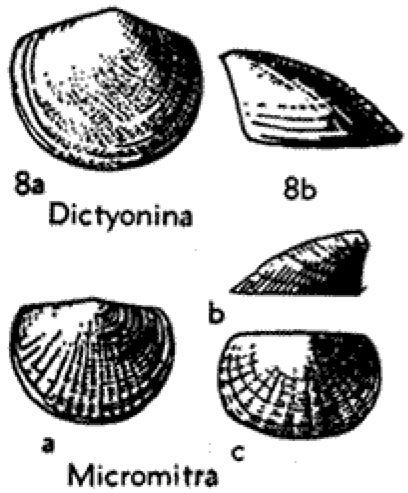
Paterinida

(Early Cambrian to Late Ordovician)

```
BRACHIOPODA
|-Linguliformea
|   |--Paterinida
|   `--Lingulata
|      |--Lingulida
|      `--Acrotretida
|         |--Discinida
|         `--Acrotretoidea
`--+--Craniiformea
   `--Rhynchonelliformea
```



Representative Paterinida:

Dictyonina, Early to Middle Cambrian. The surface is marked by obliquely intersecting rows of minute pits
Dictyonina pannula (White) (**a**, **b**, pedicle valve), Middle Cambrian, Nevada, width 3 mm

Micromitra, Early to Middle Cambrian. The surface is marked by concentric lines and low radial ridges.
Micromitra sculptilis (Meek) (**a**, **b**, pedicle valve; **c**.brachial valve), Middle Cambrian, Montana. width 4 mm

from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, pp.224-5

This small group of Linguliform inarticulate brachiopods includes only about 14 known genera. They seem to be only distantly related to all other brachiopods.

These tiny brachiopods possess chitinophosphatic shells, mostly having maximum dimensions of 2 to 7.5 mm and characterized by a distinct palintrope on the pedicle valve. The delthyrium is largely closed by a homeodeltidium. Growth of the pedicle valve is mixo-peripheral, as shown by presence of a palintrope. That of the brachial valve is hemiperipheral. The larval shells are pustulose. The cardinal margins lack setae.

A shell consisting of chitino-phosphate would seem to indicate they are typical "inarticulates", whilst the biconvex valves with their essentially straight posterior margin, well developed pseudointeraea and medianly arched plates resemble the articulates. Wright (1979) suggests they constitute one of a number of groups of "brachiophorates" which developed a skeleton independently from other stocks. The more recent classification on the EuroBrachNet site favours distant relationships with the lingulids

Previously ranked as the Superfamily Paterinacea, these brachiopods have since been elevated to ordinal, and now (perhaps undeservedly for such a small group) class status. The group is mostly limited to the early to middle Cambrian period, with a few stragglers making it through to the Late Ordovician. They are representatives of the first evolutionary wave of invertebrates (the Tommotian biota)

References

A. D. Wright, "Brachiopod Radiation", in Systematics Association Special Volume No.12,*The Origin of Major Invertebrate Groups*, ed. by M. R. House, 1979, pp.235-252, Academic Press, London and New York

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text by M. Alan Kazlev

Palaeos:

LINGULIFORMEA

BRACHIOPODA

LINGULATA

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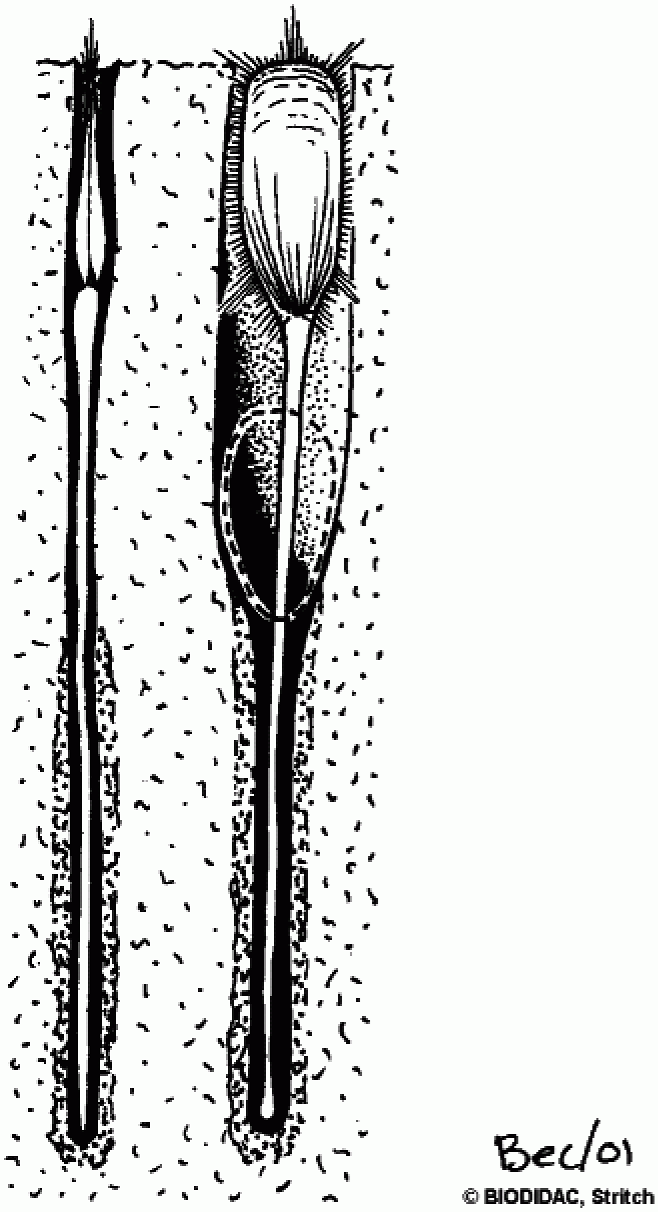
Page Next	Unit Next	Unit Home	References	Dendrogram	Glossary	Time

Lingulata

(Early Cambrian to Recent)

```
BRACHIOPODA
|-Linguliformea
|   |--Paterinida
|   `--Lingulata
|      |--Lingulida
|      `--Acrotretida
|         |--Discinida
|         `--Acrotretoidea
`--+--Craniiformea
   `--Rhynchonelliformea
```



Lingula in its natural habitat. Drawing © Rebecca Stritch, Biodidac - original url

Editor's note: Palaeos is a huge project, and hence updating it is beyond the scope of one person. For tis reason, and pending more original material, I have decided to cheat by copying (with minor editing, from Wikipedia MAK120107

The Lingulata is a class and clade of morphologically conservative brachiopods, that are little changed since the Cambrian. They represent very much the archetypal "inarticulate" brachiooids. The genus *Lingula* (Bruguiere, 1797) is traditionally considered very abcient, first appearing during the Ordovician period (but not the early Cambrian, although earlier related forms date back that far). However it has been argued that *Lingula* itself is recent, dating back nbo further than the Tertiary (the same could be said of *Sphenodon*, another tradtionally "living fossil" that has been shown to be more recent than usually believed).

The Lingulata have tongue-shaped shells (hence the name Lingulata, from the Latin word for "tongue") with a long fleshy stalk, or pedicle, with which the animal burrows into sandy or muddy sediments. They inhabit vertical burrows with the anterior end facing up and slightly exposed. The cilia of the lophophore generate a feeding and respiratory current through the lophophore and mantle cavity. The gut is complete and J-shaped.

The shells are composed of a combination of calcium phosphate, protein and chitin. This is unlike most other shelled marine animals, whose shells are made of calcium carbonate. The Lingulata are inarticulate brachiopods, so named for the simplicity of their hinge mechanism. This mechanism lacks teeth and is held together only by a complex musculature. Both valves are roughly symmetrical.

There are three orders: Acrotretida, Lingulida, and the early Paleozoic Siphonotretida

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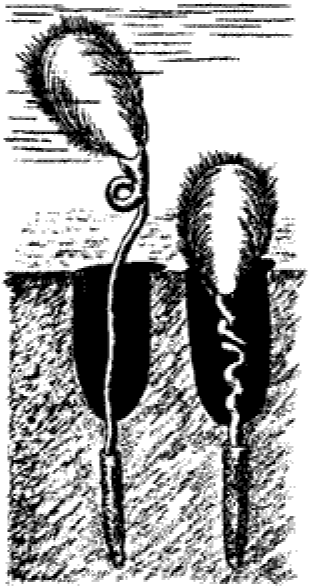
Lingulida

(Early Cambrian to Recent)

```
BRACHIOPODA
|-Linguliformea
|   |--Paterinida
|   `--Lingulata
|      |--Lingulida
|      `--Acrotretida
|         |--Discinida
|         `--Acrotretoidea
`--+--Craniiformea
   `--Rhynchonelliformea
```

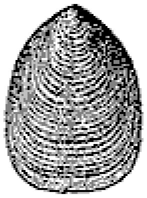


Barroisella, an extinct cousin of the living *Lingula*

Superfamily Linguloidea (Early Cambrian-Recent)
family Lingulidae Menke, 1828

Lingulids are shallow burrowing infaunal filter feeders of the shallow intertidal zone. The shell is chitinophosphatic, and characteristically shaped like a fingernail. Lingulids have a muscular pedicle which extrudes out from the posterior of the shell, between the valves, and a number of lateral muscles for manipulating their valves. The animal burrows by arching its pedicle up to force the anterior portion of the valves down. It then contracts the lateral muscles in sequence to move the valves back and forth in a scissors-like motion, thus burrowing down into the sediment. It remains with the anterior portion of the shell pointed up, and the vulnerable pedicle safely buried in the sediment, helping to anchor the animal.

The Lingulacea range from the Early Cambrian to Recent. Although occurring in normal marine environments, their fossil remains are much more common in shaley beds probably laid down in poorly oxygenated brackish waters, ill-suited for most marine invertebrates. In this environment, the group has maintained itself as "living fossils" with virtually no change in external form down to the present day.



Lingulella davisi
Furongian Epoch

Lingulids appeared in the Tommotian epoch (earliest Cambrian) with *Lingulella* (left). During the Cambrian period they were an important component of the brachiopod faunas. It does not appear that these early representatives could burrow as well as the extant genus *Lingula*. Forms very similar to that genus appeared during the Ordovician period and *Lingula* continues to the present day. *Lingula* differs markedly from earlier forms in the nature of the posterior of the valves, and most obviously in the major reduction of the pseudointerareas.

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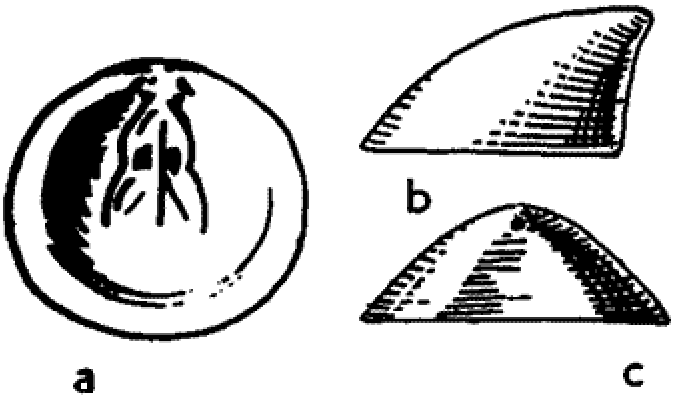
Acrotretida

(from the Early Cambrian)

```
BRACHIOPODA
|-Linguliformea
|   |--Paterinida
|   `--Lingulata
|      |--Lingulida
|      `--Acrotretida
|         |--Discinida
|         `--Acrotretoidea
`--+--Craniiformea
   `--Rhynchonelliformea
```

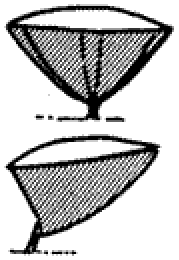


Acrotreta idahoensis Walcott
shell diameter - 2.5 mm
Furongian
image from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.224

Appearing in the earliest Cambrian (Terreneuvian Epoch), these are among the very first hard-shelled organisms. Through their long history (spanning the entire Phanerozoic) they remain quite distinct from other inarticulate brachiopods.

"Chitinous or calcareochitinous, more or less circular, conical, or flattened shells with a circular pedicle opening in the apex of the ventral valve. There is no listrium, but a pseudocardinal area is present." Twenhofel, W. H., and Shrock, R. R., *Invertebrate Paleontology,* 1935. p.287

Acrotretids are usually round with a convex, cap-shaped brachial valve, and a flat pedicle valve. They resemble the paterinids in general outline and very small size, but are distinguished by calcium



carbonate shell, the more distinctly conical form of the pedicle valve and particularly the presence of a minute pedicle foramen, located at or just behind the apex. The posterior slope of the pedicle valve commonly bears a distinct trough; but because the pedicle does not emerge at the base of this trough, next to the valve margin, the indentation cannot be interpreted to denote pressure of the pedicle against the outer side of the valve.

Life posture of Acrotreta is shown at the left. The pedicle emerges from a rounded opening between the apex of the pedicle valve and the nearest shell margin.

The basal acrotretids were most common from the Early Cambrian to Late Ordovician, with a few stragglers managing to continue on until the Devonian (Frasnian Age), when they died out, along with many other forms of life in the Frasnian-Famennian mass extinction. One specialized group, the Discinida, remain.

Systematics

In non-cladistic schemes, there is only one superfamily.

Acrotretoidea (Early Cambrian-Devonian)

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Discinida

(Early Cambrian to Recent)

```
BRACHIOPODA
|-Linguliformea
|   |--Paterinida
|   `--Lingulata
|      |--Lingulida
|      `--Acrotretida
|         |--Discinida
|         `--Acrotretoidea
`--+--Craniiformea
   `--Rhynchonelliformea
```

Superfamily Discinoidea (Early Ordovician-Recent)

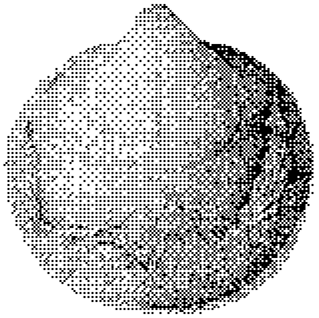
The Discinids are a small long-lived group of inarticulate brachiopods with chitinophosphatic shells. Both valves are rounded, with a convex, cap-shaped discoid to conical brachial valve, and a flat pedicle valve. The pedicle opening is a deep narrow notch indenting the posterior margin of the pedicle valve, or an enclosed narrow slit located behind the apex. Although the shell substance is dominantly chitinophosphatic, some genera have external calcareous shell laminae.

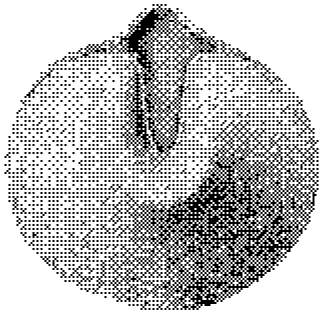
Orbiculoidea, showing attachment when alive. The pedicle valve is nearly completely flat, and circular in outline. the pedicle issues from a slit located between the centrally placed apex and margin of the valve.

The Discinida are variously included under the Acrotretida (in the *Treatise*), or with the Lingulida in the Linguliformes (the EuroBrach arrangement), or (as followed here) in both.

Trematis millipunctata Hall
time: Sandbian, (Late Ordovician-) **place:** Laurentia (North America) **habitat:** shallow water benthos
size: shell about 1.2 cm in diameter

note the pedicle slit


Top view


Bottom view

(Family **Trematidae** - Ordovician to Devonian)
ref: *Treatise on Invertebrate Paleontology*, vol. H page 283.

Trematis page

Schizocrania page

Superfamily Botsfordioidea (Early Cambrian-Middle Cambrian)

Superfamily Acrotheloidea (Early Cambrian-Early Ordovician)

In the *Treatise* these are included under the Acrotretida

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Craniiformea

(Early Cambrian to Recent)

```
LOPHOTROCHOZOA
|--MOLLUSCA
`--+--Annelida
   `--BRACHIOPODA
      |--Linguliformea
      |--+--Craniiformea
      |  |--Craniida
      |  `--+--Craniopsida
      |     `--Trimerellida
      `--Rhynchonelliformea
```

Craniiformea
Craniopsida
Craniida
Trimerellida

These are brachiopods with calcitic inarticulated shells and an unsupported lophophore. In the past they were divided among various inarticulate orders. They do not appear closely related to other brachiopods, articulate or inarticualte, and may have evolved separately from soft-bodied ancestors. There are three orders.

Classification des Brachiopoda

Craniiformea

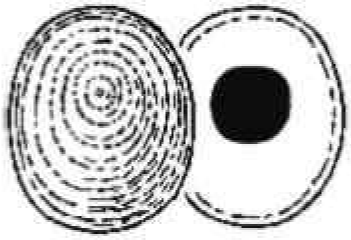
CRANIOPSIDA
Craniopsoidea (?Early or Middle Cambrian - Early Carboniferous)

CRANIIDA
Cranioidea (Early Ordovician-Recent)

TRIMERELLIDA
Trimerelloidea (Early Ordovician-Late Silurian)

Order Craniopsida

(Early Cambrian to Early Carboniferous)



Impunctate, calcite shell. No peduncle.

Family Craniopsidae

More

Image from Senckenberg Research Institute, Frankfurt

Order Craniida

(Early Ordovician - Recent)

Punctate calcite shell, anterior valve cemented to substrate.

Petrocrania scabiosa (Hall) (some 20 specimens attached to a *Raftnesquina* shell, the brachial valves ridged in a manner reflecting costac of the host shell. - diameter of latter 3.5 cm), Late Ordovician-, Indiana.

Philhedra laelia (Hall) (shells attached to a *Rafinesquina* brachial valve, - diameter of latter 3 cm), Late Ordovician-, Kentucky.

Members of the order and superfamily Craniacea have subcircular shells composed of calcium carbonate. In the *Treatise* these inarticulate brachiopods are placed in the order Acrotretida. They are now considered a separate order. According to the current classification, the Craniida are included with Craniopsida and Trimerellida in the Class Craniiformea.

Adult Craniids lack a pedicle opening but are cemented by the exterior of the pedicle valve to a foreign surface, generally another shell. Commonly, the host is a brachiopod, but it may be a coral, bryozoan colony, crinoid stem, or mollusk. Some species seem to choose a particular species of articulate brachiopod as host. They attached to its host shell when the latter was still alive, but it is never found extending onto adjoined valves, as it might if the crainacean grew on an empty shell.

A few members of this group (*Petrocrania*) have the peculiarity of reflecting rather perfectly in the markings of their brachial valve the surface of the host shell to which the craniacean is attached. This may have served the purpose of camouflage, making the animal more inconspicuous.

Superfamily Craniacea
Family Craniidae

More

Order Trimerellida

(Middle Ordovician-Late Silurian)

The Trimerellacea are a small group of quite large inarticulate brachiopods. They have moderately thick calcareous shells, which attain a width of 5 cm and a length of some 8 cm. They were originally included with the lingulids, as features of their palintropes are nearly identical with those of Lingulacea. However the more recent classification places them in a distinct order, even a distinct class. The chief distinguishing feature of the Trimerellacea is the presence of fairly broad calcareous platforms raised above the floor of both pedicle and brachial valves. The platforms are supported by septa, and they serve as a base of the attachment for muscles.

So far as known, this group is limited to the Middle Ordovician to late Silurian period.

More

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Order Craniida

(Early Ordovician - Recent)

The Craniida is a very low diversity group of brachipopods including only the single Superfamily Cranioidea Menke, 1828 and family Craniidae Menke 1828

The following extant and fossil genera are among those included: *Ancistrocrania*, *Crania*, *Craniscus* (extant), *Danocrania*, *Isocrania*, *Neoancistrocrania* (extant), *Novocrania* (extant), and *Valdiviathyris* (extant). *Valdiviathyris* and *Neoancistrocrania* were sometimes separated in a family Valdiviathyrididae although the tendency now is to include them all in a single family

Most Craniidae are long-extinct forms known only from fossils like all other Craniforma. However, some 20 species of this 470-million-year-old lineage are extant today. They include *Valdiviathyris quenstedti* which has remained essentially unchanged for the last 35 million years. Present-day *Valdiviathyris* are all but inseparable from those of the Late Eocene and the genus cannot even be divided into chronospecies. Thus, *V. quenstedti* is a true living fossil and one of the oldest and most long-lived species known to science. Some minimal evolution would obviously have taken place in the meantime, but this would have been essentially silent mutations and marginal adaptations to cooler habitat. - Wikipedia

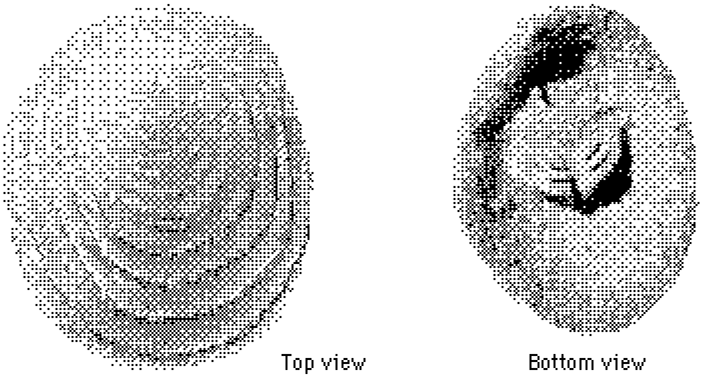
References

Robinson, Jeffrey H. & Lee, Daphne E. (2007): The Recent and Paleogene craniid brachiopod, Valdiviathyris quenstedti Helmcke, 1940. Systematics and Biodiversity 5(1): 123–131. doi:10.1017/S1477200006002179 (HTML abstract)

Brachiopoda main page

Craniopsida

Early Cambrian to Early Carboniferous of North and South America, Europe, & Asia



Craniops - original url

As with the Craniida, this is a low diversity group of inarcticulate brachipods, in this case limited entirely to the Paleozoic. The present page is even more low diversity than its Craniid counterpart, as it is essentially just a holding page, pending more detailed coverage

There is one family Craniopsidae.

Brachiopoda main page

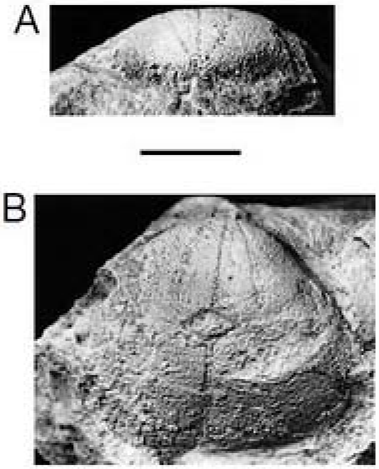


FIG. 1. — *Trimerella* sp., pedicle valve (N 1/12991), loc. 13e, Srednij Formation; **A**, posterior view; **B**, ventral view. Scale bar: 6 mm.

Specimen of *Trimerella*, from Modzalevskaya (2003), via Christopher Taylor's *Taxon Diversity*.

Order Trimerellida

Middle Ordovician to late Silurian

Shell aragonite, with muscle platform. Ordovician to Silurian.

"Brachiopods of this superfamily are both progressive and divergent from the Obolidae, with posterior platforms to which some of the muscles were attached. More advanced forms have rudimentary articulation and a generally prominent ventral cardinal area that is triangular and transversely 'striated. The shells are thick and decidedly inequivalved. Cambrian to Silurian. Trimerella (Silurian) is representative of the super- family and is an important index fossil. " - Twenhofel, W. H., and Shrock, R. R., *Invertebrate Paleontology,* 1935. McGraw- Hill Book Co., N. Y. p.287 (copyright expired)

Includes only the Superfamily Trimerellacea / -oidea.

Originally three families, the Neobolidae, Elkaniidae and Trimerellidae, were included in this superfamily, the first two formerly under the Obolidae (Obolacea). More recently, the following families are included:

- Trimerellidae
- Adensuidae
- Ussuniidae

Reference

Modzalevskaya, T. L. 2003. Silurian and Devonian brachiopods from Severnaya Zemlya (Russian Arctic). *Geodiversitas* 25 (1): 73-107.

**Brachiopoda
main page**

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Rhynchonelliformea

```
BRACHIOPODA
|--Lingulida
`--+--Craniata
   `--Rhynchonelliformea
      |--Chileata
      |--Obolellata
      |--Kutoriginata
      |--Strophomenata
      `--Rhynchonellata
```

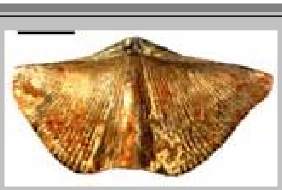
Introduction

Introduction

The Rhynchonelliformea are one of the three major clades of brachiopods. With 30 living species in 22 genera, thay are by far the most common group today. The Rhynchonelliformea include not only the "articulate" brachiopods, but a number of inarticulate forms as well. Nevertheless, they are commonly treated as coextensive with the traditional Articulata (brachiopods with specialized articular teeth, articulating with sockets that join the dorsal and ventral shells). The gut is blind and without an anus. The Rhynchonelliformea have calcareous shells with two distinct layers: a primary (outer) and secondary (inner) layer. The outer layer is lamellar and the inner layer is fibrous.

Extant species are rarely found in tropical waters, but are relatively common in deeper temperate and polar seas. However, this distribution is a relatively recent phenomenon. Paleozoic rhynchonelliforms seemed to have done better in the tropics. Similarly, living rhynchonelliforms are notable for their ability to live at a broad range of water depths. Paleozoic forms seem to have been more specialkized. Kowalewski *et al*. (2002).

In the currently accepted arrangement, the following groups are regarded as part of the Rhychonelliformea:

no image available yet				
Chileata	**Obolellata**	**Kutorginata**	**Strophomenata**	**Rhynchonellata** *Cyrtospirifer* from Virtual Fossils (Univ. di Padua)

References:

Kowalewski, M, MG Sim�es, M Carroll & DL Rodland (2002), *Abundant brachiopods on a tropical, upwelling-influenced shelf (Southeast Brazilian Bight, South Atlantic).* **Palaios** 17: 277-286.

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Subclass/superorder Chileata

Brachiopods with strophic (wide hinge-line), normally inarticulated calcite shells.

Early Cambrian - Permian

There is one order, Chileida

Brachiopoda main page

Class KUTORGINATA - Order Kutorginida

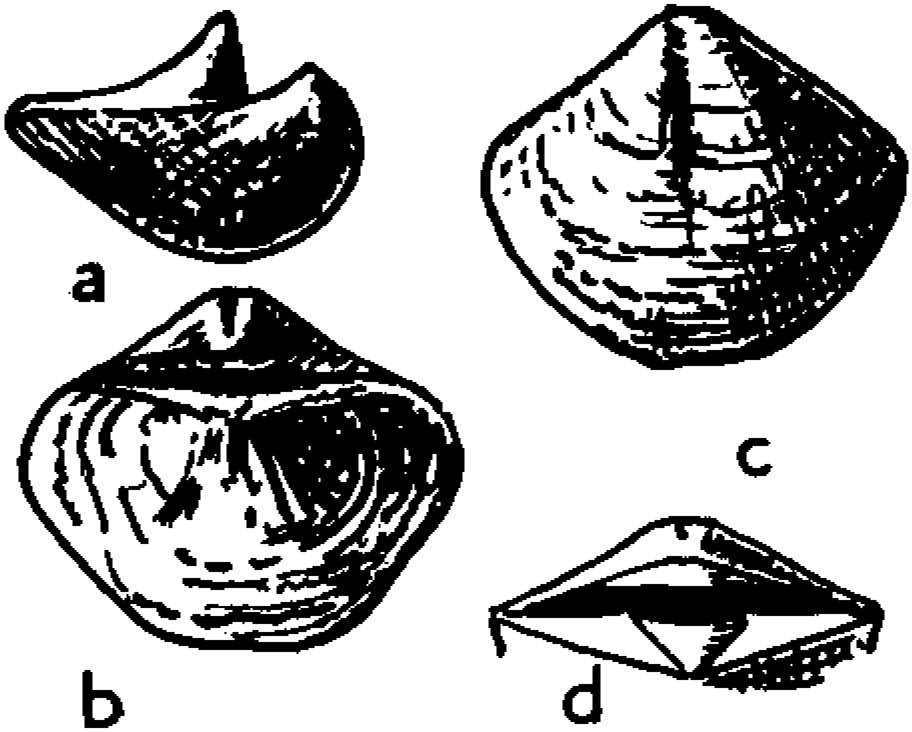
(Early to Middle Cambrian)

Systematics

Classification from *Treatise of Invertebrate Paleontology* - Part H, Revised - Brachiopoda

```
Class KUTORGINATA
        Order Kutorginida
                Superfamily Kutorginoidea (Early to Middle Cambrian)
                        Family Kutorginidae
                Superfamily Nisusioidea  (Early to Middle Cambrian)
                        Family Nisusiidae
```

Superfamily Kutorginoidea



Kutorgina cingulata (Billings)
Early Cambrian, east Laurentia (Vermont)
a, side view of shell, pedicle valve below; b, c, brachial and pedicle views;
d, interareas, showing partial closure of deithyrium by wide, narrow deltidium
width about 1.7 cm
image from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw Hill, New York, 1952, p.226

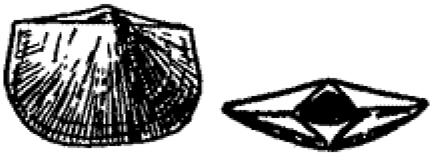
The Kutorginoidea are the earliest brachiopod order which possesses a calcareous shell, and among the earliest of all brachiopod lineages. They were originally included in the Palaeotremata, a now discarded order that was erected for supposedly ancestral members of the Articulae lineage. They were then transferred to their own order (now considered a class) of Inarticulates. There is still considerable uncertainty over their taxonomic position. The most recent classification considers them Rhynchonelliform brachiopods (distantly allied to articulates).

The shell microstructure is fibrous and impunctate. The overall morphology is ventribiconvex, with a strophic (straight) hinge.

The pedicle valve has a prominent beak which curves over interarea of the brachial valve. It also possesses a supra-foramen and an interarea (or pseudointerarea) with a very wide triangular delthyrium, which resembles the billingsellacean articulates in that it is partially closed by a pseudo- deltidium. The brachial valve has a relatively prominent interarea and a plate, equivalent to the chilidium of other articulates, which closes the space beneath the beak. The valve interiors are poorly known and understood, and the teeth and sockets characterizing the articulates have not been positively identified.

The group is entirely limited to the early to middle Cambrian period, and does not appear to be closely related to other brachiopods. They are representatives of the first evolutionary wave of invertebrates (the Tommotian biota)

Superfamily Nisusioidea



Nisusia montanaensis Bell
Middle Cambrian
West Laurentia (Montana)
width - 1.5 cm
note: the asymmetry of the left and right halves is an artifact of preservation
image from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.229

The Atdabanian epoch saw the emergence of the calcareous shelled Nisusiidae, the earliest and most primitive of the articulate brachiopods. The articulates are generally considered to have arisen from earlier inarticulates, although even in the earliest representatives of the group (*Nisusia*) possessed a well-developed hinge line and interareas. It is possible they developed from a biconvex obolid-like chitino-phosphatic stock, although this raises the biochemical problem of how the original calcium phosphate shell could change into one of calcium carbonate. Gutmann et al. (1978) have explained the development of the articulates as a gradual series of changes involving the development of the interarea and the improvement of the contact between the valves. Through hinge development, the comparatively bulky hydraulic valve opening mechanism could be reduced to a much smaller muscle system in the rear of the shell. This has the adaptive advantage of freeing two thirds of the space within the shell cavity for the function of food gathering by the lophophore. In any case, no transitional forms have been found.

Brachiopoda main page

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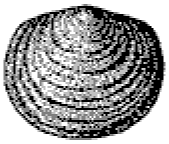
Order Obolellida

(Early to Middle Cambrian)



Obolella comleyensis
Early Cambrian
(Atdabanian to Botomian)
England

The Obolellida constitute a short-lived order, apparently becoming extinct in the middle Cambrian, whose relationship to the other "inarticulates" is obscure. They previously lumped with the Siphonotretacea, then given their own order. A. D. Wright suggests they represent a lineage distinct from other brachiopods, arising independently from a general brachiophorate ancestor and developing the ability to secrete a calcareous shell. In the most recent classification they are considered a distinct class related to the articulate line.

The Obolellids have a foliated, impunctate, biconvex (*left*) shell. As with the lingulids there is no hinge, in this respect they are typically inarticulate. Denticles on either side of a narrow delthyrium or ventral platform serve to articulate the valves. Examination of the shell structure of *Trematobolus* revealed a coarsely crystalline primary layer succeeded by a laminar secondary layer. The laminae are interpreted as being separated by protein sheets with a similar growth pattern to the modern *Crania*.

Although the obolellids have a general inarticulate external appearance and muscle scar distribution; the group is somewhat unusual in the very variable disposition of the pedicle, which may emerge from a grooved interarea, or a foramen situated either apically or anterior to the beak. In the typical Early Cambrian genus *Obolella* (above) the valves low and oval, nearly equal; and opening for the pedicle is tiny, and located near apex of the pedicle valve.

The group is entirely limited to the early to middle Cambrian period, being representatives of the first evolutionary wave of invertebrates (the Tommotian biota)

Systematics

Obolellida

Obolelloidea (Early Cambrian-Middle Cambrian)

Naukatida
Naukatoidea (Early Cambrian-Middle Cambrian)

Classification from Classification des Brachiopoda (Lophophorata)

A. D. Wright, "Brachiopod Radiation", in Systematics Association Special Volume No.12, *The Origin of Major Invertebrate Groups*, ed. by M. R. House, 1979, pp.235-252, Academic Press, London and New York

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Brachiopoda main page

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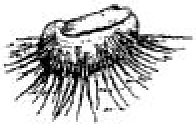
Class Strophomenata

image © Bruce Moore, Taxonomy of the Articulate Brachiopoda

The Strophomenata are a wholly Paleozoic class; one of the two classes of advanced articulate brachiopods. They first appear in the middle Cambrian and continue through to the Late Permian. From the Devonian through to the Permian they are the most abundant of all brachiopods, adopting a large range of life-styles, including bivalve-like infaunal existence, and in another group, a coral-like growth habit. There are four orders, which are shown here:

			
Billingsellida	Orthotetida	Strophomenida	Productida

Many strophomenates may be identified by their supra-apically located pedicle foramen, at least in young shells. Adult strophomenids and productids lacked an open pedicle foramen, and usually lived attached to the bottom or to other objects by the pedicle valve.

There is also a tendency among productids to cement their shells to the substrate. Strophomenids may have a scar on the umbo that was apparently the point of attachment for the juvenile stage, and some extreme productids even adopted a coral-like existence.

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Order Billingsellida

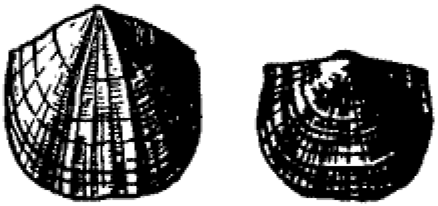
The Billingsellids are among the most primitive of all articulate brachiopods, and also among the first to appear. Originally included with the Orthids, they have since been placed closer to the Strophomenids. Currently they are included in the Class Strophomenata of the Subphylum Rhynchonelliformea

Systematics

Classification from *Treatise of Invertebrate Paleontology - Part H, Revised - Brachiopoda*, and elsewhere

```
Order BILLINGSELLIDA
        Suborder Billingsellidina (Middle Cambrian-Lower Ordovician)
        Superfamily Billingselloidea (Middle Cambrian to Early Ordovician)
                Family Billingsellidae
        Suborder Clitambonitidina (Early to Late  Ordovician)
        Superfamily Clitambonitoidea
                Family Clitambonitidae
                Family Gonambonitidae
        Superfamily Polytoechioidea
                Family Polytoechiidae
```

Suborder Billingsellidina



Billingsella perfecta
Furongian
West Laurentia (Montana)
width 1.5 cm
image from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.229

The middle Cambrian saw a new brachiopod lineage appear, the Billingsellidae. The Nisusiidae were previously included with the family Billingsellidae in the superfamily Billingsellacea, but shell structure indicates this is unlikely. The secondary shell of *Nisusia* is fibrous with a pattern identical to that of modern Terebratulides and rhynchonellides in which the calcite fibres are segregated by protein sheaths. Billingsella in contrast has a laminar secondary shell characteristic of other, quite distinct, groups of articulate brachiopods. This fundamental distinction in forms which morphologically are very similar is puzzling.

The billingsellaceans may form the ancestral stock from which all the subsequent articulate brachiopods are believed to have been derived. The superfamily has conventionally been placed in the Orthida, but is now placed with the Clitambonitidina in a separate order

Suborder Clitambonitidina

image © Bruce Moore - Taxonomy of the Articulate Brachiopoda

These persistently primitive articulate brachiopods were previously included in the Orthida, but are now considered closely related to (and probably descended from) the Billingsellidina. Ventral muscle field impressed on spondylium. The socket ridges diverge at a sharp angle, and the chilidium is convex .

They retaining the primitive features of the deltidia and chilidia. Simple spondylia or more rarely pseudospondylia are developed. The shells are impunctate. (*Invertebrate Paleontology,* 1935 p.291)

There are two superfamilies, the impunctate Clitambonitacea and the pseudopunctate Gonambonitacea, which are also distinguished by the type of radial ornamentation on the surface of the shell

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**Brachiopoda
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Order Orthotetida

(Ordovician - Permian)

The Orthotetida are derived from the Strophomenida, and are in part included in them in older classifications. There are two suborders, the Orthotetidina and the Triplesiidina, the former with a number of families

```
      Order ORTHOTETIDA
              Suborder Orthotetidina
                      Superfamily Orthotetoidea  (Early or  Middle Devonian to Late Permian)
                              Family ORTHOTETIDAE
                              Family Pulsiidae
                              Family Orthotetellidae
                              Family Derbyiidae
                              Family Meekellidae
                              Family Schuchertellidae
                      Superfamily Chilidiopsoidea (Middle or Late  Ordovician to Early
Carboniferous)
                              Family Chilidiopsidae
                              Family Areostrophiidae
              Suborder Triplesiidina
                      Superfamily Triplesioidea (Early Ordovician to Late Silurian)
                              Family Triplesiidae
```

Suborder Orthotetidina

(Early Ordovician - Late Permian)

Originally included under the Strophomenina, these unusual brachiopods appeared during the Ordovician but reached their latest culmination during the Permian period, with bizarre flattened forms like *Leptodus*. In this genus, the pedicle valve somewhat resembles an oyster, and this genus was even attached oyster-like by cementation of its pedicle valve to other shells. The interior of the pedicle valve bears a low median ridge, and on either side of it are grooves and ridges arranged normal to the median ridge. The brachial valve is extremely thin, and flat or slightly concave, fitting neatly over the pedicle valve. Lateral slits in the brachial valve overly the ridges of the pedicle interior, perhaps reflecting a pattern of a pair of long, convoluted brachia. The occurrence of *Leptodus* in Permian rocks of western Texas, but not in deposits of equivalent age nearby, shows that these forms may have been adapted to life on the flanks of Permian reefs, and were probably sensitive to variations in temperature or other environmental factors.

Triplesiidina

(Early Ordovician to Late Silurian)

image © Bruce Moore, Taxonomy of the Articulate Brachiopoda

Previously considered a distinct order (Tripleslida), this small group of Ordovician and Silurian brachiopods includes biconvex shells with well-developed fold and sulcus, either smooth or covered with costae. The brachial valve contains short crura and a prominent, branched cardinal process.

Triplesia ortoni is a characteristic Early Silurian fossil of the Ohio Valley.

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Order Productida

Ordovician - Triassic

The ***Productids*** were an extremely successful and diverse group of brachiopods, dominating late Paleozoic marine ecosystems. Productids are characterized by concavo-convex shells accompanied by development of spines, either along the posterior margin, or distributed more or less abundantly over other parts of the shell surface. Interareas, although present in some shells, are not conspicuous features. The hinge line is generally extended so as to equal or nearly equal the width of the shell. A prominent feature of many genera is the unusual convexity of the pedicle valve, accompanied by prolongation of the anterior portion of both valves so as to produce the feature called trail. In the region of the trails, the two valves are nearly or actually in contact when the valves are closed; and growth of the shell in this manner adds virtually nothing to the space of the shell interior.

> Specialization within some groups resulted in truly bizarre variations on the basic brachiopod theme, including some forms that mimicked corals. Other species were infaunal or quasi-infaunal, living partially or completely buried in sediment, like bivalves. In many forms the pedicle is lost when adult, the individuals being held in position by cementation or by spines attached to the substrate.

```
Order: PRODUCTIDA (Lower Devonian-Upper Permian, ?Lower Triassic)
         Suborder: Chonetidina
                         Superfamily Chonetoidea (Late Ordovician--Late Permian or Early Triassic)
         Suborder: Productidina
                         Superfamily Productoidea (Early Devonian-?Early Triassic)
                         Superfamily Echinoconchoidea (Early Devonian-Late Permian)
                         Superfamily Linoproductoidea (Early Devonian-Late Permian)
         Suborder: Strophalosiidina
                         Superfamily Strophalosioidea (Early Devonian-Late Permian)
                         Superfamily Aulostegoidea (Early Carboniferous-Late Permian)
                         Superfamily Richthofenioidea (Late Carboniferous-Late Permian)
         Suborder: Lyttoniidina (?Lower Carboniferous, Upper Carboniferous-Upper Permian)
                         Superfamily Lyttonioidea  (?Early or Late Carboniferous-Late Permian)
                         Superfamily Permianelloidea (Permian)
```

Chonetidina

(Late Ordovician--Late Permian/Early Triassic)

image © Bruce Moore, Taxonomy of the Articulate Brachiopoda

The Chonetids are the earliest and least derived representatives of the Productida, and can be considered ancestral to later forms. They first appear in the Late Ordovician, but the group only became more common later on

Some Devonian chonetids have unusually large spines and coarse costae; others are distinguished by denticles on the hinge margin and strong convexity of the pedicle valve. Carboniferous and Permian strata often contain useful index fossils belonging to this group. One of the best known is Mesolobus, distinguished by longitudinal corrugations of the mid-portion of the valves; it is confined to Middle Pennsylvanian

Suborder Productidina

Early Devonian-Late Permian/?Early Triassic)

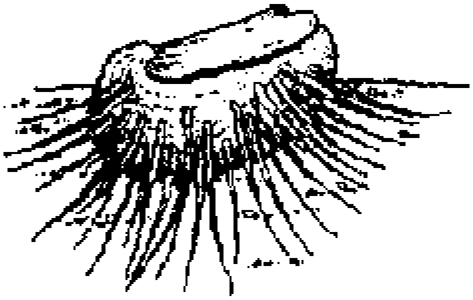


image from Benchley and Harper, *Palaeoecology*

The productids differs from their chonetid forebears in having much greater convexity of the pedicle valve and generally a more concave brachial valve. There are also a varying number of spines (which may be short or long) distributed over the surface

Productids were fairly rare during the Devonian, but become extremely numerous in the Carboniferous and Permian periods. Two main shell types are distinguished: in one, the surface is marked chiefly by longitudinal fine to coarse ribs, with few spines; in the other, spines are very numerous and costae are lacking or inconspicuous. Some members of the rib-marked group have evenly spaced concentric corrugations on the posterior part of both valves so as to produce a reticulate pattern; and the interior of the brachial valve bears looped ridges which probably are the impressions left by the lophophore.

Among the Early Carboniferous Mississippian costate productids, *Gigantoproductus* is the largest brachiopod known, attaining a width of approximately 30 cm.

The noncostate productids have shells covered by abundant obliquely disposed spines, these project backward from the posterior edge of both valves. These it would seem supported the animal in the substrate, functioning as a sort of "snowshoe," supporting and stabilizing the organism on soft muds, or allowed it to cling to seaweed or other objects

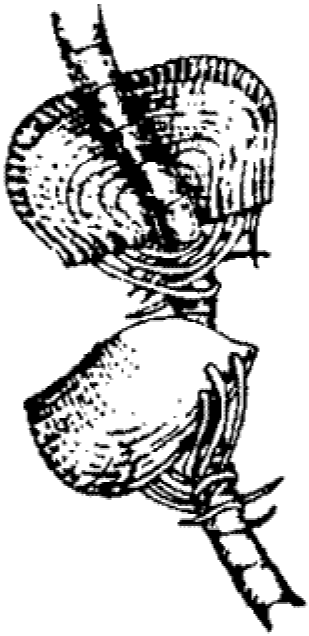


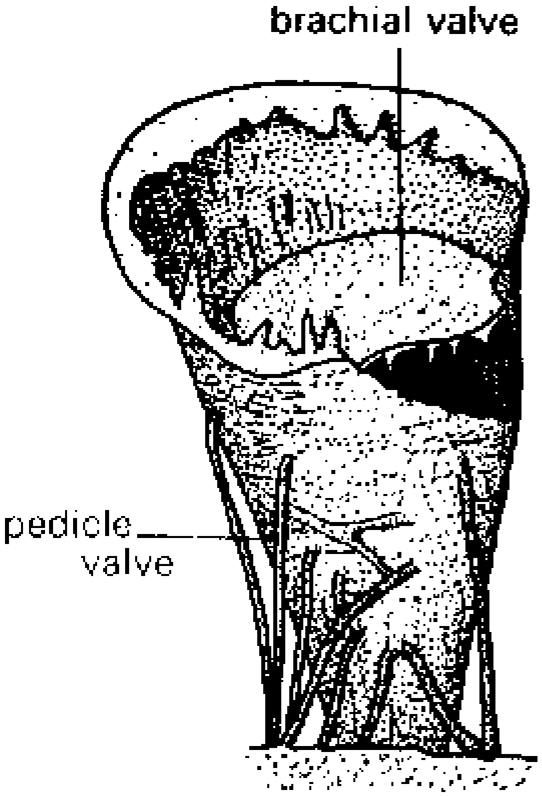
image from Benchley and Harper, *Palaeoecology*

Some of these long-spined forms are characterized by unevenness in the arrangement of the spines, others by very regular concentric rows of spines, and a Permian genus (*Waagenoconcha*) has spines arranged in curved, regularly intersecting oblique rows.

The anterior edges of productid valves were sharply angled upward in a *flange*. This flange may have been all that emerged above the sediment. The productids colonized a quasi- infaunal or almost buried (and hence protected) mode of life, one of the few brachiopod groups to imitate a bivalve (clam) lifestyle

Suborder Strophalosiidina

Early Devonian-Late Permian



The Strophalosiidines were a very strange group of brachiopods that adopted a coral-like existence. They were attached to the bottom by a cone-shaped pedicle valve, with the upper valve covering the cone like a pot lid. The unusual brachiopod *Prorichthofenia* from the Permian of Texas is one of these unusual conical forms. Superficially, the pedicle valve resembles Paleozoic horn coral and living solitary scleractinian corals. It is held in an upright position by its anchorage of outspread spines. The brachial valve is a lid-like structure which articulates with the pedicle valve at a level well below the shell edge. Near the margins of each valve on their inner side, spines are arranged in alternating position, in such a manner that when the valves are partly open, they protect the entrance to the shell interior. Some species even have a lacelike calcareous grill that arches over the brachial valve, and in these forms the inner spines are lacking.

Like the Rudist bivalves, the Richthofenioidea mimicked corals, and indeed formed large reefs. Individuals commonly grow together in clusters; and it is though that, like corals, some strophomenids bore photosynthetic algae inside their tissues that helped to supply them with food.

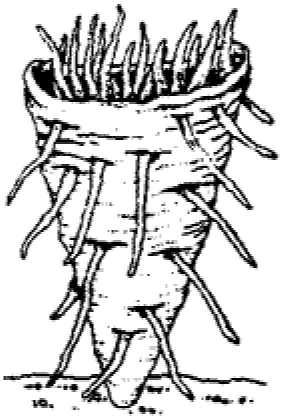


image from Benchley and Harper, *Palaeoecology*

References:

Moore, Lalicker and Fischer, *Invertebrate Fossils*

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Strophomenida

Ordovician to Carboniferous

```
Metazoa
|--Deuterostomia
`--Protostomia
   |--Ecdysozoa
   `--Lophotrochozoa
      |--Mollusca
      `--+--Annelida
         `--Brachiopoda
            |--Linguliformea
            `--Rhynchonelliformea
               |--Chileata
               |--Obolellata
               |--Kutoriginata
               |--Strophomenata
               |  |--Strophomenida
               |  `--Plectambonitoidea
               `--Rhynchonellata
```

Introduction
Anatomy
Ecology
Phylogeny and Diversity

Introduction

The order Strophomenida originally referred to a diverse Paleozoic assemblage of Brachiopods, but in the most recent classification it is used in a much more restricted sense, with the more specialised forms being placed in their own distinct orders.

Strophomenids have one valve is convex while the other is generally concave, so the living space for the animal inside is very reduced. It has a wide hinge line, and one concave valve, which may be either brachial or pedicle. The surface is ornamented by fine radiating lines (costae) and a wide hinge line is present in this group. The early strophomenids had concave-convex pseudopunctate shells, and were attached by a pedicle only in early growth stages, becoming free-lying later in ontogeny.

These are the brachiopods often referred to as "petrified butterflies." One major characteristic peculiar to this group is the presence of pseudo-punctate structure.

Appearing in the mid-Ordovician, strophomenids were both varied and abundant but declined after the Devonian. They have a well defined interarea (cardinal area) on one or both valves and lack spines.

The strophomenid body was very thin, it generally built a thick shell with muscle scars. Such shells are abundant Paleozoic fossils, and pedicle valves are exceedingly attractive. Many species have prominant growth lines that show how shapes changed with increasing size.

Systematics

Strophomenida
Strophomenoidea (Early Ordovician-Early Carboniferous)
Plectambonitoidea (Early Ordovician-Late Devonian)

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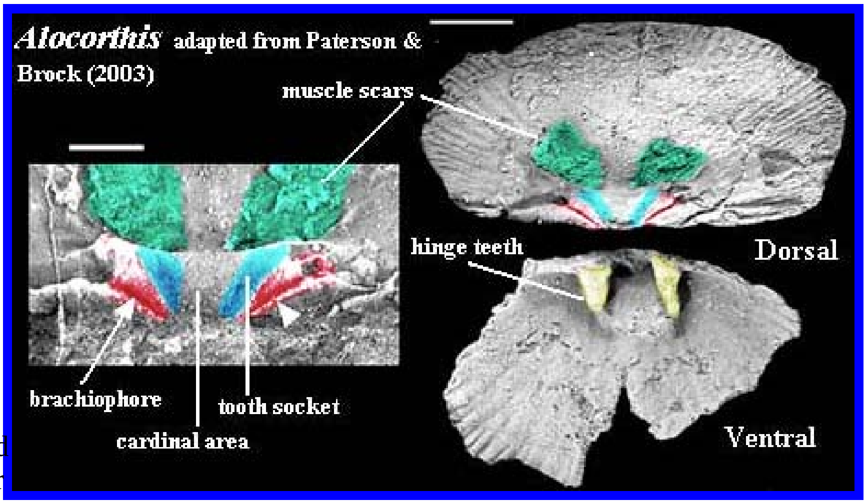
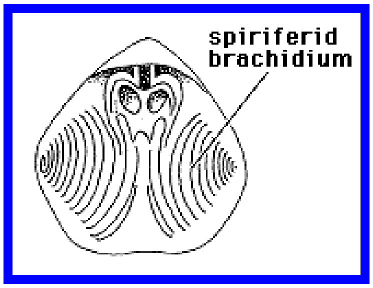
Class Rhynchonellata



This very diverse group includes the majority of articulate brachiopods, that is, brachiopods with a hinge between the two halves of the shell. The rhynchonellates range in age from Early Cambrian to Recent. Rhynchonellate shells are biconvex and articulated by teeth and sockets buttressed with brachiophores, as shown in the image of *Alocorthis* from Paterson & Brock (2003).

Most rhynchonellates have a calcified brachidium of the spiriferid type. The ***brachidium*** is a structure which supports the lophophore, the feeding organ of brachiopods. A ***spiriferid*** brachidium is a sort of dual-spring shock absorber. It consists of two coiled structures, like bedsprings, which extend off to either side and are braced against the shell. These brachidia give the lophophore of the rhynchonellates unmatched support and stability. The diagram of this arrangement is from the University of Kansas **Ancient Life** site.



The following table lists the taxa which are usually included among the Rhynchonellata, with links to some of the excellent web materials on this taxon:

no image available yet				
	Resserella from Nashville Fossils	***Cyrtospirifer*** from Virtual Fossils (Univ. di Padua)	***Pentamerus*** (source unknown)	***Beecheria*** from Catnapin Fossil Gallery
Protorthida	**Orthida**	**Spiriferida**	**Pentamerida**	**Terebratulida**

				
Unidentified rhynchonellid *in situ* from Southern Arizona Fossils	**Unidentified** atrypid from the Ammonites Page (Wroclaw Univ.)	***Composita*** from Paleobytes	***Costispiriferina*** from Palfy (2003)	***Thecidellina*** from Voskuil (1998)
Rhynchonellida	**Atrypida**	**Athyridida**	**Spiriferidida**	**Thecideida**

Links:

SYSTEMATICS- Invertebrate Paleontology Selected Classification of ...

Katedra biologie FPE ZCU v Plzni (Czech)

Ancient Life--13--Rhynchonellid Brachiopod: one of several pages on brachiopods, using a more traditional classification scheme

Early Ordovician orthide brachiopods: Full text of Paterson & Brock (2003).

References:

P�lfy, J (2003), *The Pelsonian brachiopod fauna of the Balaton Highland* **in** A V�r�s [ed.]. **The Pelsonian Substage on the Balaton Highland (Middle Triassic, Hungary)**. **Geol. Hung., Ser. Palaeontol.** 55: 139-158.

Paterson, JR & GA Brock (2003), *Early Ordovician orthide brachiopods from Mount Arrowsmith, northwestern New South Wales, Australia*. **Rec. Aus. Mus.** 55: 221-230.

Voskuil, R (1998), *On a small collection of Hawaiian Brachiopoda (Lophophorata)*. **Internet Haw. Shell News** Nov, 1998: 2-13. Republication.

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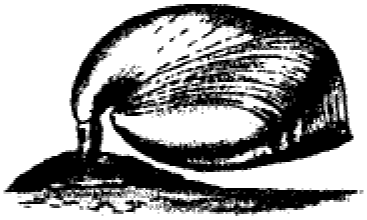
Order Athyridida

(or Suborder Athyridina)

Ordovician to Jurassic



Composita
Carboniferous
measuring 2 cm in length
illustration from Fenton & Fenton, *The Fossil Book*, 1958, Doubleday & co., p.120

The Athyridida, or Rostrospiracea as they were previously called, are a group of smooth-shelled , impunctate shells of rounded outline, having prominent beaks but no perceptible interarea on the pedicle valve

Externally, they resemble a few of the Atrypids, which also have a smooth shell. But they differ in the nature of the more complex brachidium, the athyrid brachidium sometimes bearing long pointed processes, or loops like scissor handles. Except for their spiral brachidium, directed laterally outward, they have almost nothing in common with the Spiriferida proper.

The external morphology is very variable in with group, with some genera resembling contemporary terebratulids such as *Dielasma* and *Kingena*, others being similar to *Spirifer*, and still others resembling rhynchonellids.

Athyrids were most abundant during the Silurian and Devonian periods, but still remained common during the early Carboniferous, and even as late as the Permian. One of the most abundant Carboniferous forms is *Composita* (above). This form was attached by a strong pedicle, probably in varying positions, like the living *Terebratalia*. Faunules composed mainly of *Composita* indicate an environment to which it was particularly adapted and not favored by most others brachiopods.

Athyrid ancestry is uncertain but they may have evolved from Atrypids which in turn descended from Rhynchonellids. Alternatively, they could have evolved directly from rhynchonellids independent of Atrypids.

Systematics

On the left is the classification according to the *Treatise on Invertebrate Paleontology*. On the right is the newer classification by EuroBrachNet

Treatise on Invertebrate Paleontology	**Classification des Brachiopoda**
Retziidina Retziacea (Middle Silurian-Permian) Athyrisinacea (Early Devonian-Triassic)	**Basal Taxa** Dayioidea (Late Ordovician - Late Silurian) Anoplothecoidea (Late Silurian? - Middle Devonian?) Uncitoidea **Athyrididina** Meristelloidea (Late Ordovician--Early Carboniferous) Athyridoidea (?Late Ordovician-, Early Silurian-Late Triassic, ?Late Jurassic) Nucleospiroidea (Early Silurian- Early Permian) **Retziidina** Retzioidea (Early Silurian-Late Triassic) Rhynchospirinoidea (Early Silurian-Early Devonian) Mongolospiroidea (Early Devonian) **Koninckinidina** Koninckinoidea (Early Triassic-Early Jurassic) Cadomelloidea (Early Jurassic)
Athyrididina Athyridacea (Late Ordovician--Late Triassic) Koninckinoidea (Triassic-Jurassic)	

TENDENCIES IN THE ATHYRIDID DIVERSITY DYNAMICS

Fernando ALVAREZ1 and Tatiana L. MODZALEVSKAYA2.

"The Athyridia, is a rather rich and diverse group of spire-bearing brachiopods which appeared in the late Ordovician0, Hirnantian, possibly Caradoc. At the beginning of the Silurian (Llandovery-Wenlock) the origination number shows a clear increase towards younger strata. Athyridid diversification and dispersal during the early Silurian coincides with warming of the climate and transgression of the ocean. From Wenlock, the number of originations falls towards the younger strata while extinctions show the opposite course. Geographical limitations due to the general late Silurian marine regression may have had some influence. As a result, the late Silurian was the time of the first crisis when 16 genera became extinct.

A new athyridid fauna originated (40 genera appeared) in the early Devonian when the innovation and radiation rates were the highest. These sudden innovations could explain the rise of endemic genera that took place during this period. Later both origination and extinction fall quickly. Extinctions prevailed over appearances and this caused a rapid decline in the athyridids in the late Devonian. 30 genera disappear coinciding with the extinction episode (Frasnian/Famennian). Environmental factors, such as cooling and anoxia, more than marine regression seems to have played an important role in this F-F crisis. The rate of endemism falls from mid Devonian till late Carboniferous. During the Famennian, a clear process of recovery starts. The origination numbers rise until the second half of the Carboniferous system during which a 3rd crises take place (Serpukhovian episode?) and 19 genera disappear. The late Carboniferous athyridids were the most cosmopolitan. However from that time there was a clear tendency for the rate of cosmopolitan genera to decrease while an almost continuous (except during the late Triassic) rise

> in endemism took place. During the Permian, specially during late Permian, the origination data shows a small rise, but always below the rate of extinction. At the end of Permian, coinciding with the principal mass extinction episode of the Phanerozoic, there was a considerable rise in the extinction rate, 16 genera disappear close to the Permian-Triassic boundary. In the Triassic, with the appearance of the koninckinoids, the last recovery process took place. Origination and extinction show a clear increase (29 genera appear) but extinctions clearly prevailed over appearances, causing a quick decline of the order in latest Triassic. During this period, the level of innovation was low and specialization high, the number of cosmopolitan genera decreased drastically and endemic genera increase considerable. This considerable rise of endemic genera and decline of those widely distributed coincides with the general decline of the order, a decline that began with the widely distributed genera in the late Permian and during the Triassic. By the end of the Triassic a great increase in the extinction rate took place, most of the genera disappear, and the whole order became extinct by mid Jurassic, or at the end of the Jurassic system if the presence of Ochotathyris ochotica, in Qinghai (NW China) is finally confirmed."

from **The Fourth, Millennium, International Brachiopod Congress**

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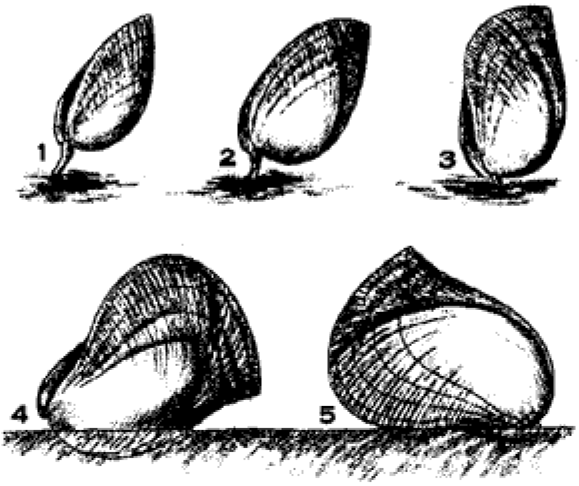
Order Atrypida

Ordovician to Devonian



Stages in growth and orientation of a large *Atrypa*. A few old shells lay in position 4, but most came to rest in position 5.
illustration from Fenton & Fenton, *The Fossil Book*, 1958, Doubleday & co., p.120

The Atrypids are the first of the spiral-lophophorate brachiopods to appear. Originally included under the order Spiriferida, they are now known to have developed the characteristic spiral lophophore independently.

Atrypids have a short hinge line, inconspicuous beak, and very inconspicuous interarea on the pedicle valve. All have a rounded outline. In longitudinal profile (below), the shells range from biconvex, which is the most common, to convexi-plane, plano-convex, and concavoconvex.

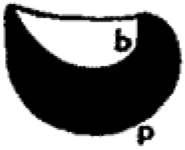
Atrypid morphologies

biconvex

image to be added

convexi-plane

plano-convex



concavoconvex

b = brachial valve p= pedicle valve

A small minority of the Atrypacea have smooth shells, others being rather finely costate or having medium to coarse plications. Some possess wide "wings," or *alate* lamellae, while in other species the lamellae fold into delicate spines. Concentric growth lines or lamellar outgrowths of shell distinguish some genera, such as *Atrypa*.

Internally, the posterior part of the pedicle valve generally bears large muscle scars. Several genera have well-developed dental lamellae, whereas others lack these structures. A distinguishing feature of the Atrypacea is the manner in which the beginnings of the spiralia bend outward so as to enclose between them the remainder of the spiral cones.

Evolutionary History

Ordovician Atrypids are moderately small biconvex shells having fine radial plications and an inconspicuous interarea on the pedicle valve. The spiral lophophore is directed inward, with the crossbar (*jugum*) connecting the outermost coil of the spires being located posteriorly in some and variably in others.

Atrypa reticularis Devonian Clark County, Indiana, USA. Matrix free silicified specimen measuring 2.8 cm across

The Silurian was characterized by smooth-shelled Atrypacea in which the spires inside the outermost loop are pointed outward or turned at right angles toward the floor of the brachial valve, as in *Atrypa.* Various species of Atrypa are the most common representatives of the Atrypacea during the Devonian. Most have fine costate ornament, but some have coarse ribs crossed by rough lamellae.

The Atrypids were among the many invertebrate groups wiped out by the Frasnian-Famennian mass-extinction.

Systematics

On the left is the classification according to the *Treatise on Invertebrate Paleontology*. On the right is the newer classification by EuroBrachNet.

Treatise on Invertebrate Paleontology	**Classification des Brachiopoda**
Atrypidina Atrypacea (Middle Ordovician-Late Devonian) Dayiacea (Middle Ordovician-Early Devonian)	ATRYPIDA **Zygospiridina** Zygespiroidea (?Early Ordovician-Middle Silurian) **Atrypidina** Atrypoidea (Late Ordovician--Late Devonian) **Lissatrypidina** Lissatrypoidea (?Middle Ordovician-Late Devonian) **Davidsoniidina** Davidsonioidea (Late Silurian-Early Devonian) Palaferelloidea (Early Devonian)

RADIATIONS AND EXTINCTIONS OF ATRYPID BRACHIOPODS: ORDOVICIAN-DEVONIAN

Paul Copper

> "Atrypid brachiopods originated during the late Llanvirn (Llandeilo) [Darriwilian -- ed.] benthic 'shelly' radiation, and the last taxa disappeared towards the Frasnian-Famennian extinction boundary, so that the order endured for close to 100Ma, commonly numerically dominating many other brachiopods in shallow water communities. All species are known to have been exclusively tropical, and preferentially subtidal carbonate shelf and ramp inhabitants: more than 200 genera and subgenera have been described. Using the latest generic diversity compilation at the stage level, including synonymies, the Caradoc (11 genera) and Hirnantian (9) mark a slow rise and arrival of the major suborders and families. The *Zygospira* group' (Anazygidina), which dominated prior to the Ordovician / Silurian boundary ,*i.e.* Hirnantian, mass extinction events, were taken over by the '*Atrypa* group' (Atrypidina) in the latest Ordovician. By the late Llandovery (Telychian), 32 genera proliferated, including many smooth-shelled taxa (Lissatrypidina), the largest expansion of the Atrypida during their history, a diversity maintained to the end of the Ludlow-Pridoli. The Early Devonian (Lochkovian) saw a decline to 20 genera, with a slow return by the end of the Pragian, a tectonically active phase marked by global sea level drawdowns, and provinciality. The late Emsian-Eifelian marked a peak in atrypoid diversity, reaching a maximum of 41 genera, coinciding with a global greenhouse setting and reef expansion, with many taxa specifically adapted to and confined to reefal carbonates. Diversity declined in the mid-Givetian, and was reduced by 50% towards the end-Givetian, with dramatic losses of reefal taxa, many at the family level. The Frasnian was a stage of low diversity (12 genera), though there was local high abundance especially in mid-Frasnian time, up to the *Palmatolepis rhenana* conodont zone: long-lived, cosmopolitan taxa dominated, with some new arrivals within the family Atrypidae. Within the latest Frasnian *P. triangularis* Zone, most regions saw fewer than two or three genera prevailing: there are no mass 'death horizons' known, and declines were stepdown events, probably tied in to sea level oscillations (T/R cycles), with virtual absence of atrypids in the uppermost meters of strata with a complete F/F succession. There are no Atrypida known from the Famennian, except as reworked Frasnian shells, thus a long-lived and highly successful group came to an end."

from **The Fourth, Millennium, International Brachiopod Congress**

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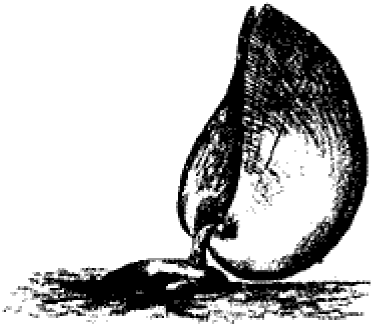
Order Orthida

(Cambrian-Permian)



The orthid brachiopods were the first important articulate group to diversify, and appeared during the Early Cambrian period, and became very diverse during the Ordovician. They are typically *strophic* (having a straight hinge line), and well developed interareas. Radiating ribs are also common in this group, as are sulcus and fold structures. Usually one valve (usually the brachial valve) is flatter than the other. The *cardinalia* (structures in the interior of the brachial valve) of orthids are usually simple. The shape is sub-circular to elliptical with the valves generally biconvex.

Evolutionary History

The orthids began with small subquadrate forms during the early and middle Cambrian. There is some controversy now over whether many of these early types really were Orthids at all, or should be separated into a distinct Order, or even, in recent classification systems, a different class. I have followed the classification scheme in use by EuroBrachNet and the revised *Treatise of Invertebrate Paleontology*, and transferred the better known of these early primitive forms to different orders and classes. Whether this arrangement will still be in use in future years and decades, or a totally different view of early brachiopod phylogeny will be adopted, remains to be seen.

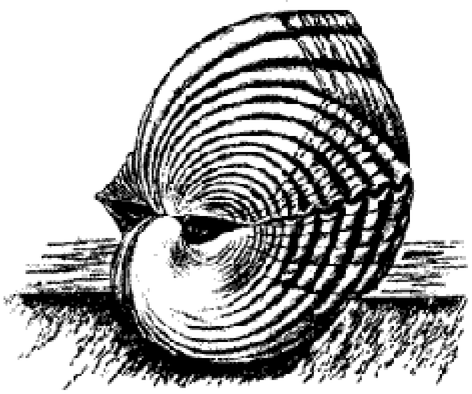
An apparently early modification in the late Early Cambrian gave rise to the more characteristic orthaceans in which the delthyrium and notothyrium are open. This implies that a pedicle rudiment was developed as a primary segment of the larva as in modern articulates. The orthaceans again have a fibrous secondary shell and are presumed to have arisen from some nisuisid stock, possibly by paedomorphic changes affecting pedicle development in particular.

By the Furongian Epoch orthids and orthid-like brachiopods achieved considerable variety and widths of 2 to 5 cm.

Furongian and earliest Ordovician genera included shells with rounded to high, pointed pedicle valves, sharp to obtuse extremities, and fine to coarse ridges (called costae).

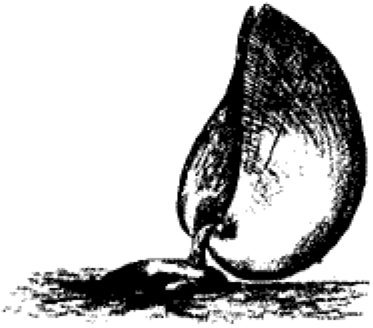
Hesperorthis
Middle Ordovician to Middle Silurian
length about 2 cm
illustration from Fenton & Fenton, *The Fossil Book*, 1958, Doubleday & co., p.120

During the mid-Ordovician, punctate shells appeared, establishing the suborder Dalmanellidina (the superfamily Enteletacea of the *Treatise of Invertebrate Paleontology*). Both the Orthodina and Dalmanellidinar suborders then gave rise to a great variety of genera and species, some of which resembled members of the other suborder and even of different orders. One Ordovician orthid looked like a strophomenid, and *Productorthis* developed both shape and ornamentation which were paralleled during the later Paleozoic by the spiny productids. *Platystrophia* anticipated the spirifers in both shape and habit and even went through similar changes in the evolution of its species.



Platystrophia
Late Ordovician- period
illustration from Fenton & Fenton, *The Fossil Book*, 1958, Doubleday & co., p.120

The Orthids were greatly reduced by the end Ordovician extinction event, although both impuncate and puncate Orthids continued through to the early Devonian. At that time the impunctate types died out, but the punctate Dalmanellidina continued on. These sometimes resembled morphotypes of earlier Orthodina. *Schizophoria*, of Devonian age, resembles the mid-Ordovician *Hebertella*. The punctate Orthids continued as a minor element of the benthic fauna until the end of the Permian.



Schizophora
Middle Silurian to Permian
length 3 cm, width 4.5 cm
illustration from Fenton & Fenton, *The Fossil Book*, 1958, Doubleday & co., p.120

Systematics

On the left is the classification according to the *Treatise on Invertebrate Paleontology*. On the right is the newer classification by EuroBrachNet, which divides the old category of Orthids into several distinct, even unrelated orders

Treatise on Invertebrate Paleontology	**Classification des Brachiopoda**	
ORTHIDA **Orthidina** Billingsellacea (Middle Cambrian-Early Ordovician) Orthacea (Middle Cambrian-Early Devonian) Enteletacea (Middle Ordovician-Late Permian) **Clitambonitidina** Clitambonitacea (Ordovician) Goniambonitacea (Ordovician) **Triplesiidina** Triplesiacea (Early Ordovician-Late Silurian)	Class Strophomenata ORTHOTETIDA **Triplesiidina** Triplesioidea (Early Ordovician-Late Silurian) BILLINGSELLIDA **Billingsellidina** Billingselloidea (Middle Cambrian-Early Ordovician) **Clitambonitidina** Clitambonitoidea (Ordovician) Polytoechioidea (Ordovician)	not Orthids
	Class Rhynchonellata PROTORTHIDA Protorthoidea (Early Cambrian-Late Devonian) Skenidoidea (Lower Ordovician-Upper Devonian)	Orthid relatives
	ORTHIDA **Orthodina** Orthoidea (Middle Cambrian-Early Devonian) Plectorthoidea (Early Cambrian-Late Silurian) **Dalmanellidina** Dalmanelloidea (Early Ordovician-Late Devonian) Enteletoidea (Middle Ordovician-Late Permian)	Orthids

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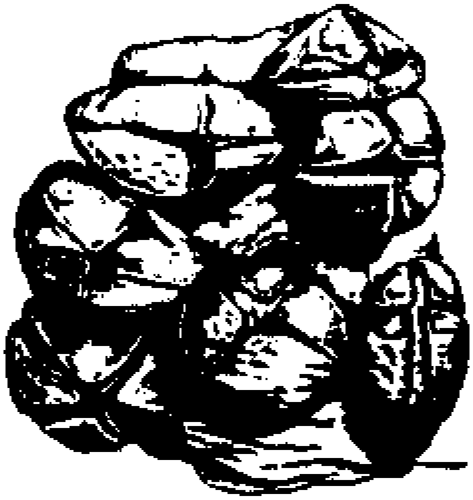
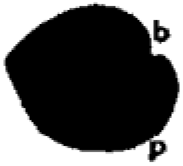
Order Pentamerida

(Cambrian-Devonian)



Pentamerids differ from other articulates in the structure of the rear portion of the pedicle valve, which has a spoon-shaped structure called a *spondylium*. The shell microstructure is impunctate. The shell is often five-sided (pentagonal) in outline - hence the name. The hinge line is short. The fold and the sulcus are reversed in regard to other brachiopods, with the fold on the pedicle valve.



These biconvex (*left*) shells appeared in mid-Canibrian seas, became common in the Ordovician, and lived on to the end of Devonian times. The Silurian *Pentamerus laevis* lived in closely packed colonies with pedicles sunk into the mud and elongate shells directed upward. Such colonies are often found on the under side of beds of fine sandstones. When cleaned and exhibited in museums, they appear upside down. Often there was pedicle attachment at all, and the animals lived in self-supporting colonies like the one illustrated above.

Systematics

Suborder Syntrophiidina

Porambonitoidea (? Early Cambrian-Early Silurian)
Camerrelloidea (Early Ordovician-Early Devonian)

Suborder Pentameridina

Pentameroidea (Late Ordovician--Late Silurian)
Clorindoidea (? - ?)
Stricklandioidea (Early Silurian-Late Silurian)
Gypiduloidea (Early Silurian-Late Devonian)

Classification from **Classification des Brachiopoda (Lophophorata)**

**Brachiopoda
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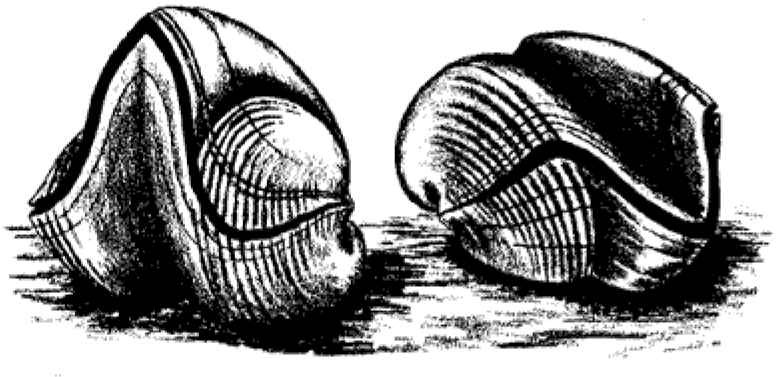
Order Spiriferida

(Ordovician-Jurassic)

The spiriferids are a very variable group of brachiopods. Members of this group can have punctate or impunctate shell microstructure, strophic or astrophic hinge line, and of any of a number of gross shell morphology. Their only defining quality is the presence of a spiral brachidium; that is, a spiral support for the lophophore (spiralia). This admittedly is not a very reliable feature, in view of the common brachiopod tendency to homeomorphy, and it has recently been suggested that some if not all of the four main suborders of Spiriferids are actually distinct, even unrelated orders which independently evolved the distinctive spiral brachidium. I have followed the most current classification in separating the Atrypids and Athyrids into separate orders. Both of these groups are thought to have descended from rhynchonellid ancestors. The punctate spiriferids are a small but varied (possibly artificial) assemblage and are here retained within the order Spiriferida.

Order Spiriferida

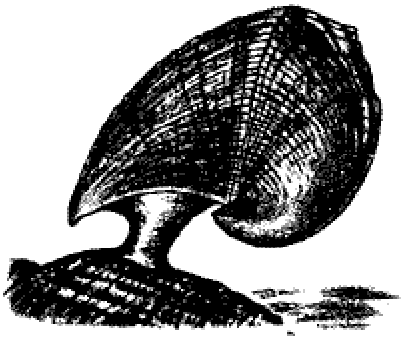
or Suborder Spiriferidina



Paraspirifer
early and Early Devonian
length about 4 cm - width about 4.5 cm
mode of life: attached when young, but its pedicle disappeared in maturity and the shells lay in the mud.
illustration from Fenton & Fenton, *The Fossil Book*, 1958, Doubleday & co., p.120

The Spiriferids proper are characterized usually by the familiar "spirifer" shape with wide or extended hinge line; in fact the hinge-line is often the widest part of the shell, and in some genera (e.g. *Mucrospirifer*) it is greatly elongated. Nearly all shells bear costae or plications, and they are almost invariably marked by a well-developed sulcus on the pedicle valve and a fold on the brachial valve. The surface is either plicate or coilate and may bear much finer markings. The beak is prominent, and a curved, generally obtuse-angle interarea occurs on the pedicle valve. Directly beneath the beak, the interarea is interrupted by the delthyrium, which may be partly closed by a deltidium.

The spiral brachidium of these brachiopods is remarkably developed, the cone-shaped coils on either side of the median plane being formed of many turns. The spiral brachidia extend outward toward the extremities rather than into the brachial valve. Internal structures are varied, and in some shells they are important in generic diagnosis. Generally, there are large muscle scars, stout dental lamellae, closely coiled, outwardly pointed spiralia, and simple jugum.



Brachyspirifer
Early Devonian
length about 3 cm - width about 4.5 cm
mode of life: had a thick pedicle that probably was attached to large shells, corals, etc., throughout the animal's life
illustration from Fenton & Fenton, *The Fossil Book*, 1958, Doubleday & co., p.120

Evolutionary history

The spiriferids evolving from the orthids at the end of the Ordovician, developing a coiled brachium independently of the Atrypids and Athyrids. The Spiriferids remain rare during the Silurian, but undergo a dramatic evolutionary radiation during the following, Devonian period, reaching a peak development in variety and numbers at that time. a prominent brachiopod assemblage. Devonian forms were very diverse, including some types with a nonplicated fold and sulcus, various others with evenly spaced coarse or medium to fine plications, and one lineage that is planoconvex in form (i.e. one valve flat, the other bulbous). *Cyrtina*, with its deep pedicle and opening for a large pedicle, is a well-known Devonian genus. The group undergoes something of a decline during the Early Carboniferous, although still remaining very common (second only to the productids in abundance). *Spirifer*, a typical genus of this time (top of page), is characterized by plicate shells with a wide hinge line. Late Carboniferous and Permian Spiriferids are characterized especially by bifurcation and bundling of plications on the shell surface. Only a few punctate-shelled forms (which may or may not belong to a distinct order) make it through to the Jurassic.

- **Spriferidina** (Late Ordovician--Late Permian)
  - Cyrtioidea (Late Ordovician--Early Devonian)
  - Spinelloidea (Late Silurian -- Late Devonian)
  - Theodossioidea (Early Devonian-Early Carboniferous-?Late Carboniferous)
  - Cyrtospiriferoidea (Early-Late Devonian)
  - Ambocoelioidea (Late Silurian-Late Permian)
  - Martinioidea (Late Silurian-Late Permian)
  - Spiriferoidea (Late Devonian-Late Permian)
  - Brachythyridoidea (Early Devonian-Late Permian)
  - Paekelmanelloidea (Late Devonian-Late Permian)

Delthyridina (Early Silurian-Late Permian.
  Delthyridoidea (Early Silurian-Early Devonian)
  Reticularioidea (Early Silurian-Late Permian)

Order Spiriferidida or Suborder Spiriferinina

Cyrtinidina (Early Devonian-Early Jurassic).
  Cyrtinoidea (Early Devonian-Early Carboniferous)
  Suessioidea (Early Carboniferous-Early Jurassic)
  Spondylospiroidea (Late Triassic)
  Pennospiriferinoidea (Late Devonian-Early Jurassic)
  Spiriferinoidea (Middle Triassic-Early Jurassic)

The Spiriferidida, previously called Punctospiracea, are distinguished from other spire-bearing (spiriferid) brachiopods by their punctate shell structure. As with other groups of punctate shells, such as terebratulids and dalmanellaceans, the presence of puncta constitutes a basis which is presumed to justify this separation. In all other respects though this is a very variable group, and may perhaps be polyphyletic. For the time being I have left these forms with the Spiriferids proper. Many of these forms had high cardinal areas and coarse plications, although others were much more like conventional (impunctate) spiriferids.

Classification from Classification des Brachiopoda (Lophophorata)

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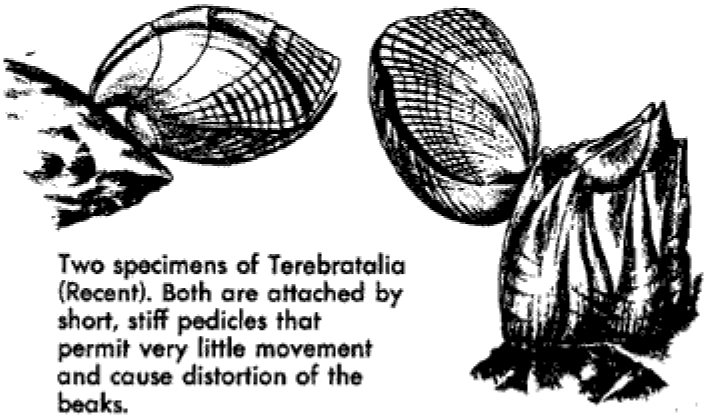
Order Terebratulida

(Devonian - Recent)

Terebratulids are one of the only two living orders of articulate brachiopods, the other being the Rhynchonellida. They are bulbous in shape, commonly circular or ovoid in outline, and have a simple calcareous loop supporting the lophophore. Terebratulids are also distinguished by a very short hinge line, and the shell is punctate in microstructure. Surface ornamentation is variable, with a single species sometimes showing both smooth-shelled and ribbed forms. There is a circular pedicle opening, or foramen, located in thebeak. The characteristic shape of terebratulids resembles that of ancient oil lamps, and thus the common name for brachiopods is "lamp-shells".



Two specimens of Terebratalia (Recent). Both are attached by short, stiff pedicles that permit very little movement and cause distortion of the beaks.

illustration from Fenton & Fenton, *The Fossil Book*, 1958, Doubleday & co., p.120

Terebratulid success may be due to their unique adaptation of *transapical resorption*. During ontogeny the fold in the deltidium becomes relatively larger, which allows enlargement of the pedicle with increasing size. This allowed larger species to have much strong attachment to the substrate

Terebratulids may have evolved from Atrypids during the early or Middle Silurian. Early genera were almost circular to elongate-oval, with smooth or finely costate shells. During the Cretaceous and Tertiary periods, many shells became coarsely plicate. Terebratulids are important today, especially on the Pacific coast of North America. Despite their antiquity, living terebratulids are advanced organisms, able to out-perform molluscan bivalves in filter feeding efficiency under certain conditions. Some species inhabit rocky shores, though others prefer quiet, and cold deep water environments.

Systematics

Suborder Centronellidina

Stryingocephaloidea (Early Devonian-Late Permian)

Suborder Terebratulidina

Dielasmatoidea (Early Devonian-Late Jurassic)
Cryptonelloidea (Early Devonian-Late Permian)
Terebratuloidea (Early Triassic-Recent)
Dyscoloidea (Early Jurassic-Recent)
Cancellothyroidea (Early Jurassic-Recent)
Loboidothyridoidea (Early Jurassic-Late Cretaceous)

Suborder Terebratellidina

Terebratelloidea (Paleocene-Recent)
Zeillerioidea (Early Triassic-Recent)
Kingenoidea (Triassic-Recent)
Laqueoidea (Cretaceous-Recent)
Megathyridoidea (Early Cretaceous-Recent)
Bouchardioidea (Cretaceous-Recent)
Kraussinoidea (Miocene-Recent)
Platidioidea (Late Cretaceous-Recent)
Gwynioidea (Jurassic-Recent)

Order Thecideida or Suborder Thecideidina

Thecospiroidea (Early Triassic-Recent)
Thecideoidea (Early Triassic-Recent)

Classification from Classification des Brachiopoda (Lophophorata)
superfamilies from Treatise on Invertebrate Paleontology

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THECIDEID PHYLOGENY, HETEROCHRONY, AND THE GRADUAL ACQUISITION OF CHARACTERS.

Glenn Jaecks

> "The classification of thecideid has been contentious: they have been included in the strophomenates, spire-bearers and terebratulides, all within the last three decades. Each of the evolutionary scenarios implied by these alternative classifications have been supported by emphasizing different character suites, shell microstructure and median septum morphology in particular. Most recently they have been afforded order status because they share few characters with any one group. While phylogenetic analysis has so far been little help in resolving this issue, it has provided a clearer picture of gradual character evolution within Thecideida ...
>
> "Characters often associated with Thecideida appear piece-meal and are often homoplastic: the often basal thecideid, *Thecospira*, is smaller than most outgroup members, yet larger than most other thecideids, suggesting a gradual decrease in size. Likewise, *Thecospira* does not have a dorsal median septum as an adult, suggesting the acquisition of this character later in the group's history. The other prominent feature in thecideid evolution, the expansion of the shell primary layer (or reduction of the secondary layer), occurs in derived taxa, and may occur more than once. Both shell microstructure and median septum characters played were needed to resolve thecideid relationships, and both character suits are less homoplastic than average thecideid characters. "

from The Fourth, Millennium, International Brachiopod Congress

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Order Rhynchonellida

(Ordovician-Recent)

This distinctive group of brachiopods - easily recognized by their strongly ribbed wedge-shaped or nut-like shells - first appeared with an evolutionary radiation during the Middle Ordovician and remained prominent throughout much of the Palaeozoic. They were especially common during the Early Carboniferous period. Although much diminished by the terminal Paleozoic extinction they experienced a revival during the Early Jurassic period, and became the most common brachiopods of the Mesozoic Era. The rhynchonellids are one of the three groups of living articulate brachiopods, the other two being the Terebratulida and the very uncommon Thecideida. Today they represented only a fraction of their past glory. This very morphologically conservative group has changed little since their appearance during the Ordovician.

Rhynchonellids lack any brachidium, and are therefore able to extrude their lophophore out from the shell into the water for more efficient food-gathering. It has been suggested this is why they survived the Devonian and end Permian, and Jurassic extinctions while many other brachiopods with a brachidium failed to do so.

The rhynchonellid shell has a very short hinge line. The hinges come to a point (as in most bivalve mollusk shells), this being the non-strophic condition. The loss of the hinge line was an important evolutionary innovation, rhynchonellids being the first truly non-strophic shells with a purely internal articulation (teeth-sockets).

Strong radiating ribs are common in this group, and there are generally very strong *plications* or accordion like folds on the sulcus (the long middle section) of the shell. **All rhynchonellids are biconvex (have a bulbous shell), and have a fold located in the brachial valve. All this means that the commisure, the line between the two valves or shells, is zigzagged, a distinguishing characteristic of this group. Some species are excellent index fossils; others belong to superficially similar genera that can be distinguished only by internal characters. The prominent beak of the pedicle valve usually overlaps that of the brachial valve, in order to allow the shell to open and close. There is usually a functional pedicle although the delthyrium may be partially closed. The shell microstructure of most groups is impunctate, but there are a few punctate forms.**

The rhynchonellids seem to have evolved from pentamerids and in turn gave rise to the first atrypids and athyrids, both of which are characterized by the development of a complex spiral brachidium.

Systematics

list of superfamilies

Ancistrorhynchoidea (Middle Ordovician-Early Devonian)
Rhynchotrematoidea (Middle Ordovician-Early Carboniferous)
Uncinuloidea (Early Silurian-Late Devonian)
Camarotoechioidea (Early Silurian-Early Carboniferous)
Rhynchotetradoidea (Late Devonian-Early Triassic-?Middle Jurassic)
Lambdarinoidea (Late Devonian-Late Carboniferous)
Wellerelloidea (Early Devonian-Late Jurassic)
Rhynchoporoidea (Early Carboniferous-Late Permian)
Dimerelloidea (?Late Devonian-Early Triassic-Recent)
Stenoscismatoidea (Early Devonian-Late Permian)
Rhynchonelloidea (Early Triassic-Recent)
Pugnacoidea (Early Devonian-Recent)
Norelloidea (Early Triassic-Recent)
Hemithiridoidea (Middle Triassic-Recent)

Classification from Classification des Brachiopoda (Lophophorata) based in turn on Treatise on Invertebrate Paleontology

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Brachiopoda
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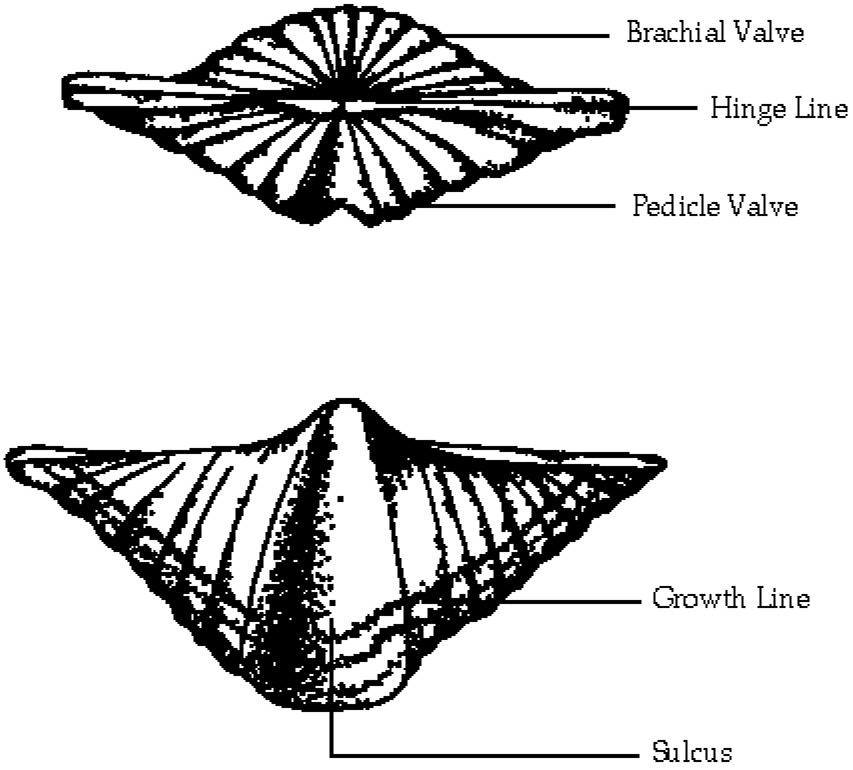

Shell external structure

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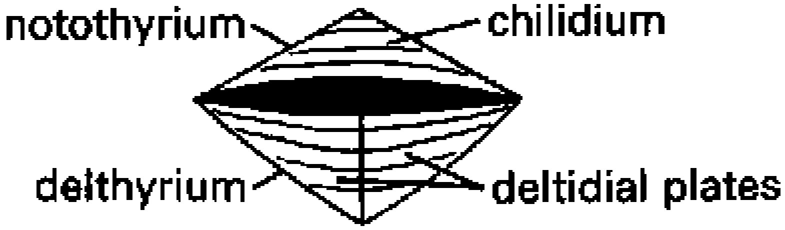
Shell external structure



Beak - pointed extremity (front) of shell that marks the beginning of shell growth

Chilidium - plate extending across the notothyrium, partly closing it

Delthyrium - notch beneath beak of pedicle valve for passage of pedicle, extends to the

Interarea - generally flat surface between beak and posterior margin of either valve

Notothyrium - triangular opening at middle of interarea of the brachial valve, furnishing an opening (with deltyrium) for the pedicle

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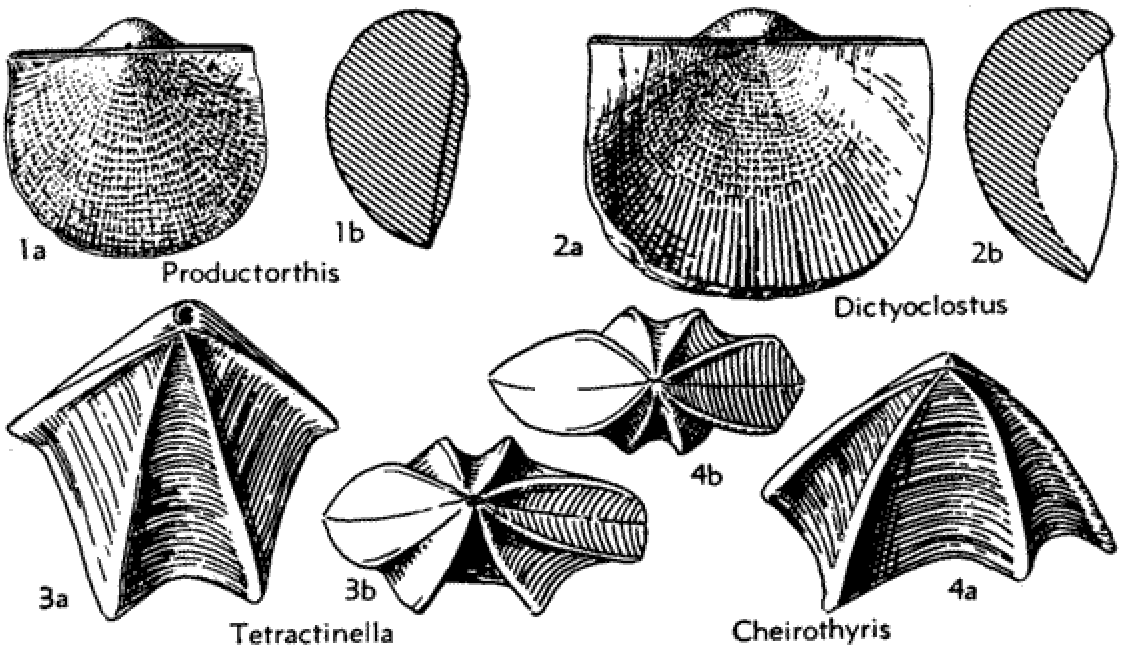
Homeomorphy of brachiopod shells

Simulation of one shell morphotype by another constitutes *homeomorphy*, and resemblances of this sort are quite numerous among brachiopods. The near identity in appearance can be very misleading, and it is necessary to take into account shell structure and internal features. Homeomorphs often not only belong to different genera, but they maybe classed in different families and even (as the following examples show) different orders. Some lived at the same time, others were separated by many millions of years.



1a, b, *Productorthis eminens* (Pander), brachial view and median longitudinal section showing shell form, Middle Ordovician, Russia. Width 1.5 cm. This impunctate shell belongs to the superfamily Orthacea and order Orthida.
2a, b, *Dictyodostus americanus* Dunbar & Condra, brachial view and median section, Late Pennsylvanian, Kansas, width 6 cm. This is a pseudopunctate shell belonging in the family Productid (order Strophomenida)

3a, b, *Tetractinella trigonella* (Schlotheim), brachial and posterior views, length and width 1.8 cm. An impunctate spire-bearing brachiopod (order Spiriferida); Middle Triassic, Italy.
4a, b, *Cheirothyris fleuriausa* (d'Orbigny), brachial and posterior views, width 2 cm; a punctate loop-bearing shell of the order Terebratulida. Late Jurassic, Germany.

from Moore, Lalicker and Fischer, *Invertebrate Fossils*, McGraw-Hill Book Company Inc, 1952, p.218

Brachiopoda
main page

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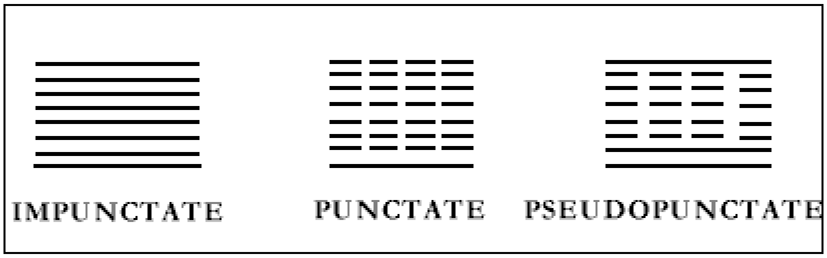
The following diagram shows the differences between the three types of brachiopod shell micro-structure:



Shell Microstructure

The micro-structure is very important in determining classification.

- The ***impunctate shell*** is solid all the way through
- The ***punctate shell*** has tiny open tubes extending almost to the outer surface.
- The ***pseudopunctate shell*** has instead of tubes slender solid rods of calcite that end within the fibrous layer.

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The Classification of the Brachiopoda

The brachiopods have for a long time been traditionally divided into two classes, the Inarticulata and the Articulata. The Inarticulata are so-called because they possess two valves that do not have an articulating hinge. Recently it has been suggested that hinge articulation is not a good way to classify brachiopods anyway, that the traditional organization of the Brachiopoda is erroneous, and that the "Inarticulata" is probably an artificial group and should perhaps be broken up into several classes. Cladistic analysis of the Brachiopoda has resulted in a major revision of the supra-ordinal taxa of the Brachiopoda, which has become widely accepted, although the traditional classification as used in the Treatise on Invertebrate Paleontology, is still standard.

The taxonomy of brachiopods is complicated by homeomorphy, or similarity due to convergent evolution. In any case newer cladistically-based arrangements (see Brachiopod Systematics and Classification des Brachiopoda) give a much more complex classification arrangement than the familiar Treatise on Invertebrate Paleontology, with a large number of higher taxa. These are compared in the following table:

[***Key***: **SUBPHYLUM**, **Class**, ORDER, Suborder, Superfamily]

Treatise	**New Arrangement**
Class Inarticulata	**LINGULIFORMEA** **Lingulata** LINGULIDA Linguloidea Discinoidea Acrotheloidea ACROTRETIDA SIPHONOTRETIDA **Paterinata**

LINGULIDA Linguloidea Trimerellacea ACROTRETIDA Acrotretidina Craniidina PATERINIDA OBOLELLIDA KUTORGINIDA	PATERINIDA **CRANIIFORMEA** **Craniata** CRANIOPSIDA CRANIIDA TRIMERELLIDA **Rhynchonelliformea** **Chileata** CHILEIDA DICTYONELLIDA **Obolellata** OBOLELLIDA NAUKATIDA **Kutorginata** KUTORGINIDA
Class Articulata ORTHIDA Orthodina Triplesiidina Clitambonitidina	**Strophomenata** STROPHOMENIDA PRODUCTIDA Chonetidina Productidina Strophalosiidina Lyttoniidina ORTHOTETIDA Orthotetidina Triplesiidina BILLINGSELLIDA Billingsellidina Clitambonitidina **Rhynchonellata**

ORDER UNCERTAIN
Dictyonellidina

STROPHOMENIDA
Strophomenidina
Chonetidina
Productidina
Oldhamadina

PENTAMERIDA
Syntrophiidina
Pentameridina

RHYNCHONELLIDA

SPIRIFERIDA
Atrypidina
Retziidina
Athyrididina
Spriferidina

TEREBRATULIDA
Centronellidina
Terebratulidina
Terebratellidina

ORDER UNCERTAIN
Thecideidina

PROTORTHIDA

ORTHIDA
Orthodina
Dalmanellidina

PENTAMERIDA
Syntrophiidina
Pentameridina

RHYNCHONELLIDA

ATRYPIDA
Zygospiridina
Atrypidina
Lissatrypidina
Davidsoniidina

ATHYRIDIDA
Athyrididina
Retziidina
Koninckinidina

SPIRIFERIDA
Spriferidina
Delthyridina

SPIRIFERINIDA
Cyrtinidina

THECIDEIDA
Thecideidina

TEREBRATULIDA
Centronellidina
Terebratulidina
Terebratellidina

It seems to me that this newer version, based as it is on Cladistics, gives a grossly inflated number of higher Linnaean taxa for the "Inarticulates". What was previously a simple class is now divided into no less than *three* subphylum and six classes! To give the idea of a subphylum, the entire Vertebrata (Vertebrate animals) are in the Linnaean arrangement a subphylum of the phylum Chordata. The taxonomic diversity of a very morphologically conservative group like the "Inarticulates" certainly does not seem to justify such a high ranking. This is typical of the sort of problems that come about when trying to integrate Cladistic and Linnaean systems. Such attempts often lead to a huge taxonomic inflation of ancestral ("basal") taxa.

The Articulates meanwhile are in the newer arrangement split into two classes and a greater number of orders, some of which may indeed be warranted (for example four rather one order of "Spirifid" brachiopods can be justified if it can be shown that the Spirifid condition evolved in four different and unrelated lineages).

The relationship of the Phoronida (burrowing worm-like lophophorates) is another problem. Although a number of authors still regard Phoronida as constituting a separate phylum. Several recent evolution trees show the Phoronida and Brachiopoda as closely interrelated, with the Brachiopoda possibly a paraphyletic group. It is becoming increasingly accepted that the constitute a single clade together with the Brachiopoda, possibly as a class within the phylum Lophophorata, which also includes the Bryozoa, and Brachiopoda, all three groups sharing a ciliated lophophore and a number of other features (although the status of the Bryozoa awaits molecular confirmation).

It has even been suggested that brachiopods are polyphyletic, and that is, that different brachiopod groups evolved separately from soft-bodied phoronid-like ancestors.

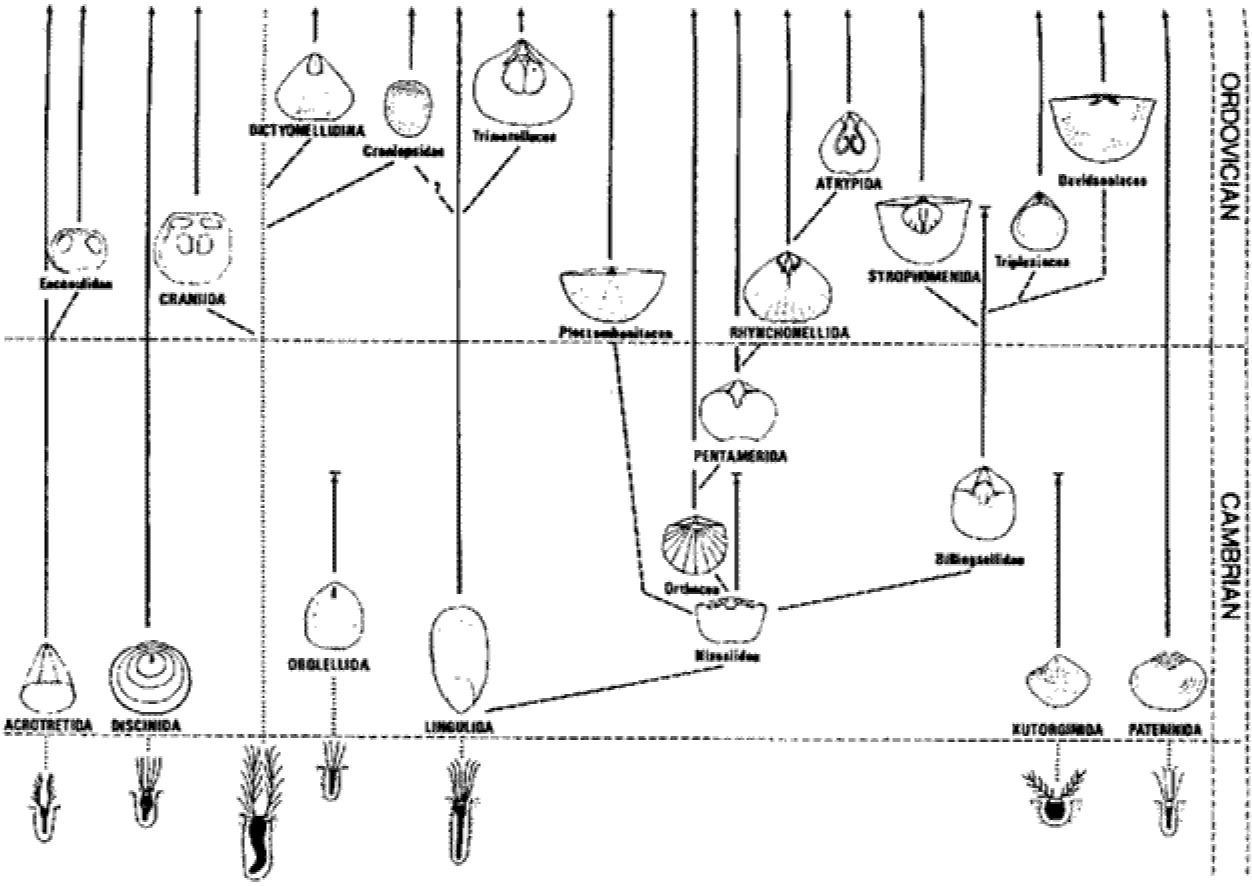


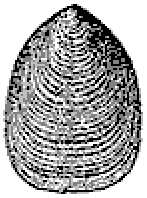
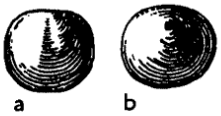
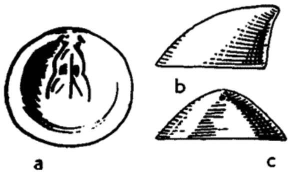
diagram from A. D. Wright, "Brachiopod Radiation", in Systematics Association Special Volume No.12, *The Origin of Major Invertebrate Groups*, ed. by M. R. House, 1979, p.249, Academic Press, London and New York

This might explain the way in which a number of distinct brachiopod lineages appear in the earliest Cambrian with no intermediate forms.

Note, in the following classification, diagnosis for the most part follows Sean Robson

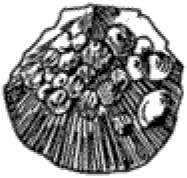
Subphylum Linguliformea

Brachiopods with organophosphatic inarticulated shells, valves lacking teeth and sockets.
The lophophore is unsupported. They have a true gut with an anus.
Early Cambrian - Recent

Lingulata Linguliform brachiopods with smooth or pitted larval shell; marginal setae form continuous rows along mantle margin; digestive tract recurved with anteriorly placed, functional anus.				**Paterinata**
				
Lingulida	**Discinida**	**Acrotretida**	**Siphonotretida**	**Paterinida**

Subphylum Craniiformea

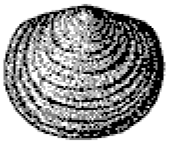
Brachiopods with calcitic inarticulated shells.
The lophophore is unsupported. They have a true gut with an anus.
Early Cambrian - Recent

Craniata		
	**no image available yet**	**no image available yet**
Craniida	**Craniopsida**	**Trimerellida**

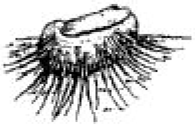
Subphylum Rhynchonelliformea (including "Articulata")

Brachiopods with calcitic articulated shells. Teeth and sockets are usually present, except in some primitive "inarticulate" forms, but can be lost secondarily. The gut is blind and without an anus. The Articulata have calcareous shells whose valves, like Bivalve mollusk shells, are hinged (articulated) by well-developed teeth and sockets. The shell is divided into two distinct layers, primary (outer) and secondary (inner). The outer layer is lamellar (consisting of layers) and the inner layer is fibrous, made up of calcareous fibers.

Primitive ("Inarticulate") forms

Chileata		**Obolellata**		**Kutorginata**
no image available yet	**no image available yet**		**no image available yet**	
Chileida	**Dictyonellida**	**Obolellida**	**Naukatida**	**Kutorginida**

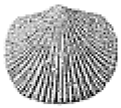
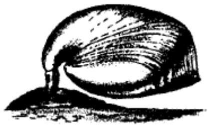
Advanced ("articulate") forms - the Strophomenids

Strophomenata Articulate brachiopods with variable profile in productids; commonly planar to weakly concavoconvex in strophonmenides. middle Cambrian - Late Permian			
			
Billingsellida	Orthotetida	Strophomenida	Productida

Advanced ("articulate") forms - the rest of the Articulates

Rhynchonellata

Articulate brachiopods with biconvex, strophic or astrophic shells articulated by deltidiodont or cyrtomatodont teeth and sockets buttressed by brachiophores. Early Cambrian - Recent

no image available yet		**no image available yet**		**no image available yet**
Protorthida	**Orthida**	**Spiriferida**	**Pentamerida**	**Terebratulida**
no image available yet	**no image available yet**		**no image available yet**	**no image available yet**
Rhynchonellida	**Atrypida**	**Athyridida**	Spiriferidida	Thecideida

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Links

Links

Brachiopods - this European Web site includes up-to-date information on Brachiopoda, references, systematics, diagnoses...) a directory of specialists working on brachiopods (Brachiopodologists - yes, there is such a term!).

Brachio-Philes - Sean Robson's Brachiopod site - see his Brachiopod Systematics page

The classifications on both these sites are based on Williams, Carlson, Brunton, Holmer, and Popov, 1996: A Supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London. Series B.* Volume 351, pgs.1171-1193.

Brachiopoda main page

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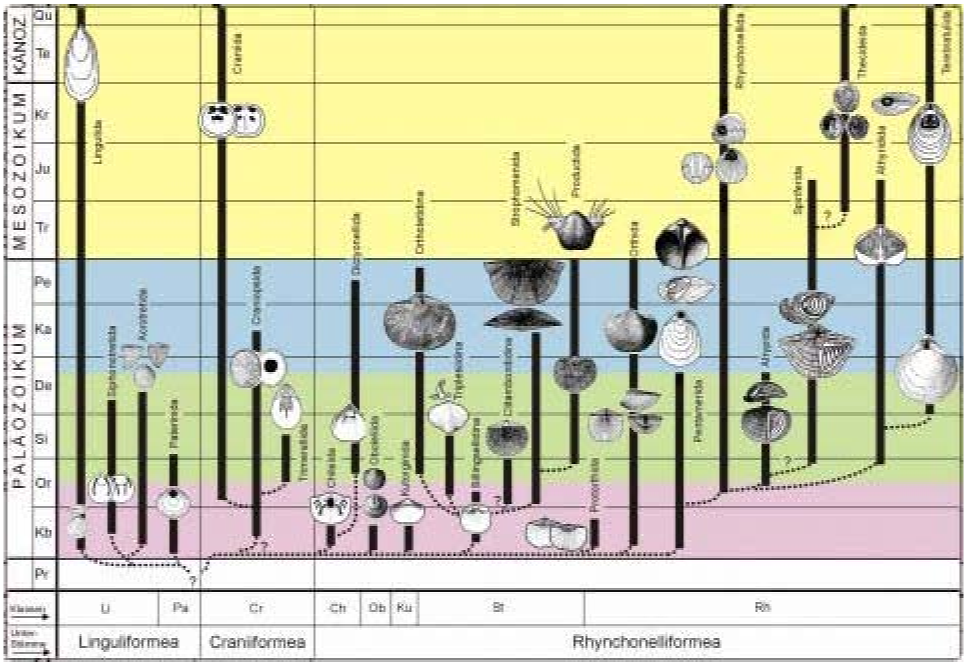
Brachiopoda - Dendrogram

The following very useful diagram is from

Image from Senckenberg Research Institute, Frankfurt



The bottom row lists the three subkingdoms, the next the classes, and finally the time-line and phylogeny shows the orders, along with represemntative illustrations. Many of these ordinal groups are likely paraphyletic, as shown here. However the exact relationships of some of these taxa remains speculative (and hence are usefully represented by evolutionary systematic style dotted lines)

The following dendrogram is based on this phylogeny (from Access Science). It gives the illusion that brachiopod systematics and phylogeny is pretty well worked out. Nothing could be further from the truth. Endemic homoplasy means that, above superfamily level, exact phylogenetic relationshiops remain frustratingly unclear. The only difference is that we have retained the three main clades (with Phoronida as a fourth one) as an unresolved polytomy. It is likely that proto-brachiopods radiated rapidly at this time, (at the start of the Cambrian explosion), making precise phylogenetic determination difficulat (and always, morphology may give one version, molecular phylogeny another, and differemnt molecular phylogenies different topologies). Especially, the positions of a number of taxa (e.g. Phoronida, Thecideida) is difficult to determine. MAK120107

```
o Brachiopoda
|?--Phoronida
|--o Craniiformea / Craniata
|  |--Craniida
|  `--+--Craniopsida
|     `--Trimerellida
|--o Linguliformea
|  |-- Paterinata / Paterinida
|  `--o Lingulata
|     |--Acrotretida
|     `--+--Lingulida
|        `--Siphonotretida
`-o Rhynchonelliformea
  |--o Obolellata
  |  |--Obolellida
  |  `--Naukatida
  |--o Chileata
  |  |--Chileida
  |   `--Dictyonellida
  `--+--Kutorginata / Kutorginida
     |--o Strophomenata
     |  |--Strophomenida
     |  |--Billingsellida
     |  `--+--Orthotetida
     |     `--Productida
     `--o Rhynchonellata
        |--+--Protorthida
        |  `--Orthida
        `--+--Pentamerida
           `--+--+--Rhynchonellida
              |  `--+--Atrypida
              |     `--+--Terebratulida
              |        `--Athyridida
              |        ?--Thecideida
              `--+--Spiriferida
                 `--Spiriferinida
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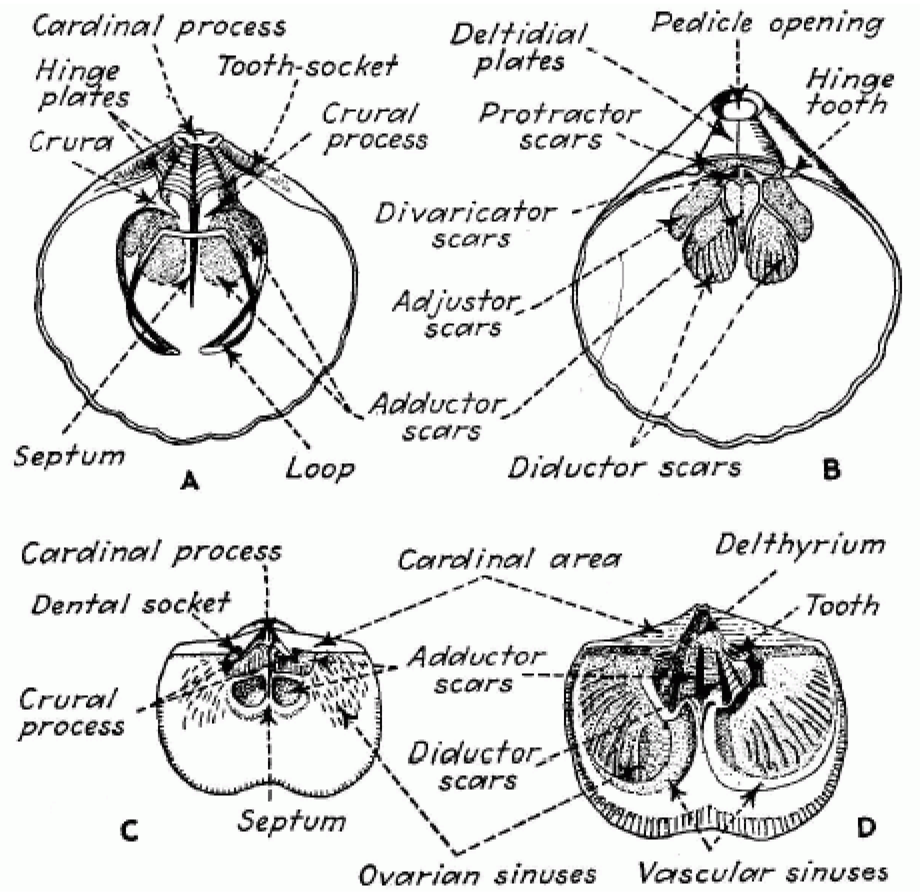
page M. Alan Kazlev 120107

Brachiopoda - Glossary

Editor's note: at some point we intend to have a proper glossary here. See also the main brachiopod page for more



A-B. *Magellania flavenscens*, a modern terebratellid brachiopod: A, view of interior of dorsal valve, with all organic matter removed; B, ventral interior showing various muscle scars. C-D. *Hebertella*, a very common fossil brachiopod in Upper Ordovician strata: C. *H. occidentalis*, dorsal interior. D. *H. insculpta*, ventral interior - diagram and caption from Twenhofel, W. H., and Shrock, R. R., *Invertebrate Paleontology,* 1935. McGraw- Hill Book Co., N. Y. p.287 (

See Access Science - Brachiopoda for further diagrams

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Bryozoa

The freshwater bryozoan *Lophopus crystallinus* (Pallas, 1768)
Phylactolaemata > Plumatellida > Lophopodidae
image Creative Commons Attribution Non Commercial Share Alike, © Natural History Museum, London, via EOL

Bryozoa are a phylum of common, small, colonial, mostly marine but sometimnes freshwater, often encrusting, lophotrochozoans. Like brachiopods they possess a fringe of complex hollow feeding tentacles called a lophophore. Because of this they are generally grouped together with brachiopods and phoronids on morphologicalgrounds, but molecular phylogeny tends to place them in a more basal position. Their position being for this reason unresolved and controversial , they are for the time being interpreted as general lophotrochozoa

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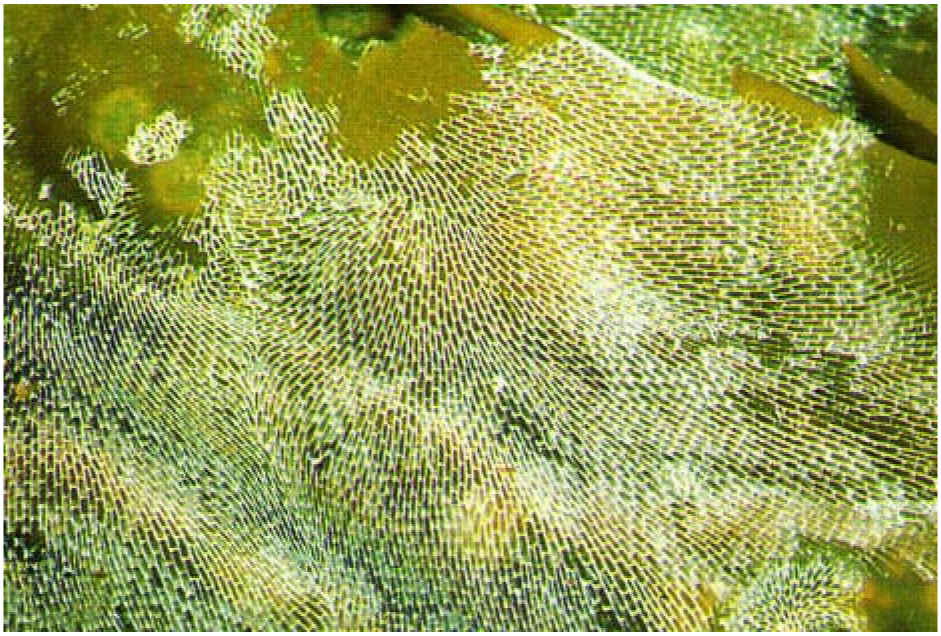
Bryozoa

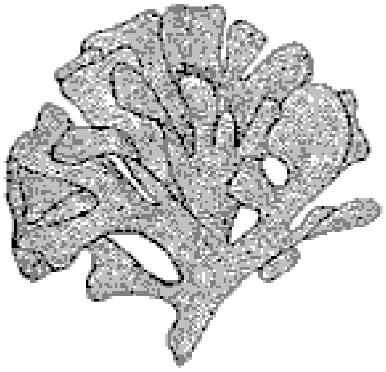
Early Ordovician to Recent



The encrusting bryozoan, *Membranipora membranacea*; Gymnolaemata > Cheilostomida > Membraniporidae. The encrusting habit is characteristic of many bryozoa, although some have erect colonies that resemble miniature corals. Bryozoa are commonly encountered even in intertidal rockpools, or found cemented on other organisms such as kelp or seashells.
Image from: USGS, via Wikipedia, public domain

Bryozoans, or "moss animals," are aquatic, mostly marine, colonial organisms, superficially rather like coral. A few to many millions of these individuals may form one colony. The colonies range from millimeters to meters in size, but the individuals that make up the colonies are tiny; usually less than a millimeter long. Usually they encrust rocky surfaces, shells, or algae. The colonies may be soft-bodied or calcareous like corals. It is the latter that are most often fossilized. There are about 5000 living species, with several times that number of fossil forms known.

After approximately 250 years of scientific study, the sum total of accumulated human wisdom on the subject of bryozoan phylogeny is Nil. Zero. Nada. It would be fair to state that we know as much about the phylogeny of entirely hypothetical Martian cryptobionts. Those, at least, have been the subject of intense speculation by learnèd folks who can get away with such speculations in the semi-popular press. Bryozoologists just throw their hands up -- like so many zoöids waving their happy lophophores about. Maybe they'll catch onto something that way -- but we are not



optimistic.

For taxonomic purposes, the Bryozoa are classified as follows:

PHYLUM BRYOZOA
- **Class Stenolaemata**
  - Order Cyclostomata
  - Order Hederellida
  - Order Trepostomatida
  - Order Cystoporida
  - Order Cryptostomida
  - Order Fenestrida
- **Class Gymnolaemata**
  - Order Ctenostomata
  - Order Cheilostomata
- **Class Phylactolaemata**

MAK990511 ATW050910.

The following phylogeny is proposed by *Palaeos* contributer Christopher Taylor on the basis of Prothero, 1998. and should not be considered more authoritative than other phylogenies (assuming their are any). We have only included here because what would *Palaeos* be without its dendrograms? MAK121001

```
Bryozoa
    |--Ctenostomata
    `--+--Cheilostomata
       `--+-- Stenolaemata
          `-- Phylactolaemata
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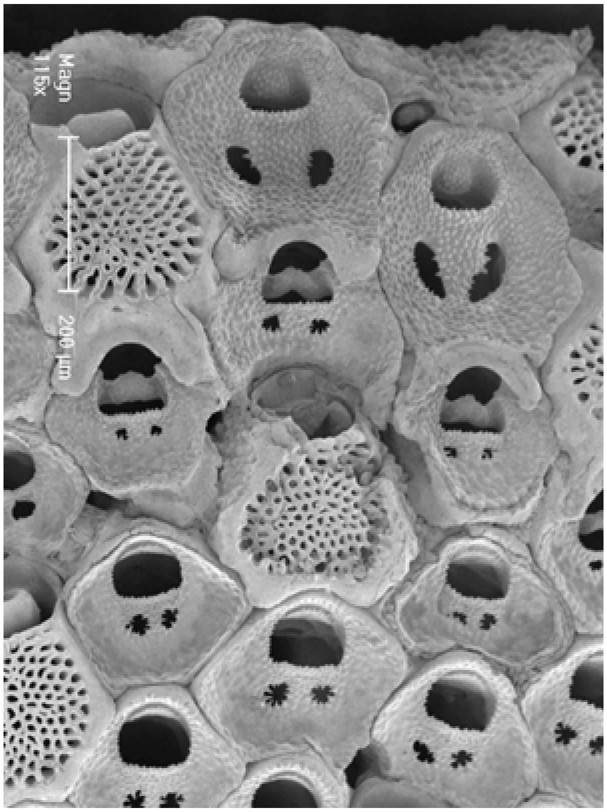


Scanning electron micrograph of part of a bryozoan colony showing male and female brooding zooids and feeding autozooids..

Class Stenolaemata

These are marine bryozoans with tubular zooids with strongly calcified walls. The lophophore is protruded by action of annular muscles. Most forms lack an operculum. This was the predominant Bryozoan group during the Paleozoic. Some grew as lacy or fan-like colonies that became important reef builders and in some regions form an abundant component of limestones. Their numbers were greatly reduced by the terminal Permian extinction event.

Order Cyclostomata (= Tubuliporata)

Bryozoa with encrusting or erect colonies, many with communication pores. The skeletal structure is typically laminated. The aperture for each zooid (little animal) is either circular or polygonal. Late Ordovician to Recent. - about 250 genera

Representative types	**Systematic Classification**
...	SUBORDER PALEOTUBULIPORINA SUBORDER TUBULIPORINA SUBORDER FASCICULINA SUBORDER ARTICULINA SUBORDER CANCELLATA SUBORDER CERIOPORINA SUBORDER RECTANGULATA

Order(?) Hederellida

A group of bryozoans similar to cyclostomatids; of uncertain relationships. Late Ordovician to Carboniferous.

Order Trepostomatida

Colonies generally robust; dendroid, encrusting, or massive. Ordovician to Triassic - 200 genera

Tabulipora acadica - (Family: Stenopridae) - Early Carboniferous of Nova Scotia

Order Cystoporida

Colonies encrusting or erect, robust or delicate. Crescent-shaped thickened strip or projections (*lunarium*) around each aperture. Early Ordovician to Late Permian - 100 genera

Representative types	**Systematic Classification**
...	SUBORDER CERAMOPORINA SUBORDER FISTULIPORINA

Order Cryptostomida

Colonies erect, typically delicate; foliate, dendroid.(tree-like), or bilaminar sheets. Skeletons without communication pores
Early Ordovician to Late Permian - 90 genera

Representative types

...

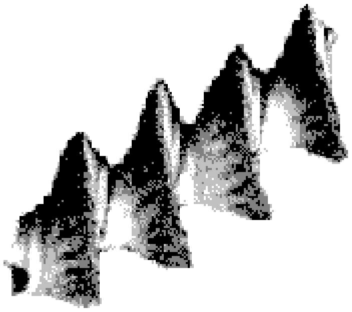
Systematic Classification

SUBORDER PTILODICTYINA
SUBORDER RHABDOMESINA
SUBORDER TIMANODICTYINA
SUBORDER GOLDFUSSITRYPINA
SUBORDER STREBLOTRYPINA

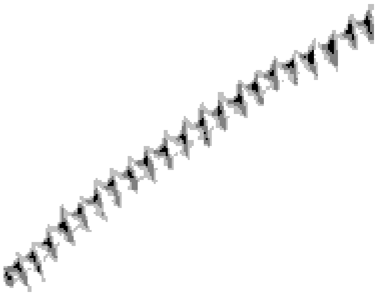
Order Fenestrida (=Fenestrata)

Includes some of the most amazing bryozoa. The colonies are erect, typically delicate; reticulate (net-like) or pinnate (fern-like). This order was previously included under the Cryptostomata.
Early Ordovician to Late Permian - 100 genera

Representative types



close up



entire colony

Family FENESTELLIDAE
Archimedes wortheni Hall
Early Carboniferous (Warsaw Formation - Early Visean, Arundian epoch)
west Laurussia

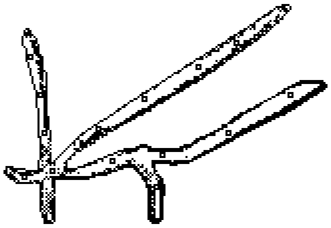
Class Gymnolaemata

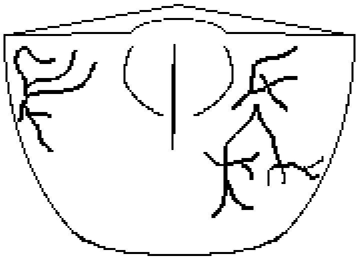
Mostly marine bryozoans with cylindrical or flattened zooids. Lophophore is protruded by action of muscles pulling on frontal wall. Includes the majority of living bryozoan species..

Order Ctenostomata

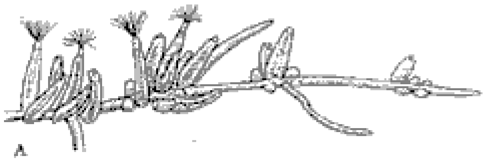
Uncalcified forms, including several that bore into calcareous substrates. Skeleton membranous or gelatinous. Opercula rare. Eggs brooded in body cavity. Almost all fossils are traces of boring forms Ordovician to Recent - 50 named genera

Representative types





Suborder STOLONIFERINA
Superfamily TEREBRIPOROIDEA
family VINELLIDAE
Vinella repens Ulrich, 1890 (above)
Blackriveran (Sandbian)
North America
width of shell illustrated on top right: 3 cm
more on *Vinella*
(from the Union College Geology Department site)



Suborder VESICULARINA
Superfamily VESICULARIOIDEA
family VESICULARIIDAE
Bowerbankia
recent - widespread

Systematic Classification

SUBORDER ALCYONIDIINA
SUPERFAMILY ALCYONIDIOIDEA

SUBORDER FLUSTRELLIDRINA
SUPERFAMILY HAYWARDOZOONOIDEA
SUPERFAMILY FLUSTRELLIDROIDEA

SUBORDER VICTORELLINA
SUPERFAMILY VICTORELLOIDEA

SUBORDER PALUDICELLINA
SUPERFAMILY PALUDICELLOIDEA

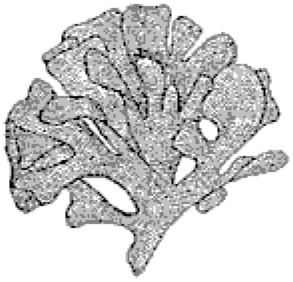
SUBORDER VESICULARINA
SUPERFAMILY VESICULARIOIDEA

SUBORDER STOLONIFERINA
SUPERFAMILY TRITICELLOIDEA
SUPERFAMILY AEVERRILLIOIDEA
SUPERFAMILY VALKERIOIDEA
SUPERFAMILY ARACHNIDIOIDEA
SUPERFAMILY TEREBRIPOROIDEA
SUPERFAMILY HISLOPIOIDEA
SUPERFAMILY PENETRANTIINA

Order Cheilostomata

These are calcified forms, usually with an opercula. Short-box-like zooeica (chambers for the little animal). The eggs are usually brooded in ovicells (swollen spherical chambers in which the fertilized egg develops into a larva). The suborders are distinguished according to frontal calcification and mechanism of lophophore protrusion. This order includes the majority of recent Bryozoa
Late Jurassic - Recent. 1000 genera

Representative types



Infraorder FLUSTRINA
Superfamily CALLOPOROIDEA
family Flustridae
(*Flustra foliacea* Linnaeus, 1758)

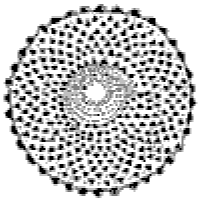
Systematic Classification

SUBORDER PROTOCHEILOSTOMATINA
SUPERFAMILY LABIOSTOMELLOIDEA

SUBORDER INOVICELLINA
SUPERFAMILY AETEOIDEA

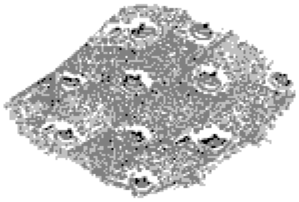
SUBORDER SCRUPARIINA
SUPERFAMILY SCRUPARIOIDEA

(Recent - Europe and the Arctic)



Suborder NEOCHEILOSTOMINA
Superfamily CALLOPOROIDEA
family CUPULADRIIDAE
Cupuladria
Pliocene to Recent
Atlantic, Carribean, Indo-Pacific

Suborder ASCOPHORINA
Infraorder LEPRALIOMORPHA Gordon, 1989
Superfamily SMITTINOIDEA
Family BITECTIPORIDAE
Pentapora
Recent - Europe and Atlantic



Infraorder LEPRALIOMORPHA
Superfamily SCHIZOPORELLOIDEA
Family SCHIZOPORELLIDAE
Schizoporella - recent - widespread

SUBORDER MALACOSTEGINA
SUPERFAMILY ELECTROIDEA

SUBORDER NEOCHEILOSTOMINA
INFRAORDER FLUSTRINA
SUPERFAMILY CALLOPOROIDEA
INFRAORDER CELLULARIOMORPHA
SUPERFAMILY BUGULOIDEA
SUPERFAMILY MICROPOROIDEA
SUPERFAMILY CELLARIOIDEA

SUBORDER ASCOPHORINA
INFRAORDER ACANTHOSTEGOMORPHA
SUPERFAMILY CRIBRILINOIDEA
SUPERFAMILY BIFAXARIOIDEA
SUPERFAMILY NEPHROPOROIDEA
SUPERFAMILY CATENICELLOIDEA
INFRAORDER HIPPOTHOOMORPHA
SUPERFAMILY HIPPOTHOOIDEA
INFRAORDER UMBONULOMORPHA
SUPERFAMILY ARACHNOPUSIOIDEA
SUPERFAMILY ADEONOIDEA
SUPERFAMILY PSEUDOLEPRALIOIDEA
SUPERFAMILY LEPRALIELLOIDEA (UMBONULOIDEA)
SUPERFAMILY CHLIDONIOPSOIDEA
INFRAORDER LEPRALIOMORPHA
SUPERFAMILY SMITTINOIDEA
SUPERFAMILY SCHIZOPORELLOIDEA
SUPERFAMILY URCEOLIPOROIDEA
SUPERFAMILY DIDYMOSELLOIDEA
SUPERFAMILY EUTHYRISELLOIDEA
SUPERFAMILY SIPHONICYTAROIDEA
SUPERFAMILY MAMILLOPOROIDEA
SUPERFAMILY CELLEPOROIDEA
SUPERFAMILY CONESCHARELLINOIDEA

Class Phylactolaemata

Non-calcareous freshwater bryozoans with no zooid polymorphism. Horse-shoe shaped lophophore.. No fossil record except for a few statoblasts (resistant wintering structures) from Quaternary sediments.

Representative types	**Systematic Classification**
...	ORDER PLUMATELLIDA

Credits

illustrations from the former The "Lesser" Protostome and Lophophorate Phyla page at University of Sydney Biological Sciences, from Brusca and Brusca, *Invertebrates*.1990.

References

Prothero, D. R. 1998. *Bringing Fossils to Life: An introduction to paleobiology*. WCB McGraw-Hill: Boston.

Links

The Bryozoa Home age - Recent and Fossil Bryozoa

Introduction to the Bryozoa - "Moss animals"

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(originally uploaded on Kheper site uploaded 11 May 1999)

Mollusca

Abbreviated Dendrogram

```
SPIRALIA
|--BRACHIOPODA
`--+--ANNELIDA
   |
   `--MOLLUSCA
      |--Aculifera
      |  |==Mattheviidae
      |  |   `--Aplacophora
      `--Conchifera
         |==Tryblidiida (Monoplacophora)
         |  `--Cephalopoda
         `==Helcionelloida
              |==Rostroconchia
              |  `-- Scaphopoda
              |--Bivalvia
              `--Gastropoda
```

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The European Common Cuttlefish, *Sepia officinalis* (Cephalopoda, Coleoidea, Sepiida, Sepiidae)
Photo © Hans Hillewaert, Creative Commons Attribution Share Alike, WoRMS image

Mollusca: Contents

Part 1: Alphabetical Listings

A. Glossaries of terms and abbreviations.

- Overall Glossary
  - Bivalve Glossary
  - Cephalopod Glossary
  - Gastropod Glossary

B. Taxon Index: alphabetical list of taxa.

Very incomplete taxon list

C. References: literature citations by author.

- Overall References
  - Cephalopod References

Part 2: Phylogenetic Listings

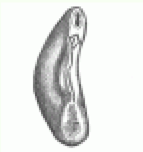
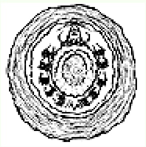
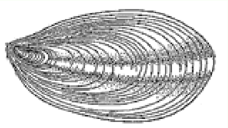
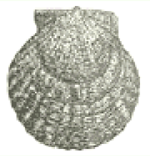
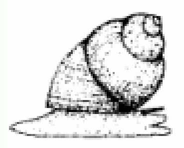
A. Dendrograms ("Cladograms")

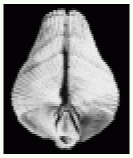
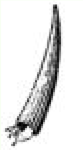
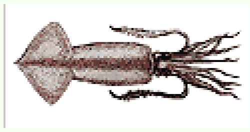
- Summary Dendrogram
- Molluscan Phylogeny
  - Bivalve Dendrogram
  - Cephalopod Dendrogram
  - Helcionelloida Dendrogram   Gastropod Dendrogram

B. Descriptions

Molluscan phylogeny is a highly controversial subject. The introduction of both molecular phylogeny and cladistic methodology has if anything only obscured things, with a molecular consensus emerging totally at odds with both morphology and paleontology (e.g. bivalves and gastropods as sister taxa). The revised units also need to be uploaded

Under Construction

	**Solenogastres** (= Neomeniomorpha; Aplacophora in part)	no fossil record	very small creeping worm-like soft bodied shell-less forms
	**Caudofoveata** (= Chaetodermomorpha; Aplacophora in part)	?Silurian to Recent	very small deep sea worm-like soft bodied burrowing shell-less forms. The Silurian *Acaenoplax*, which resembles both Solenogastres, Caudofoveata and Polyplacophora, may be an early form of this lineage.
	**Polyplacophora** (= Amphineura in part)	Furongian to Recent	The chitons, which have eight plates or "valves" which are overlapping in post-Mesozoic forms. The foot is broad; the head reduced. The soft parts show some segmentation. The animal generally lives attached to rocks in the inter-tidal zone. Appear to be distantly related to the Solenogastres and Caudofoveata (as ancestors/cousins), and the Tryblidiida
	**Tryblidiida** (= Monoplacophora *sensu stricto* = Tryblidiida = Tergomya in part)	Furongian to Recent	Creeping cap-shelled forms with paired muscle attachments. The most primitive conchiferan group. A few dozen deep water recent species remain as "living fossils". As with the Polyplacophora the soft parts show some segmentation. Probably evolved from a soft-bodied ancestor, possibly Polyplacophora relationships.
	**Stenothecidae** (= Monoplacophora in part)	Early to Middle Cambrian	Small group of little known bivalved forms. There relationship with other molluscan groups is unclear, and it is not agreed whether they qualify as class status. No descendents, ancestors unknown.
	**Helcionelloida** (= Monoplacophora in part; paraphyletic)	Earliest to Late Cambrian	an ancestral lineage or grade. Consist of creeping or weakly infaunal forms with cap-shaped or spiral shell. Probably evolved from a soft-bodied ancestor, as the direction of shell coiling is opposite that of the Tryblidiida, which they predate in any case. Generally considered directly or indirectly the ancestors of all conchiferan mollusks other than the Tryblidiida.
	**Bivalvia** (= Pelycopoda)	Early Cambrian to Recent	mostly sedentary or burrowing forms with a shell of two valves hinged dorsally. The foot is generally hatchet-shaped (hence the name "Pelycopod"); the head lacking; a very diverse group, includes epifaunal or infaunal forms, mostly marine but some freshwater species. Clams oysters, mussels, etc. Generally considered to have evolved from rostroconches , although this would relate them to helcionelloids , if not actually Scaphopods and Cephalopods, and the weight of current molecular and cladistic evidence indicates the bivalves diverged from the main Conchiferan lineage quite early.
	**Paragastropoda**	Early Cambrian to Devonian	Small group of superficially snail-like forms, and perhaps snail-like habits, distinguished by lack of torsion. Evolved from helcionelloids , no descendents. It is not even certain if this is a natural or a polyphyletic group.
Tergomya	**"Tergomya"** in part (= Monoplacophora in part; polyphyletic)	Furongian to Devonian	A probably artificial assemblage of creeping cap- or partly spiral shelled forms with single or paired muscle attachments. The Tryblidiida are usually included here but they are certainly a more basal group. Non- tryblidiidan Tergomya may have evolved probably several times from helcionelloids , although some may be related to the Tryblidiida. Some of the helcionelloid -descended forms would seem to be related to the Gastropods
	Gastropoda	Furongian to Recent	Diverse group of shelled or shell-less forms, evolved from a spiral-shelled helcionelloid or helcionelloid -descended "tergomyan" ancestor that underwent torsion. The body is usually asymmetrical, with a distinct head, pair of eyes, and one or two pairs of tentacles. The shell is usually spirally-coiled, but may (in the case of limpets) be cap shaped, and in some species is vestigial or completely absent. The

			foot is broad and used to creep along the substrate. Includes marine, freshwater, and terrestrial species (the only mollusks to invade the land). Snails, slugs and their relatives
	**Rostroconchia**	Early Cambrian to Late Permian	A Paleozoic group of infaunal forms. The shell consists of two valves joined in adults by an enclosed hinge. Evolved from helcionelloids . The posterior of the shell is usually produced into an elongate tube, presumably for inhalant and exhalent siphons. Originally considered to have given rise to both Scaphopods and Bivalves, as they share many similarities with both those groups. But relationships among early molluscan classes remain controversial
	**Scaphopoda**	Devonian to Recent	small semi-infaunal forms, the tubular shell open at both ends and resembles a miniature elephant's tusk, with one end larger than the other. The foot is conical; there are no gills. Probably evolved from rostroconches . Shown to be related to the Cephalopods.
	**Cricoconarida** (= Tentaculitoidea)	Middle Cambrian to Devonian	very small pelagic forms with tubular shells. They are thought to be related to the Cephalopods, and seem to have born a number of arms.
	**Cephalopoda**	Latest Cambrian to Recent	diverse group of large intelligent predaceous forms, with a large external shell (most Paleozoic and Mesozoic forms, and current Nautilus), a vestigial internal shell, or (in the case of the octopus) the shell is lost altogether. The head is large with well-developed eyes, and armed with horny chitinous jaws and many arms or tentacles for grasping prey; the head fused to the foot (hence the name). Evolved from helcionelloids .
	**Hyolitha**	Earliest Cambrian to Permian	Enigmatic animals with small conical shells, shell- microstructure indicates close to mollusks but experts do not agree whether they actually were mollusks .

Part 3: Specific terminology

The Shell
The Radula

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Phylum Mollusca

Abbreviated Dendrogram

```
SPIRALIA
|--BRACHIOPODA
`--+--ANNELIDA
   |
   `--MOLLUSCA
      |--Aculifera
      |  |==Mattheviidae
      |  |--Aplacophora
      |  `-- Polyplacophora
      `--Conchifera
         |==Tryblidiida
(Monoplacophora)
         |  `--Cephalopoda
         `==Helcionelloida
              |==Rostroconchia
              |  `-- Scaphopoda
              |--Bivalvia
              `--Gastropoda
```

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1. Mollusca

PRODUCTS OF MOLLUSC EVOLUTION

page from Volume 2 of the three volume set *The Science of Life* by H. G. Wells, Julian Huxley and G. P. Wells (1929-39).
image from More images of devilish aquatic creatures

Introduction

The Mollusks are a large and diverse group of soft-bodied unsegmented animals. Nearly 130,000 recent species are known, and some 35,000 fossil species. They include many familiar animals, like snails, clams, squid, octopi, etc, as well as others not so well known. They range in size from microscopic forms to the giant squid (Architeuthis), and have a long and venerable history appearing during earliest Cambrian time, if not before.

Physiology

All mollusks possess some or all of the following characteristics:

- a muscular fleshy foot which with gastropods (snails) is used to crawl along with but in cephalopods is modified into tentacles
- a visceral mass containing the digestive, excretory, and reproductive organs
- a mantle, usually two folds that enclose the gills or lungs, and also secretes the protective shell
- a radula, a tongue-like feeding organ, essentially a sort of built-in saw equipped with rows of microscopic teeth that is incredibly effective at scraping food off hard surfaces or grinding through any substance (some carnivorous snails are able to bore a whole through the shells of other mollusks)
- a special respiratory gill (the ctenidium)
- a shell made of calcium carbonate. This fossilizes easily, which explains the rich fossils record the mollusks possess.

Although not all mollusks share all these characteristics, generally all mollusks have at least some of them.

Molluscan Diversity

Despite sharing these common features, the mollusks are an incredibly diverse group. The following diagram shows the major classes, which as can be seen are all based on variation in this same body plan.

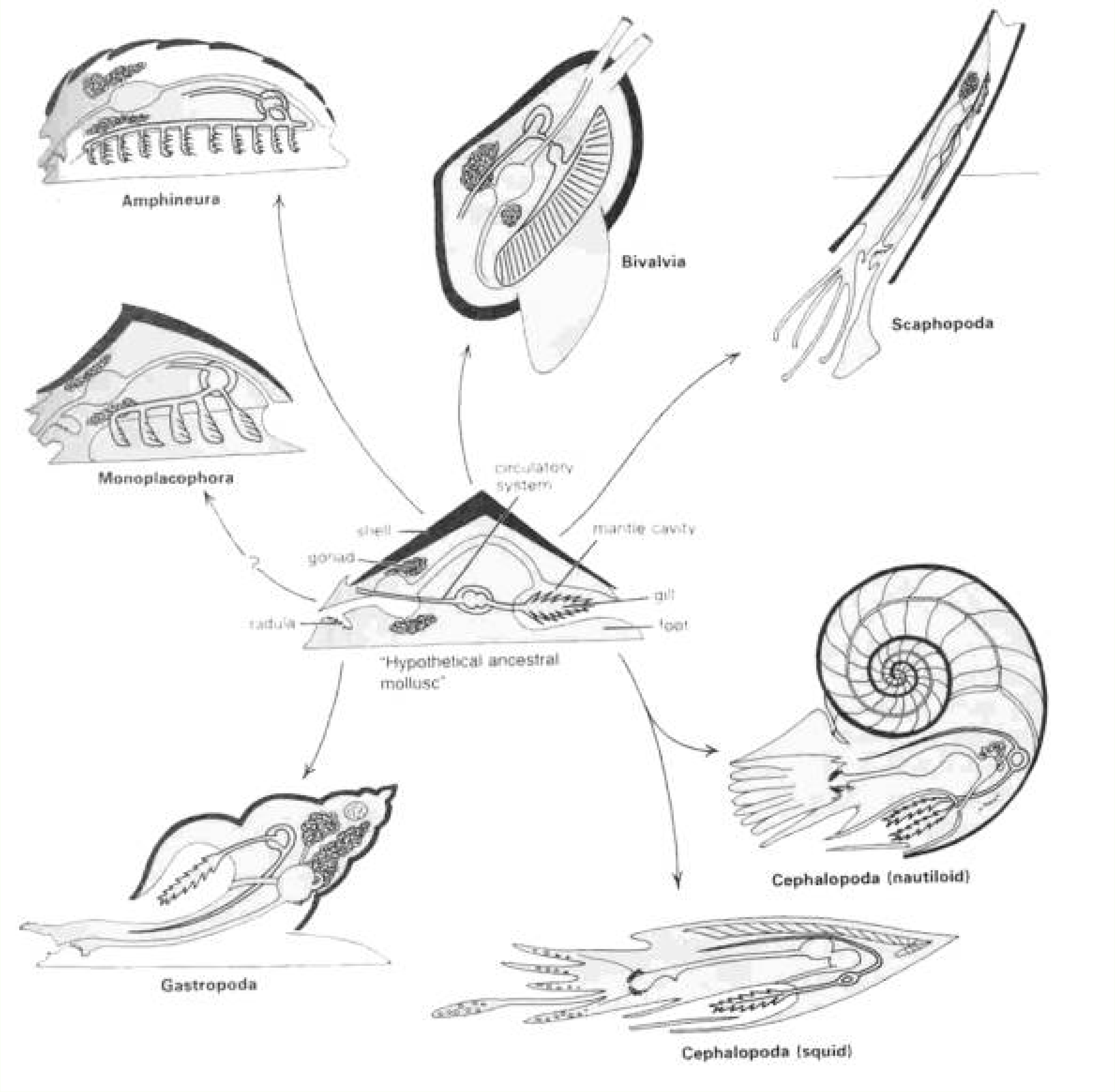

Figure from D. R. Prothero, 1998, *Bringing Fossils to Life*, McGraw-Hill, p. 277; from Clarkson, 1993 - this image from LAB 3 Chapter 8: Phylum Mollusca and Biological Diversity and Evolution through Time

This diagram presents a stylized relationship between the different Molluscan groups, with all evolving from a "hypothetical ancestral mollusk". It is now known that molluscan phylogeny is a lot more complex than this.

Habitat

As one of the most successful forms of animal life, the mollusks have conquered almost every habitat and exist in all the oceans (from shallow tidal pools to the deepest trenches), in fresh water, and on land. The only environment they cannot cope with are very dry regions, as their moist skin is easily desiccated. Even so, the greatest diversity of mollusks species is to be found in marine environments

Taxonomic History

When Linnaeus was formulating his system of binomial nomenclature the mollusks were grouped (along with most invertebrates) under *vermes*, worms. The name Mollusca (from the Latin *mollis* "soft"), was first used by the great French zoologist Cuvier in 1798 to refer to cephalopods like squids and cuttlefish. It was later extended to include other organisms of this group, such as snails and bivalves.

Evolutionary History

The mollusks first appeared during the earliest Cambrian (Tommotian), at the very start of radiation of coelomate animals. The 35,000 fossil species that are known are without doubt only a small fraction of those that have ever lived. As the Cambrian period progressed, many types appeared that soon died out. Although previously included among the conventional classes of mollusks it is increasingly argued that these represent distinct classes, early experiments in molluscan evolution, or transition forms. However, the exact number of extinct classes remains debatable

By the Ordovician period the three main classes - Gastropoda, Bivalvia, and Cephalopoda - had increased greatly in number and diversity. This was a period of major evolutionary diversity for the phylum, and they became common in most marine ecosystems

The Devonian saw bivalves invade freshwater, and the first land snails appeared during the Carboniferous. During the Devonian also, the ammoniod took over from the nautiloids as the dominant cephalopod group, and these creatures continued to flourish throughout the entire Mesozoic, living alongside species of bivalves and gastropods not very different to modern forms. (Oysters for example were common during the Jurassic and Cretaceous, while scallops date back to the Paleozoic). By mid Cretaceous most mollusks, like most invertebrates and fish, were essentially like modern forms, except for the Cephalopods which were still represented largely by the Mesozoic ammonites and belemnites. The ammonites were decimated by the K-T extinction event, as were the reef-building rudist bivalves (although these were on the decline for some time), but the coleoids (soft-bodied squids, octopi etc) continued to evolve quite happily.

Systematics

Traditionally seven classes are recognized: Aplacophora (primitive worm-like shell-less forms), Polyplacophora (chitons, these were at one tile included with the Aplacophora), Monoplacophora (primitive ancestral forms), Gastropoda (snails and slugs), Bivalvia (clams, mussels, oysters, etc), Scaphopoda (tooth and tusk shells), and Cephalopoda (squids, octopus, nautilus, cuttlefish), of which only Gastropoda, Bivalvia, and Cephalopoda have large numbers of species and a strong fossil record. However it is becoming increasingly recognized that there were more groups that have since died out.

Descriptions

Mollusca Linnaeus 1758

Range: Fr ECambrian

Phylogeny: Spiralia (=Lophotrochozoa) **:** Brachiopoda + (Annelida + * **:** Aculifera + Conchifera) (see also Phylogeny page)

Characters: shell-secreting mantle (in primitive shell-less forms secretes instead calcareous spicules,), a single muscular foot (sometimes highly modified), radula (rasping file-like organ, secondarily lost in bivalves and some

Solenogastres), unique nervous system with two main pairs of nerve cords, and pectinate gills. (Nielsen (2001, via Jack R. Holt Systematic Biology)

Description: The second largest phylumj in the animal kingdom (surpassed only by the arthropods), a highly diverse phylum that includes both familiar animals such as snails and slugs, periwinkles, whelks, limpets, mussels, oysters, scallops, clams, squid, octopus, cuttlefish and many other forms. Although many are distinguished by a hard external shell, others such as slugs and octopus lack any trace of shell.

Links: Phylum Mollusca - a good brief introduction to the Mollusks; The Living World of Molluscs - another very good intro, a bit more detailed; Mollusca Tree of Life project; Malacology - from the Australian Museum On-line; Mollusca - a good introduction, from Biomedia (Glasgow University Zoology Museum); Index of Mollusks by Ralph Body - mostly still under construction, although the Aplacophora are well covered; The Classes of Phylum Mollusca - short overview of each of the extant classes; Phylum Mollusca Systema Naturae 2000 / Classification - ; LAB 3 Chapter 8: Phylum Molusca - some lecture notes and images.

page from Volume 2 of the three volume set *The Science of Life* by H. G. Wells, Julian Huxley and G. P. Wells (1929-39).
image from More images of devilish aquatic creatures

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page uploaded 29 September 2002
page by M. Alan Kazlev 020929, checked ATW050731, last revised MAK120607

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Shell Morphology

Abbreviated Dendrogram

```
SPIRALIA
|--BRACHIOPODA
`--+--ANNELIDA
   |
   `--MOLLUSCA
      |--Aculifera
      |  |==Turrilepadida
      |  `-- Polyplacophora
      `--Conchifera
         |==Tryblidiida (Monoplacophora)
         |  `--Cephalopoda
         `==Helcionelloida
              |==Rostroconchia
              |  `-- Scaphopoda
              |--Bivalvia
              `--Gastropoda
```

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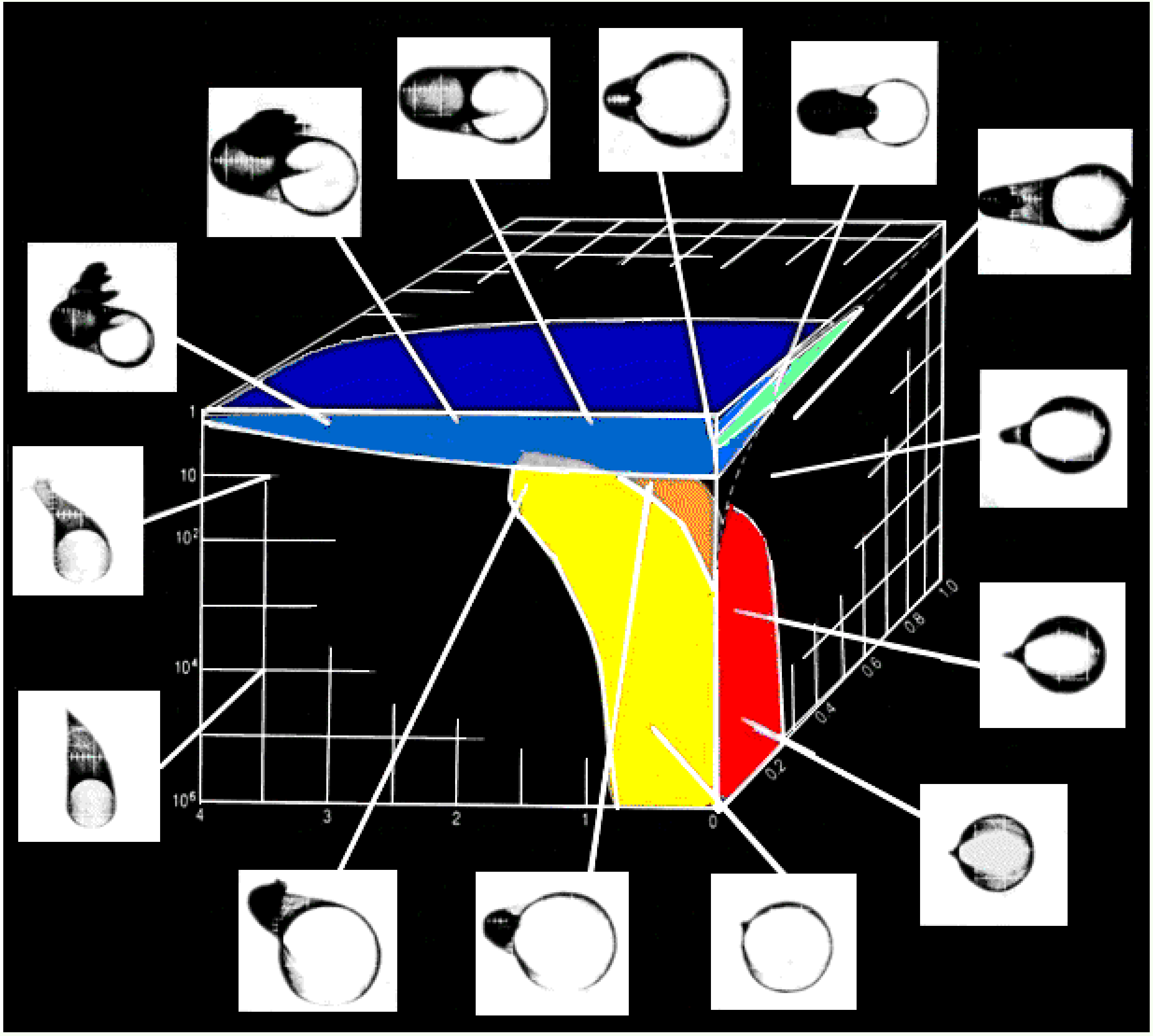

Shell morphology, according to the mathematical model of David Raup. Blue represents Gastropods, green Cephalopods, yellow Bivalvia, and Red Brachipoda

image from Equiangular Spiral Mollusca

The work of D'Arcy Wentworth Thompson - especially his opus *On Growth and Form*, was seminal in understanding the elegant mathematical basis of the forms found in nature, such as mollusk shells, plant growth, and so on. Of later studies regarding the theoretical morphology of the coiled shell, the work of David Raup (1962, 1966) is the best-known. Raup used a computer-based graphical method to produce a range of hypothetical coiled shapes and was then able to see how many of these possible types had in fact been adopted in nature. [Clarkson, 1979 p.141].

Dr Raup was able to generate a large number of ideal shapes using only four parameters, three of which are shown here:

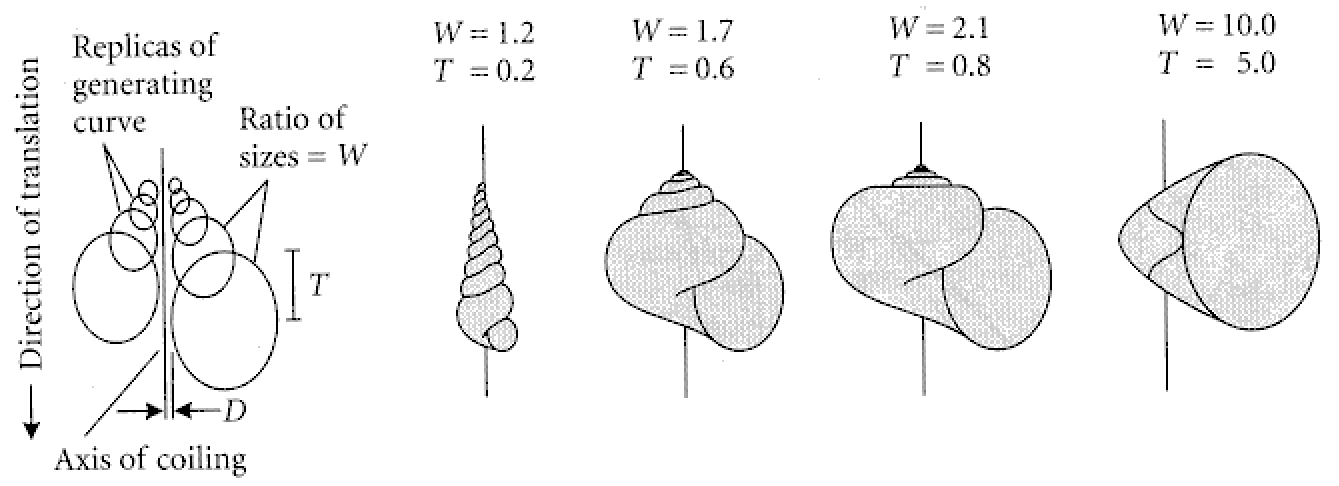

image from Raup Model from Raup 1962)

> "A simple model of variation in the rate of growth in several dimensions accounts for variation in the form of gastropod shells. The model specifies the shape of the aperture, or generating curve, the axis of coiling, the size ratio (W) of successive generating curves, the distance (D) of the generating curve from the axis, and the proportion (T) of the height of one generating curve that is covered by the successive gyres."

image from Futuyma 1997, after Raup 1962, cited in Raup Model

Taking the example of a helically coiled gastropod, and assuming that its shell is no more than a long hollow cone growing at the aperture end and coiling about a vertical axis as it grows, these parameters are:

- The shape of the tube in section, known as the shape of the *generating curve*. This is basically the same as the shape of the aperture, and may vary greatly in various molluscan species, especially in shelled cephalopods.
- The rate of whorl expansion after each revolution around the axis, represented by the letter **W**. W affects the rate at which the diameter of the tube grows. Higher values mean opening of the shell becomes wider with each rotation. So if, for example, W=2, that means that the diameter of the tube after a single revolution is twice what it was one whorl before. Hence short broad shells have a high W value, while long high spired ones (or serpenticone ammonoids) have a low W value.
- The position and orientation of the generating curve with respect to *distance* from the axis, represented by the letter **D**. D affects the distance of the center of the tube from the axis of coiling. Higher values mean tube of the shell forms further from the coiling axis, resulting in a wider columella or hollow center
- The rate of *whorl translation* along the axis, represented by the letter **T**. This is the relative distance between successive revolutions along the axis as compared with away from the axis. T affects the distance of the center of the tube from the previous rotation along the axis of rotation. Higher values mean the shell is taller, lower values shorter. Where T = 0 the shell is isotrophic [planispiral]. Where T is negative it is orthostrophic (most gastropods), where T is positive it is hyperstrophic (paragastropods).

Some transitional forms are shown in the following diagram, from Futuyma 1997, after Raup 1962

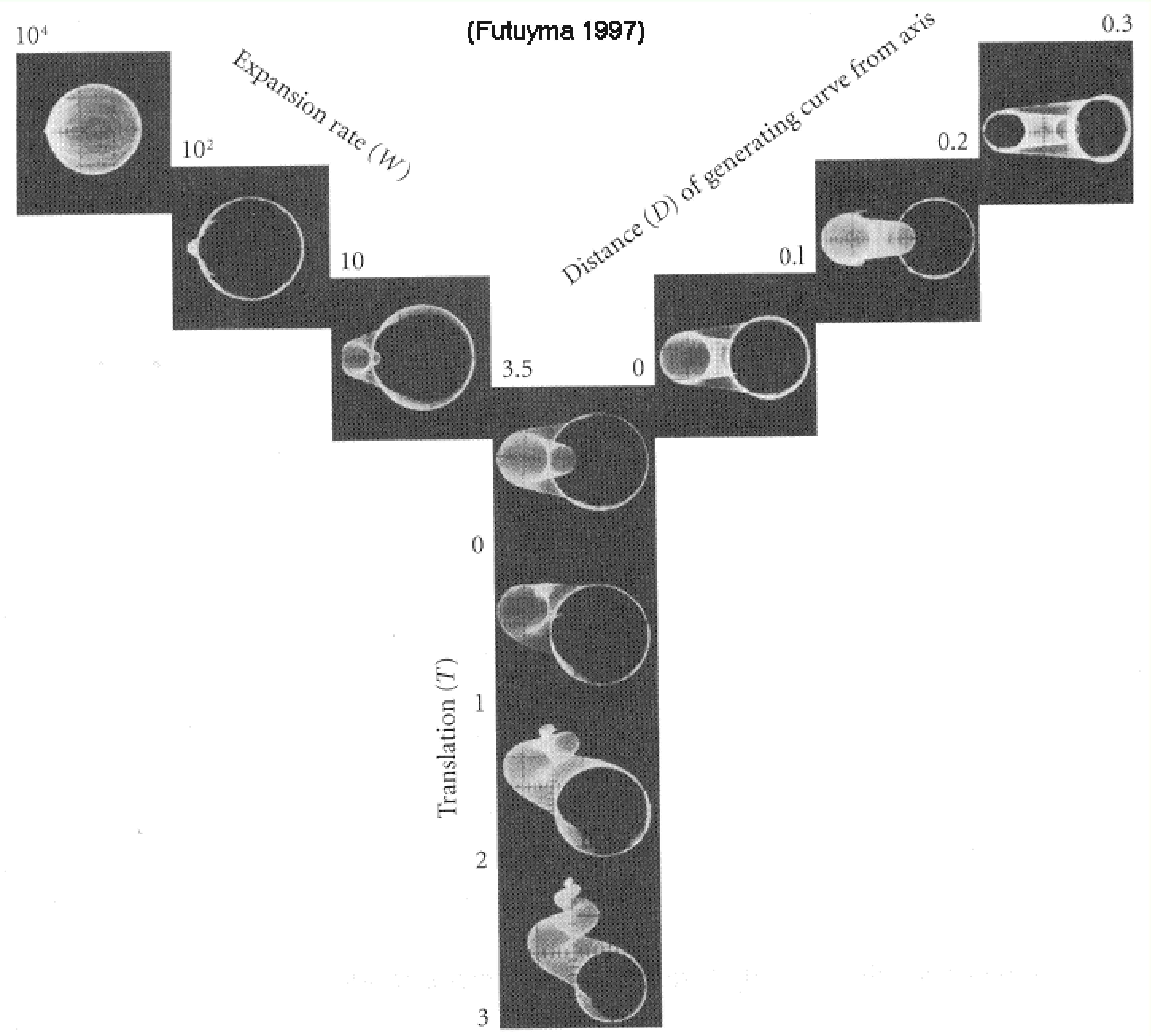

image © xxxx, from Futuyma 1997, after Raup 1962 (see Raup Model)

Originally, the shell shapes were projected onto an oscilloscope screen. Four decades later, anyone can access experiment by means of a simple java applet available on the Web

One can easily see how some molluscs, and indeed some spiral forms in nature (since these principles can be widely applied) developed shells where certain parameters have a high value, and others a low value. This is because each form evolved to different functional ends. Thus gastropods are usually helically coiled and tend to have a low W but T is very variable and may be anywhere from fairly low (giving squat broad shells) to extremely high, giving very tall high-spired shells. A few planispiral gastropods have T of value 0 (giving a shell equivalent in shape to coiled cephalopods, but lacking septa), and in one extinct lineage, the Euomphalids, T that is positive. In contrast, paragastropods have T that is positive in value, and may be very low to moderate. In bivalves T is always low and W is always very high, giving shells with a wide open curve and very rapidly expanding apertures. In brachiopods W is also high but T always equals O. Cephalopods are with only a few exceptions T=0 (planispiral), but unlike Brachiopods W is almost always very low (although some endocerids and other brevicones had short broad shells, but even here W is much lower even than in limpet gastropods). The following diagram shows some variations in form with only two parameters. The vertical axis here = W, the horizontal axis = D.

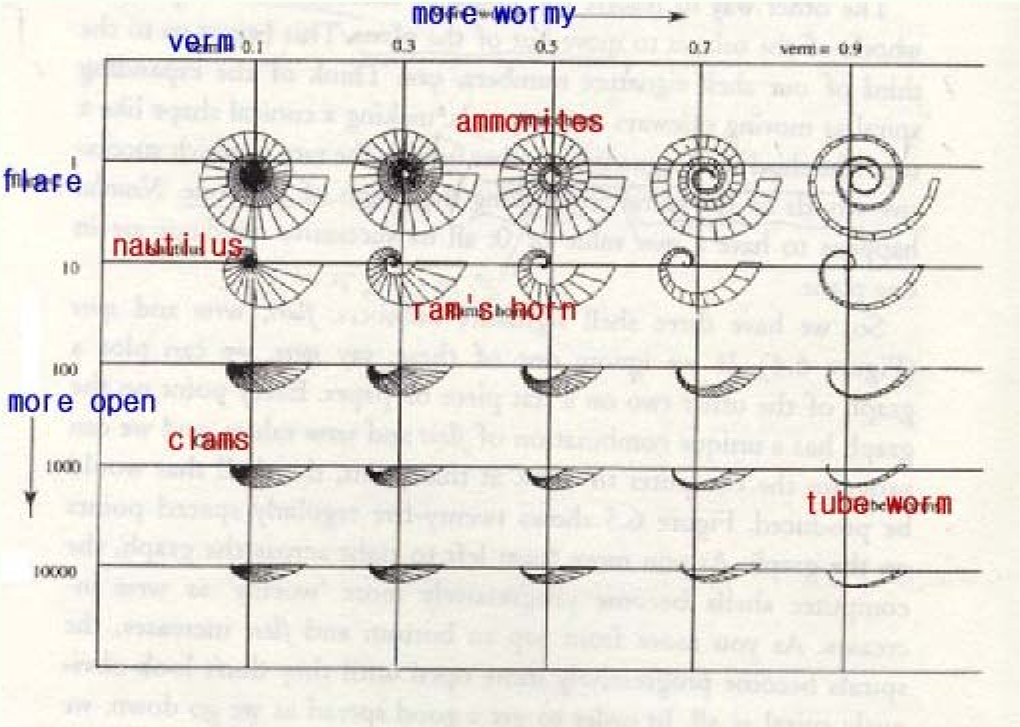

image © xxxx from Equiangular Spiral Mollusca

Dr Raup showed that coiled molluscs occupied only a small part of available geometric morphospace. Of all the possible shell shapes he was able to generate only relatively few have been found biologically useful, and these shapes were thus been adopted repeatedly within certain groups. Other types have not been able to be put to useful functional purposes and so are rarely, if ever, found in any living or fossil group. [Clarkson, 1979 p.142]. Choice of particular form can be the result of a complex process. The distribution of ammonoid shells does not appear to represent the optimization of any single functional factor, but rather is a geometric region which minimizes several problems. [Saunders et al 2002].

Links

Links

Computer generated snail shells - This applet lets you create images of shells using Raup's mathematical model of shell form.

Raup Model - more images according to Raup 1962

Computational Paleontology - includes modeling ammonoid ribs, ammonite sutures, Graptolite growth, Logarithmic spirals (e.g. mollusk shells), Ammonoid septa, and Coral septa

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page by M. Alan Kazlev
checked ATW050713
page uploaded 28 December 2002

Molluscan Cladograms

Abbreviated Dendrogram

```
SPIRALIA
|--BRACHIOPODA
`--+--ANNELIDA
   |
   `--MOLLUSCA
      |--Aculifera
      |  |==Mattheviidae
      |  |   `--Aplacophora
      |  `-- Polyplacophora
      `--Conchifera
         |==Tryblidiida (Monoplacophora)
         |  `--Cephalopoda
         `==Helcionelloida
             |==Rostroconchia
             |  `-- Scaphopoda
             |--Bivalvia
             `--Gastropoda
```

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References

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Working Phylogeny
Tentative Molluscan Phylogeny

Working Phylogeny

Our working phylogeny of the mollusks differe somewhat from Alan's Phylogeny below, probably because Alan actually thought about it, while we were more concerned with matters of format. Directory structure on the web enforces a species of heirarchical, somewhat Linnaean, organization which is sometimes antithetical to good phylogenetics. It doesn't have to be this way, but we are all heirs to the legacy of DOS -- and Aristotle, for that matter. In any event, our *working* phylogeny (much abbreviated and coded to match our current directory structure) looks like this: ATW

```
MOLLUSCA
|
ASAL MOLLUSCA
|--Aplacophora
`--Testaria
   |--Polyplacophora
   `--Conchifera (Helcionelloida)
      |--Monoplacophora
      `--+--Diasoma
         |  |--Rostroconchia
         |  `--BIVALVIA
         `--+--CYRTOSOMA
            |  |--Scaphopoda
            |  `--Cephalopoda
            |     |--Nautiloidea
            |     `--Neocephalopoda
            |        |--Ammonoidea
            |        `--Coleoidea
```

```
            `--GASTROPODA (stem group)
               |--Paragastropoda
               `--Tergomya (grossly paraphyletic)
                  |
                  Gastropoda (crown group)
                  |--Eogastropoda
                  |  |--Euomphalida
                  |  `--Patellogastropoda
                  `--Orthogastropoda
                     |--Vetigastropoda
                     `--APOGASTROPODA
                        |--Caenogastropoda
                        `--HETEROBRANCHIA
                           |--Opisthobranchia
                           `--PULMONATA
```

Tentative Molluscan Phylogeny

The following cladogram is based on a number of sources, as well as arguments presented in these pages regarding some of the more radical placements. The position of the Bivalvia remains controversial. On the basis of molecular and some cladistic evidence, it belongs near the bottom of the conchiferan crown group, possibly prior to the Helcionellid-derived Gastropoda + Cephalopoda + Scaphopoda clade). But on the basis of cladistic evidence from transitional Cambrian forms, Bivalvia is much closer to the Rostrochochia. The Scaphopoda are here derived from the Rostrochonchia, with the Cephalopoda very tentatively derived from related Yochelcionellid Helcionellids. MAK021228

```
<==o MOLLUSCA
   `--+--o SOLENOGASTRES
      `--+--+-- †Acaenoplax hayae
         |  `--o CAUDOFOVEATA
         |     |-- Limifossoridae
         |     |-- Prochaetodermatidae
         |     `-- Chaetodermatidae
         `--o TESTARIA
            `--+--o POLYPLACOPHORA
               |  `--+--†Mattheviidae
               |     |--†Septemchitonida
               |     `--+--†Chelonida
               |        `--+--Lepidopleurida
               |            |--†Scanochitonida
               |            `--Chitonida
               `--o CONCHIFERA
                  |--o Tryblidiida ("Tergomya" in part)
                  |  `--o Tryblidoidea
                  |     `-- Neopilinidae
                  | ?-- STENOTHECOIDA
                  `--+--?? BIVALVIA (on basis of molecular phylogeny)
                     `--o Unnamed Clade (Higher Conchifera)
                        `--o †Helcionellidae (Helcionelloida)
                           |--+--+-- †Yochelcionellidae [Helcionelloida = "Quasirostroconchs"]
                           |  |  `?-- CEPHALOPODA
                           |  | ? -- †CRICOCONARIDA
                           |  `--+--†Stenothecidae [Helcionelloida; = "Pararostroconchs"]
                           |     |--+--+-- †Heraultipegma varensalense
                           |     |  |  `-- †Watsonella crosbyi
                           |     |  `--? BIVALVIA (on basis of transitional forms)
                           |     `--+--+-- †Taurangia paparua
                           |        |  `-- †Pseudomyona queenslandica
                           |        `--+-- †ROSTROCONCHIA
                           |           `-- SCAPHOPODA
                           | ?-- †Palaeacmaeidae
                           |--+-- †Helcionella subrugosa
                           |  `--+--†Helcionella subrugosa comleyensis
                           |     `--o †Scenellidae (Helcionelloida)
                           |        `--+-- †Scenella reticulata
                           |           `-- †Kiringella pyramidalis "Tergomya"
                           `--+--†Coreospiridae (Helcionelloida)
                              |--+-- †Euomphalopsis involuta
                              |  `-- †Macluritella? walcotti
                              |--o †PARAGASTROPODA
                              |  |--o †Pelagielloidea
                              |  `--o †Onychochilioidea
                              |?-- †Hypseloconoidea "Tergomya"
                              `--+-- †Cyrtolites "Tergomya"
                                 `-+-- †Chippeaella patellitheca
                                   `-- GASTROPODA
```

Revised Phylogeny

The following revised phylogeny is just as provisional and uncertain as the above two, but takes into account new findings from molecular phylogeny. For reasons stated elsewhere, we have retained a paraphyletic aculifera MAK120607

```
MOLLUSCA
|== †Acaenoplax etc
|   |==†Turrilepadida,
|   |   |--Caudofoveata
|   |   `--Solenogastres
|   `--+---Phthipodochiton
|      `---Polyplacophora
`--CONCHIFERA
   |--+--Tryblidiida (Monoplacophora)
   |   `--+==†Hypseloconidae
   |      `--Cephalopoda
   `--†Helcionellidae [Helcionelloida]
       |--+-- †Yochelcionellidae [Helcionelloida]
       |  ` --+--†Stenothecidae [Helcionelloida]
       |      `--+-- †Rostroconchia
       |          `-- Scaphopoda
       |--+-- †Watsonella
       |  `--Bivalvia
       |    |--Protobranchia
       |    `--Heterodonta
       `--+--†Coreospiridae [Helcionelloida]
           `--+-- †Paragastropoda
              `--+-- †"Tergymya"
                  `-- Gastropoda
```

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Content by ATW, MAK , checked ATW050713, page uploaded 28 December 2002, last revised MAK120607

Molluscan Phylogeny

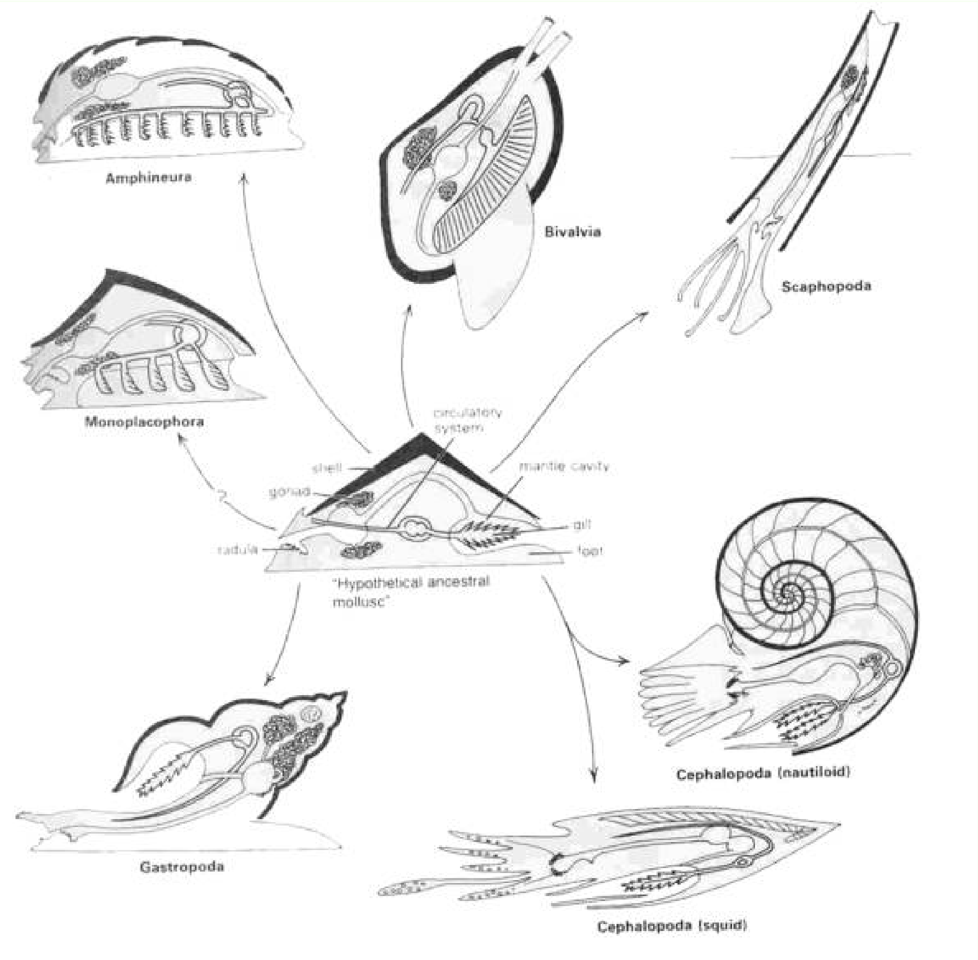
Abbreviated Dendrogram

```
SPIRALIA
|--BRACHIOPODA
`--+--ANNELIDA
   |
   `--MOLLUSCA
      |--Aculifera
      |  |==Mattheviidae
      |  |--Aplacophora
      |  `-- Polyplacophora
      `--Conchifera
         |==Tryblidiida (Monoplacophora)
         |  `--Cephalopoda
         `==Helcionelloida
              |==Rostroconchia
              |  `-- Scaphopoda
              |--Bivalvia
              |  |--Protobranchia
              |  `--Heterodonta
              `--Gastropoda
                 |=="Archaeogastropoda"
                 `--+--Caenogastropoda
                    `--+--Opisthobranchia
                       `--Pulmonata
```

The Ur-Mollusc Paradigm
Cyrtosoma and Diasoma
Yochelson's Archi-mollusk
Stasek's Aculifera - Polyplacophora - Conchifera model
Salvini-Plawen and the Neontological Perspective
The Tergomya and the Helcionelloida
Diasoma-Cyrtosoma vs Helcionellid
Waller's Cladistic Research
Molecular Analysis
The Aplacophora
Bivalves, Rostroconcha, and Scaphopods
Comparisons
Rival hypotheses
Recent deveolpments

The Ur-Mollusc Paradigm

The following diagram presents a stylized relationship between the different Molluscan groups, with all evolving from a "hypothetical ancestral mollusk", which people consider to show shared ancestral characters for the group Mollusca



Radiation of the mollusks from the “hypothetical ancestral mollusk

Figure from D. R. Prothero, 1998, *Bringing Fossils to Life*, McGraw-Hill, p. 277; from Clarkson, 1993 - this image © xxxx from LAB 3 Chapter 8: Phylum Molusca (former site) and Biological Diversity and Evolution through Time (former site)

Useful as this diagram may be for illustrating the diversity among extant classes of mollusks, it really does nothing to explain the relationships of the various clades that make up the phylum. For this understanding, we must turn to the various hypotheses that have been proposed by paleontologists and neontologists over the last several decades. We can begin with an idea that has laid the foundations for much of our understanding of molluscan phylogeny, but has itself been later challenged - the Cyrtosoma-Diasoma hypothesis.

Cyrtosoma and Diasoma

The view of molluscan evolution, which for some time assumed that the various classes developed from a hypothetical ancestral shelled ancestor, was revolutionized by an elegant model proposed by Bruce Runnegar and John Pojeta in 1974, and developed in a series of subsequent papers. This can be best represented by the following diagram:

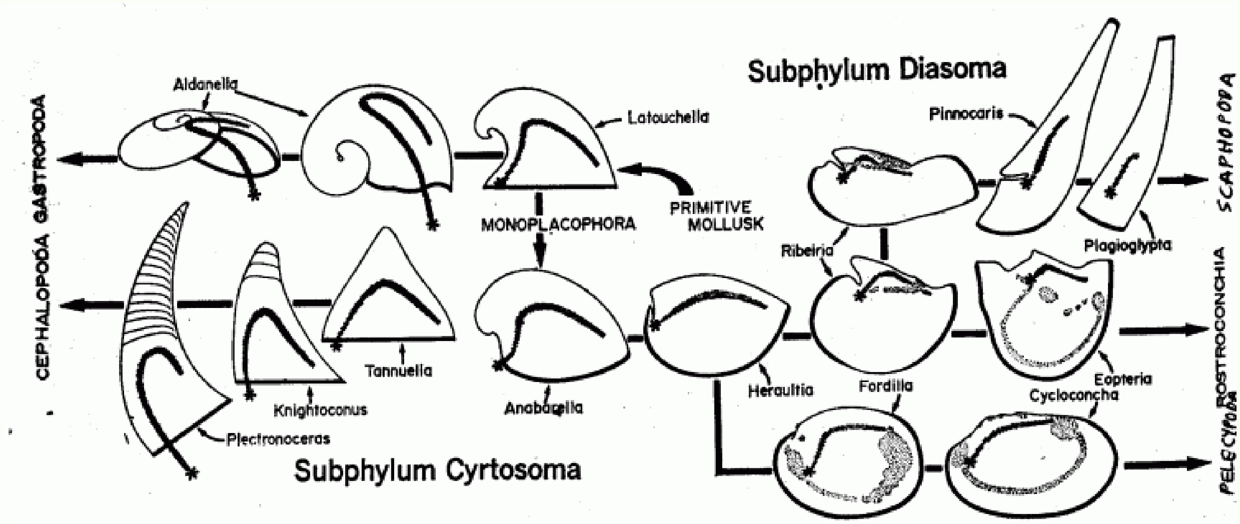


image from 1974 p. 314

As indicated here, the Conchiferan (shell-bearing) mollusks are divided into two main sub-phyla, linked by a number of early transitional forms.

The *Cyrtosoma* (hunchback-body) includes the Monoplacophora, Gastropoda and Cephalopoda. The Monoplacophora gave rise to the Gastropoda, Cephalopoda, and the Rostroconchia (which latter is included in the second group). The Monoplacophora, Gastropoda, and Cephalopoda all are characterized primitively by 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"-shape or (with gastropods) twisted on account of torsion. Most are surface-dwelling (epi-faunal) grazers or carnivores.

In the *Diasoma* (through-body) the gut is essentially straight. This group includes the classes Rostroconchia, Bivalvia and Scaphopoda, with the two latter derived from the Rostroconchia. These three classes 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.

But although the Cyrtosomes - including as they do the Monoplacophora - are the ancestors of the Diasomes (and hence not strictly a monophyletic clade), both subphyla began to diversify within a few million years in the Early Cambrian.

Runnegar and Pojeta also suggest that the Polyplacophora can be derived from the Monoplacophora instead of (as usually suggested) a more primitive ancestral stock.

While not universally accepted, the Cyrtosoma-Diasoma paradigm presented an integrated paleontological perspective that complemented neontological discussions.

Yochelson's Archi-mollusk

Yochelson (1978) rejects the Cyrtosoma-Diasoma model on the grounds that the differences between the shelled taxa remain too great, and that it would be foolish to speculate too much on the soft anatomy of animals known only from hard shells and a few rare muscle scars. Instead of a small number of classes linked by intermediate Cambrian shelled forms, he suggests a large number of different taxa that developed from a non-shelled ancestor or Archi-mollusk. This is represented in the following diagram

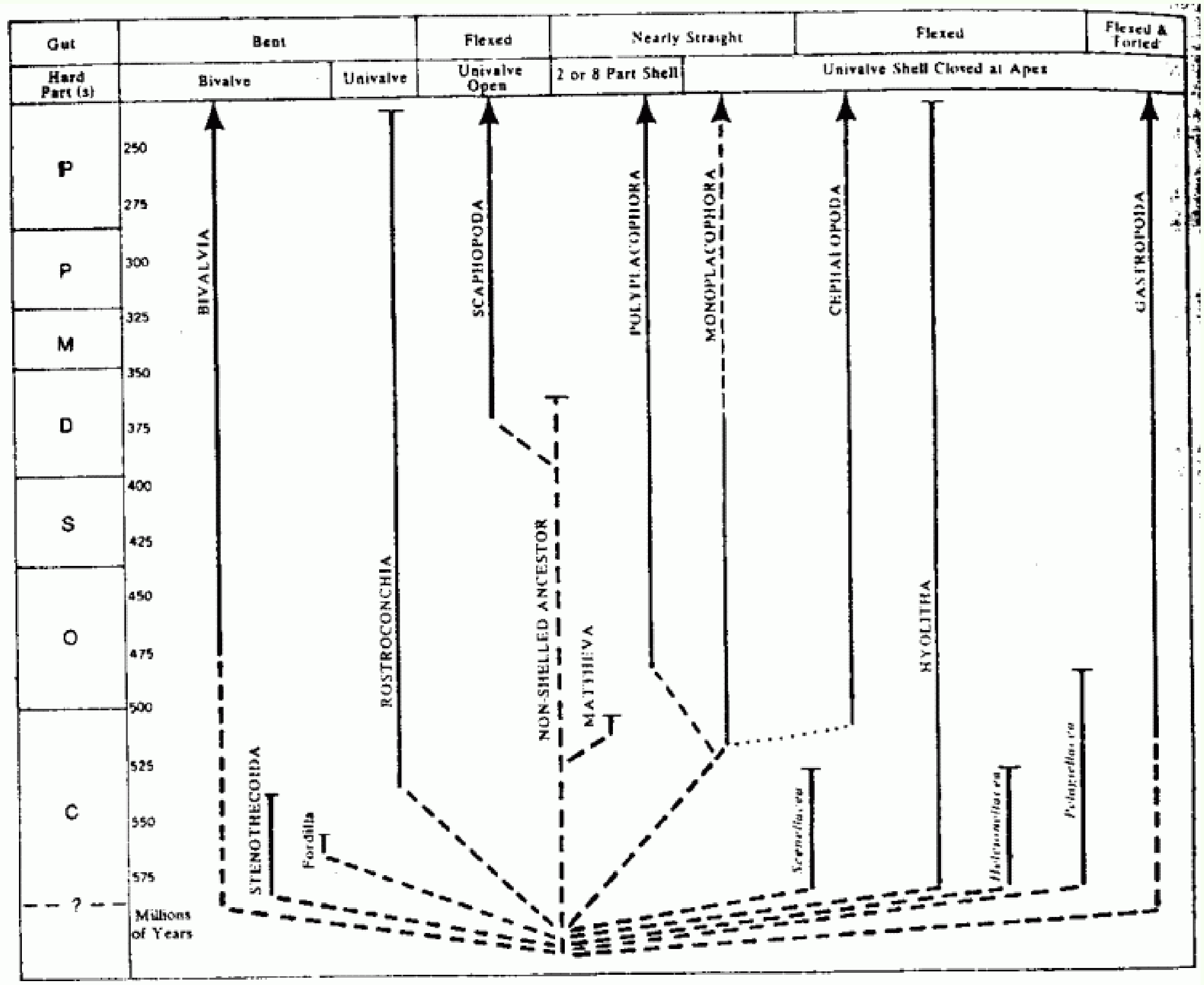


image © from Yochelson 1978 p. 166

Here we are back to the original position at the top of the page, except that the ancestral form lacks a shell, and there are many early short-lived taxa that cannot be pigeonholed into the main classes.

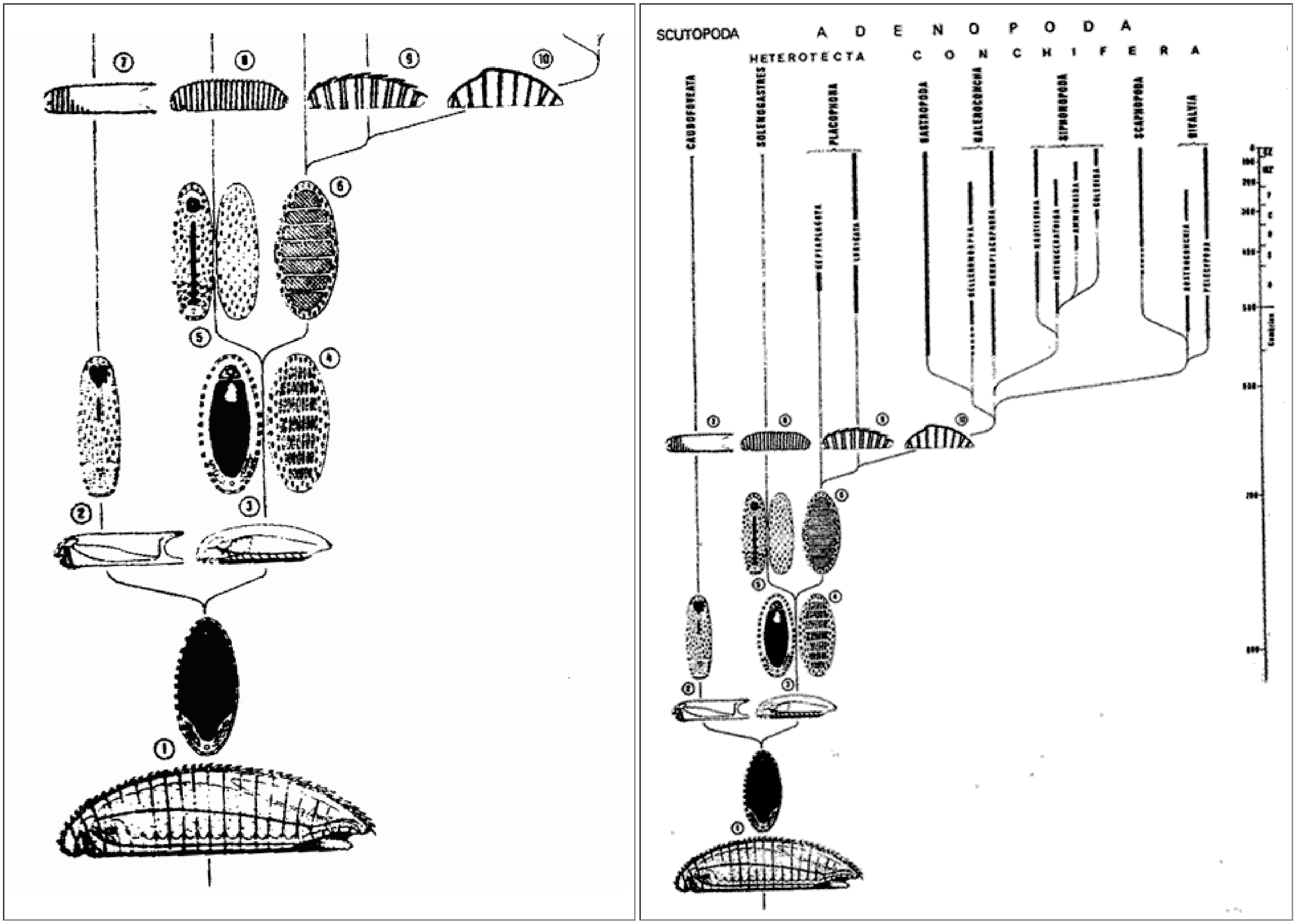
This is reminiscent of the controversy between Gould and Conway-Morris' position regarding the Cambrian explosion and the number of extinct high level taxa. One sees a disorderly bush with a large number of separate early experiments, the other an orderly tree in which the branches can be carefully mapped out.

Stasek's Aculifera - Polyplacophora - Conchifera model

In 1972 C.R. Stasek theorized that the extant mollusks are the progeny of three separate lineages that separated before the phylum was well established. He stated no known fossil or living genera can bridge the gaps between any two of the three lineages, and treated each as a separate subphylum. These are (i) the *Aculifera* Hatscheck 1891, containing only the class Aplacophora, derived from the most primitive ancestor; (ii) the subphylum *Placophora* von Jhering 1876, containing only the class Polyplacophora, and emphasizing the pseudometamerism of its more advanced premolluscan ancestor; and (iii) the subphylum Conchifera Gegenbaur 1878, containing the remaining shelled mollusks - the Monoplacophora and the other classes derived from it.

Salvini-Plawen and the Neontological Perspective

Salvini-Plawen (1980) provided a reconsideration of the phylogenetic relationships among the various molluscan groups by studying various extant forms, including the little known soft-bodies vermiform types that had previously been called "Aplacophora" and lumped with the chitons under the now rejected class "Amphineura". On the basis of this analysis he proposed a phylogenetic line by which an original archi-mollusc gives rise to the main Conchiferan groups as well as a number of side-branches. All in all there are four stages of progressive differentiation. The first has an early side branch called the Scutopoda dividing from the main line, and eventually becoming the Caudofoveata (a class of Aplacophora). The other line is represented by the Adenopeda, which include the ancestors of all other mollusks. From the Adenapoda the shell-less Solenogastres (the second class of Aplacophora) separate from the shell-bearing Testaria. Within the Testaria thePolyplacophora, or "Placophora", divide from the Conchifera. Finally, the Conchiferan ancestor gives rise to the various extant classes, along with the extinct Galeroconcha (Monoplacophora plus Bellerophontida, the latter here considered to be untorted). The Aplacophora are rejected, as the Placophora and Solenogastres are tied together by a number of shared unique characteristics (synapomorphies), in contrast to the merely symplesiomorphic (shared primitive) characters in Solenogastres and Caudofoveata. This can be represented by the following diagram:



"Diagram of the phylogenetic radiation of me Mollusks (black bars indicate fossil records, time-scale in millions of years, logarithmic). (1) Hypothetical archi-mollusc (main organization. and ventral view) with overall ventral gliding surface (black), postero-lateral mantle cavity, scale-bearing mantle, straight midgut pouched laterally, serial dorsoventral muscle bundles, gonopericardial system. and main nervous system with terminal sense organ(s). (2) Evolutionary branch of burrowing Scutopoda (lateral and ventral) with cerebrally-innervated section of locomotor surface (= pedal shield, black) and reduction of its ventrally- innervated section. (3) Evolutionary branch of gliding-creeping Adenopoda (lateral and ventral) with ventrally-innervated section of locomotor surface (= foot, black) including the pedal gland, with rudiment of head, and with peripedal-preoral mantle cavity. (4) Level of primitive Heterotecta (dorsal view), dorsal mantle with seven transverse rows of juxtaposed scaly bodies. (5) Level of Solenogastres (ventral and dorsal) with narrowed body and toot, mantle cavity reduced to preoral sensory pit (atrial sense organ) and to internal tubes (spawning ducts); adult mantle cover altered again to homogeneous arrangement of scales (6) Level of early Placophora (= Heptaplacota; dorsal view) with consolidation of juxtaposed scaly bodies to seven shell plates. (7) Regressive dorsoventral musculature in Caudofoveata. (8) Serial arrangement of dorso- ventral musculature in Solenogastres; compare (1). (9) Serial arrangement of dorso- ventral musculature in recent Placophora, concentrated according to the eight shell plates (8 x 2 = 16). (10) Primitive Conchifera with further concentration of the placophoran dorso-ventral musculature (9) according to the homogeneous conchs (see *Neopilina*)" - images and text © Institute of Malacology and Field Museum of Natural History, from Salvini-Plawen 1980 figure p. 258, caption page 259

The above represents what might be called the *Adenopoda hypothesis.* This is complimentary to the Cyrtosoma-Diasoma hypothesi, the former pertaining to the most primitive molluscs, the latter to more advanced types.

The alternative to the Adenopoda hypothesis is the Aculifera hypothesis. This is simpler than Stasek's original hypothesis as it has only two subphyla, the Aculifera (spiny mollusks) and the Conchifera (shell bearing mollusks).

The subphylum *Aculifera* comprises the most primitive group - all those mollusks that do not produce a complete shell. Instead they have a hard exterior skin called a cuticula. This cuticula additionally is protected by calcareous spines (spiculi). Two classes belong to the Aculifera:

- Aplacophora
    - Chaetodermomorpha (= Caudofoveata)
    - Neomeniomorpha (= Solenogastres)
- Polyplacophora (Chitons).

The *Conchifera* includes those mollusks that have a complete shell (although this may be lost in some more derived forms). Included here are the gastropods, bivalves, cephalopods, and other lesser groups, as follows:

- Monoplacophora (Trybliida)
- Visceroconcha
    - Gastropoda
    - Cephalopoda
- Loboconcha
    - Scaphopoda
    - Bivalvia

The Visceroconcha containing the classes Gastropoda and Cephalopoda, and the Loboconcha containing the classes Scaphopoda and Bivalvia, are clearly the neontological equivalents to Runnegar and Pojeta's Cyrtosoma and Diasoma [Mizzaro-Wimmer and Salvini-Plawen 2001]

The Tergomya and the Helcionelloida

John S. Peel reinterpreted the Cyrtosoma and Diasoma by rejecting the old "wastebasket" taxon Monoplacophora, and replacing it with two distinct and only distantly related early classes. These are the exogastrically-curved Class Tergomya (the superfamily Tryblidiacea), based upon a subclass of the same name described by Horny (1965a, b) and including the order Tryblidiida with the recent *Neopilina*; and a group of endogastrically coiled univalved mollusks, the Class Helcionelloida (the former superfamily Helcionellacea), including a range of primitive extinct firms, including some with cap shaped shells, others with high shells, even forms with "snorkels". The Helcionelloida is considered to be the direct ancestor of the Class Rostroconchia and members of this latter class are also interpreted here as endogastric mollusks. The model of diasome evolution proposed by Runnegar & Pojeta is replaced by one in which two parallel lineages are recognized within the former Diasoma: Tergomya - Bivalvia, and the Helcionelloida - Rostroconchia.

The scaphopods are tentatively derived from the Rostroconcha (although they may come from either lineage), and the Cephalopoda from the helcionelloids rather than from high-shelled conical Tergomya such as *Knightoconus* [Yochelson *et al* 1973). This, together with the derivation of the Gastropoda from the Tergomya or tergomyan-like forms, suggests that the Cyrtosoma is also not monophyletic.

Diasoma-Cyrtosoma vs Helcionellid

During the 90s the two competing hypotheses of evolutionary relationships among conchiferan molluscs: the Diasoma-Cyrtosoma concept recognizing the clades (Tryblidiida, (Bivalvia, Scaphopoda), (Gastropoda, Cephalopoda)); and the Helcionellid concept with (Tryblidiida, (Bivalvia, (Gastropoda, Scaphopoda, Cephalopoda))). The rostroconches were either stem group diasomes or stem group scaphopods (Runnegar & Pojeta, 1974; Salvini-Plawen, 1980; Steiner, 1992; Engeser & Riedel, 1996; Runnegar, 1996); if the latter the Bivalvia stood alone as a monophyletic clade.

Both of these hypotheses have problems. The Diasoma results in convergent evolution of elongated dorso-ventral body axes in Scaphopoda and Cyrtosoma (Gastropoda, Cephalopoda), of multiple cephalic tentacles and ring-shaped muscle attachment in Scaphopoda and Cephalopoda. The Helcionellid concept has to account for convergent similarities in the development of the mantle-shell, the typical burrowing foot, and the nervous system in Bivalvia and Scaphopoda. [Steiner and Dreyer

2002]

Waller (1998) proposed a third alternative, that the Scaphopoda and Cephalopoda are sister groups within the subphylum Cyrtosoma. Waller's cladogram is shown below.

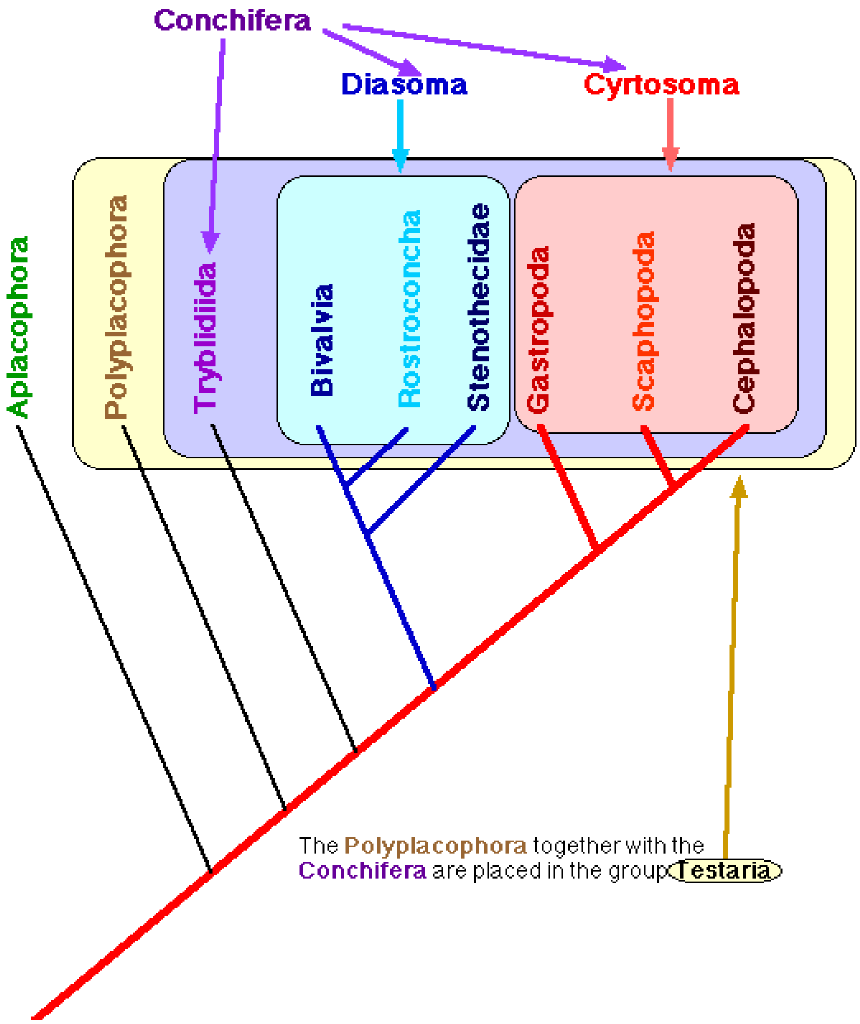
```
o MOLLUSCA
   `--+-- Aplacophora (= Solenogastres +
Caudofoveata)
      `--+-- TESTARIA
         `--+-- Polyplacophora
            `--+-- CONCHIFERA
               |-- Tryblidiida
                --+--o DIASOMA
                  |    `--+--†Stenothecidae
                  |        `--+--
†Rostroconchia
                  |            `-- Bivalvia
                   `--o CYRTOSOMA
                     `--+-- Gastropoda
                        `--+-- Scaphopoda
                           `-- Cephalopoda
```

This established the new view by which extant conchiferan classes are grouped as follows (Tryblidiida, (Bivalvia, (Gastropoda, (Scaphopoda, Cephalopoda)))). The following represents a diagramatic interpretation of the Cyrtosoma - Diasoma hypothesis.

Steiner and Dreyer [2002] used molecular analysis and a 18S rDNA data set containing 17 Bivalvia, 6 Gastropoda, 17 Scaphopoda, 4 Cephalopoda, and 3 Polyplacophora. All the resulting trees showed Cephalopoda and Scaphopoda as sister groups with the Gastropoda connecting to their common stem. So far this supports Waller. However Bivalvia here appear paraphyletic at the base of the conchiferan ingroup. This is perhaps more a problem with the unreliability of current molecular phylogeny, due to "long branch attraction", than an actual representation of the early history of the group.

Cladogram for Phylum Mollusca (Waller, 1998)

Note: this author put the Class **Monoplacophora** inlcuding the 'living fossil' *Neopilina* within the larger group **Tryblidiida**. The **Rostroconcha** are an extinct group, as are the **Stenothecida**, and together these are placed in the **Diasoma**. He places the **Scaphopoda** with the **Gastropoda** and **Cephalopoda** as sister groups in the Subpylum **Cyrtosoma**. The **Tryblidiida** together with the **Diasoma** and **Cyrtosoma** are called the **Conchifera** (shell-bearers)



The **Polyplacophora** together with the **Conchifera** are placed in the group **Testaria**

image and text by Ellen Thomas - from Biological Diversity and Evolution through Time [http: ethomas. web. wesleyan. edu/ scie639/ bivalve.htm]

The Aplacophora

In 2000, Gerhard Haszprunar argued that the two aplacophoran taxa, the Solenogastres and Caudofoveata do not form a single clade. Based on current knowledge and available data, he concluded that the arrangement (Solenogastres (Caudofoveata (Polyplacophora + Conchifera))) is the most parsimonious one, with the Aplacophora as a basic, paraphyletic assemblage. The monophyly of the Testaria (Polyplacophora + Conchifera) is well supported by several characters, and the Aculifera (Polyplacophora + Aplacophora) rejected. The Adenopoda (Solenogastres + Testaria) of Salvini-Plawen is shown to be polyphyletic in this interpretation.

Further insights have been provided by the discovery of the Silurian spiny worm-like soft-bodied plated mollusk *Acaenoplax hayae*, which combines characteristics of both the Caudofoveata and the Polyplacophora, and can be seen as a sister clade to the Caudofoveata, and a sort of missing link or transitional form between these two groups [Sutton et al 2001], although this interpretation has been challenged by Steiner and Salvini-Plawen 2001, who claim *Acaenoplax* is a polychaete worm; an interpretation that is unlikely if only because of the similar number of transverse plates and bristles in both *Acaenoplax*, chitons, and larval Solenogastres, implying a close relationship between all these groups.

Bivalves, Rostroconcha, and Scaphopods

Steiner and Dreyer 2002 suggest a scenario for the evolution of the higher conchiferan taxa. Acquiring an infaunal life style occurred independently in the early Rostrochonchia-Bivalvia lineage and, later, in Scaphopoda, rendering the relevant characters convergent. After the separation of the gastropod lineage, the stem-group of Scaphopoda and Cephalopoda comprised high-shelled, dorsoventrally elongated helcionellids with a deep mantle cavity, multiple cephalic feeding tentacles, and a circular area of muscle-shell connection. Shell-chambering for buoyancy then led to the first cephalopods, and anterior mantle elongation and transient forms with posterior shell slits or snorkels in response to an increasingly infaunal habit gave rise to the tube-shelled scaphopods.

Thus, all rostroconches and some helcionellacean univalves technically become stem group bivalves. This is because the total group is thought to have originated at the latest common ancestor of the Bivalvia and the Cyrtosoma; Cytosoma here being (Gastropoda (Cephalopoda, Scaphopoda)). [Runnegar 2002].

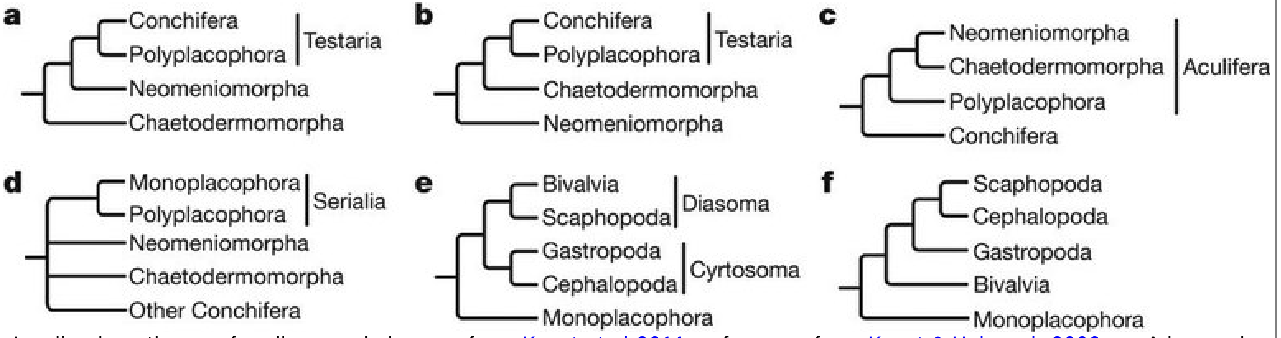
Comparisons

While molluscan phylogeny is mostly concerned with extant, well-known taxa, as these can provide the most data, this avoids the fact that during the early Paleozoic molluscs were far more diverse than they are now, and included a large number of types that don't fit into the crown group taxa, and which for this reason provide useful phylogenetic data. The comparison of the various hypotheses as regards the status of various little known fossil groups. as well as better known extant classes, can be shown as follows

Hypothesis	Runnerger & Pojeta	Yochelson	Peel	Waller	Wagner	Steiner and Dreyer
Conchifera evolution	Cyrtosoma-Diasoma	Archi-mollusk	Helcionellid-Tergyma	Cyrtosoma-Diasoma	--	--
Hyolitha	extinct related phylum	extinct class of Molluscs	--	--	--	--
extinct classes	Rostroconchia only	at least three and probably more	Rostroconchia and Helcionelloida	Rostroconchia only	--	--
Mathevia	polyplacophoran	extinct class	--	--	--	--
Monoplacophora	Highly diverse	Restricted to a few forms	Restricted to a few forms (Tergmya)	--	--	--
Stenothecoides	bivalved monoplacophoran	extinct class	extinct class	--	--	--
Helcionellida	Monoplacophora	probably extinct class	extinct class	stem grade	stem grade	stem grade
Rostroconcha	Diasoma	archi-mollusk derived	Helcionellid-derived	Diasoma - Stenothecidae derived	Stenothecidae derived	Helcionellid-derived
Bivalvia	Diasoma - Rostroconcha derived	archi-mollusk derived	Tergmya derived	Diasoma - Rostroconcha sister group	Rostroconcha sister group	Rostroconcha derived
Fordilla	Diasoma	extinct class	--	Early Bivalve	Early Bivalve	--
Gastropoda	Cyrtosoma	archi-mollusk derived	Tergmya derived	--	"Tergmya" derived	Cyrtosoma
First Gastropods	Early Cambrian	Furongian	Furongian	--	Furongian	--
Aldanella	early gastropod	not a mollusk	--	--	--	--
Pellagiellacea	Early Gastropod	possibly extinct class	--	--	Paragastropod	--
Scaphopoda	Diasoma - Rostroconch derived	archi-mollusk derived	Helcionellid Rostroconch derived	Cyrtosoma - sister group Cephalopods	--	Helcionellid derived - sister group to Cephalopods
first Scaphopoda	Mid-Ordovician	Devonian or Early Carboniferous	--	--	--	--
Cephalopoda	Cyrtosoma - Hypseloconid derived	archi-mollusk derived	Helcionellid derived	Cyrtosoma - sister group Scaphopoda	--	Helcionellid derived - sister group Scaphopoda

Rival hypotheses

By the start of the 21st century, morphology-based cladistics and molecular phylogeny had resulted in a number of conflicting hypotheses, some more popular than others. Some of these are summarised in the following diagram.



Leading hypotheses of molluscan phylogeny, from Kocot et al 2011, references from Kocot & Halanych 2009. **a**, Adenopoda hypothesis placing Chaetodermomorpha basal (Salvini-Plawen 1972, 1980, 1985, 1991, 2003). **b**, Hepagastralia hypothesis placing Neomeniomorpha basal (Salvini-Plawen and Steiner 1996). **c**, Aculifera hypothesis placing Aplacophora sister to Polyplacophora (Ivanov 1996, Scheltema 1993, 1996, Kocot et al 2011, Smith et al 2011), modified version with Polyplacophora ancestral to Aplacophora (Sigwart & Sutton 2007, Vinther et al 2011). **d**, Serialia hypothesis allying Polyplacophora and Monoplacophora (Giribet et al 2006). **e**, Diasoma and Cyrtosoma hypotheses allying bivalves to scaphopods and gastropods to cephalopods, respectively (Runnegar and Pojeta 1974, Salvini-Plawen 1980, Simone 2009). **f**, Unnamed hypothesis, allying scaphopods and cephalopods (Giribet and Wheeler 2002, Haszprunar 2000, Passamaneck et al. 2004, Steiner and Dreyer 2002, 2003, Waller 1998). (not figured) Conchifera, grouping together Monoplacophora, Gastropoda, Bivalvia, Cephalopoda, and Scaphopoda (Wingstrand 1985) and Testaria, with Polyplacophora (but not aplacophora) sister to Conchifera (Salvini-Plawen 1972, 1980, 1985, Salvini-Plawen and Steiner 1996, Haszprunar 2000.), unnamed clade grouping Scaphopoda, Gastropoda, Bivalvia (Smith et al 2011), unnamed clade with Monoplacophora and Cephalopoda as sister taxa (Smith et al 2011), and Pleistomollusca allying Gastropoda and Bivalvia (Kocot et al 2011)

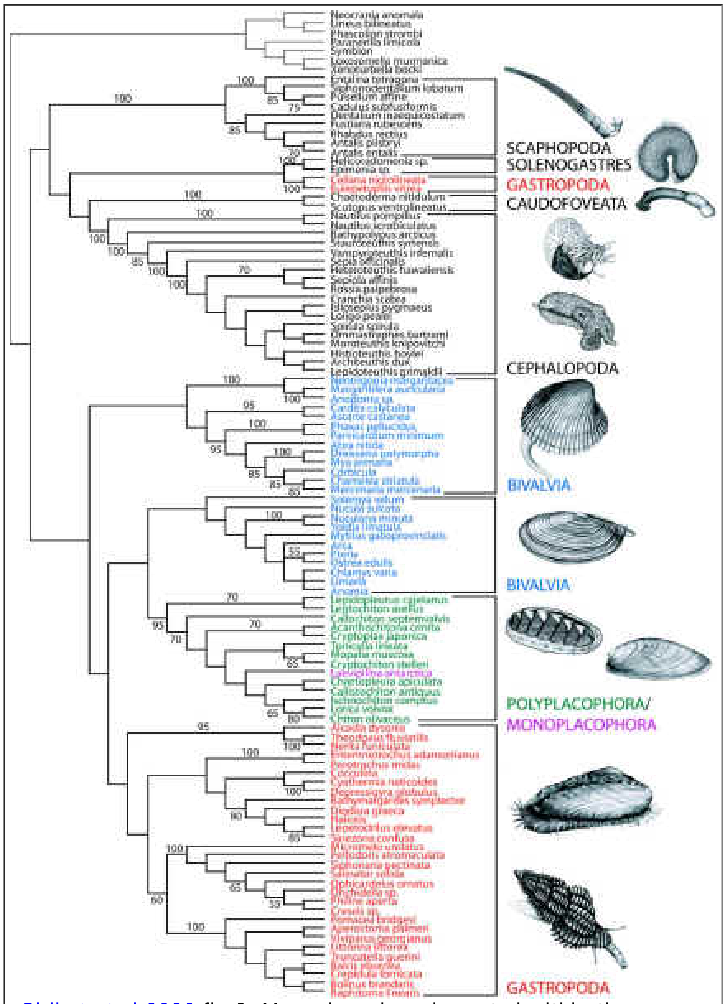
Recent developments

Over the past decade or so, developments in both molecular phylogeny and cladistic methodology have if anything only obscured rather than contributed further insights, with lack of clear consensus between morphology and molcules, and even different molecular phylogenies The following two paragraphs are taken from Wikipedia, tending a more comprehensive coverage on our part.

"It is uncertain whether the ancestral mollusc was metameric (composed of repeating units) (which would suggest an origin from an annelid-like worm (Jacobs et al 2000). According to Giribet et al 2006 that the repetition of gills and of the foot's retractor muscles were later developments, while Sigwart & Sutton 2007 concluded that the ancestral mollusc was metameric, and that it had a foot used for creeping and a "shell" that was mineralized. In one particular one branch of the family tree, the shell of conchiferans is thought to have evolved from the spicules (small spines) of aplacophorans; however this is difficult to reconcile with the embryological origins of spicules (Henryetal2004).

The molluscan shell appears to have originated from a mucus coating, which eventually stiffened into a cuticle. This would have been impermeable and thus forced the development of more sophisticated respiratory apparatus in the form of gills. Eventually, the cuticle would have become mineralized (Runnegar & Pojeta 1974, using the same genetic machinery (engrailed) as most other bilaterian skeletons (Jacobs et al 2000). The first mollusc shell almost certainly was reinforced with the mineral aragonite (Porter 2007).

Morphological analyses tend to recover a conchiferan clade that receives less support from molecular analyses (Winnepenninckx et al 1996), although these results also lead to unexpected paraphylies, for instance scattering the bivalves throughout all other mollusc groups (Passamaneck et al 2004).



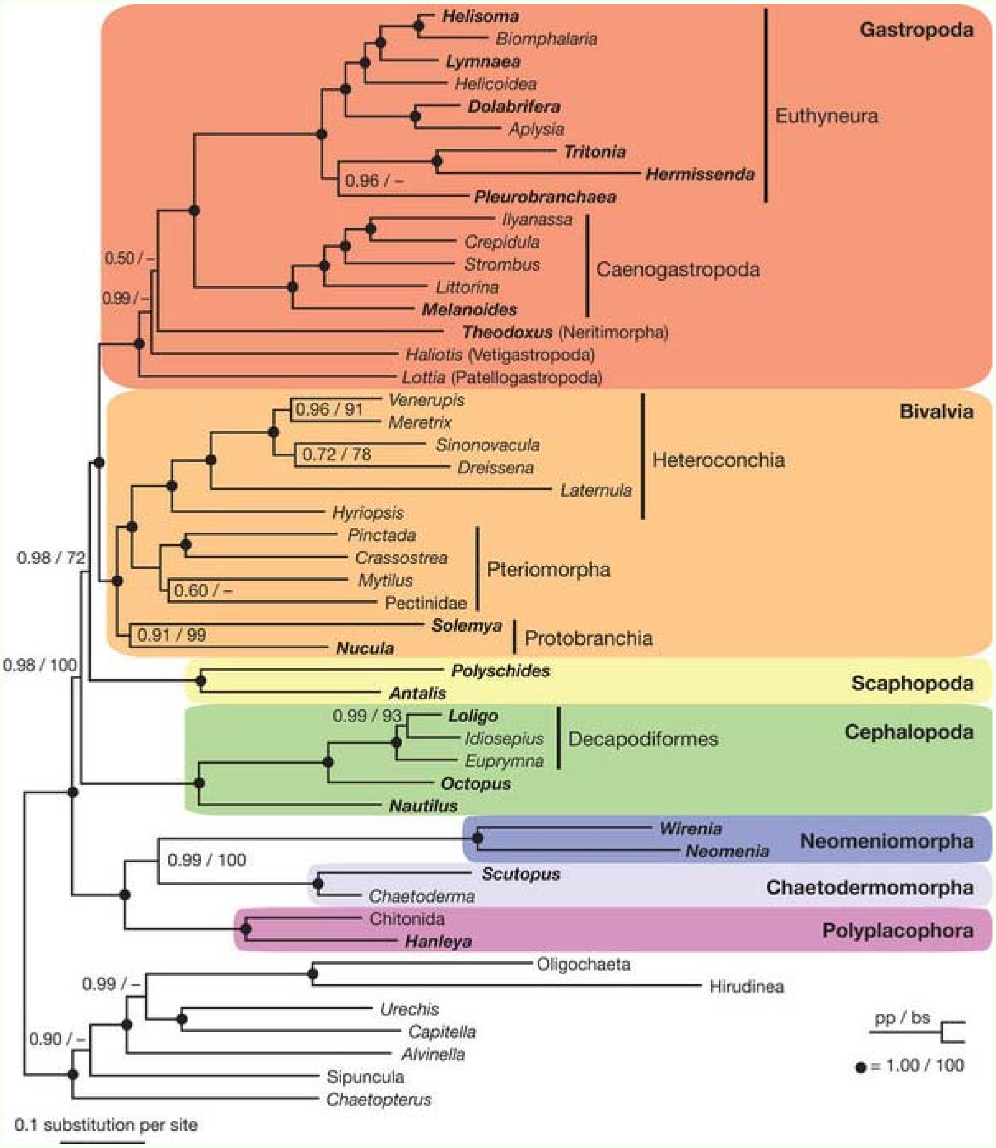
Giribet et al 2006 fig.2. Monoplacophora is nested within the Polyplacophora. Bivalvia emerges as a paraphyletic group. Scaphopoda, Solenogastres (Neomeniomorpha), Caudofoveata (Chaetodermomorpha), and the Cephalopoda make a monophyletic clade. (via Taxa of Life)

However, an analysis in 2009 that used both morphological and molecular phylogenetics comparisons concluded that the molluscs are not monophyletic; in particular, that Scaphopoda and Bivalvia are both separate, monophyletic lineages unrelated to the remaining molluscan classes—in other words that the traditional phylum Mollusca is polyphyletic, and that it can only be made monophyletic if scaphopods and bivalves are excluded (Goloboff et al 2009). A 2010 analysis managed to recover the traditional conchiferan and aculiferan groups, but similarly concluded that the molluscs are not monophyletic, this time suggesting that solenogastres are more closely related to the non-molluscan taxa used as an outgroup than to other molluscs (Wilson et al 2010). Current molecular data is insufficient to constrain the molluscan phylogeny, and since the methods used to determine the confidence in clades are prone to over-estimation, it is risky to place too much emphasis even on the areas that different studies agree (Wägele et al 2009. Rather than eliminating unlikely relationships, the latest studies add new permutations of internal molluscan relationships, even bringing the conchiferan hypothesis into question (Vinther et al 2011)." -- Wikipedia

Some of these problems can be explained as due to this being still early days of molecular phylogeny, others to the fact that original molluscan evolution was part of the Cambrian explosion which involved a very rapid radiation of new lineages, and that molecular sequencing does not have the resolution to unravel the particular order of branching and new clades (this is the same problem as with metazoa in general). It is possible however that better sampling and more broad ranging studies will improve resolution. In 2011, two deep phylogeny analyses produced a molecular consensus emerging totally at odds with both morphology and paleontology; for example bivalves and gastropods as sister taxa. Pending a more comprehensive review, the cladograms each produce are shown here:

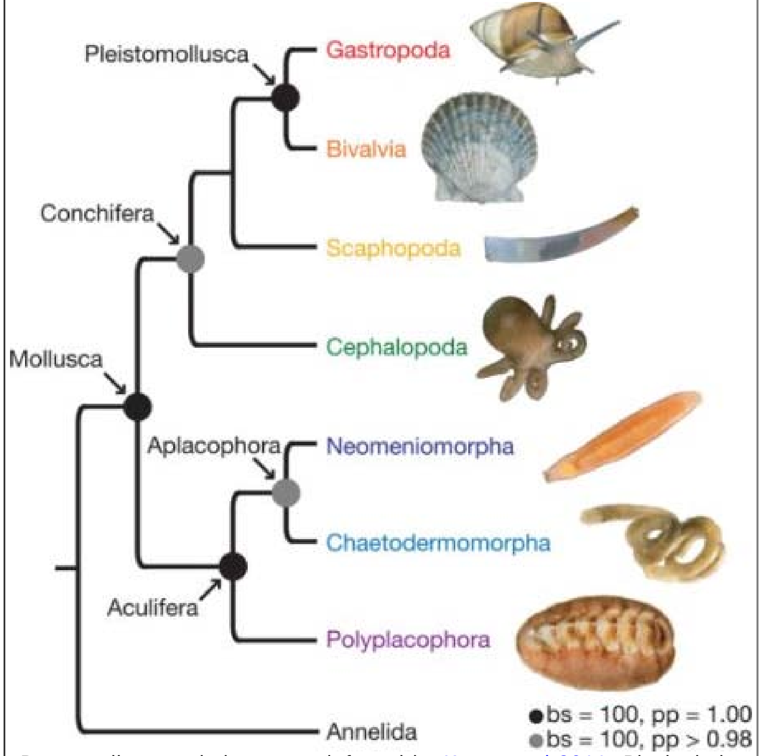
From Kocot et al 2011 (abstract below) and phylogram (*right*):

> "Evolutionary relationships among the eight major lineages of Mollusca have remained unresolved despite their diversity and importance. Previous investigations of molluscan phylogeny, based primarily on nuclear ribosomal gene sequences or morphological data, have been unsuccessful at elucidating these relationships. Recently, phylogenomic studies using dozens to hundreds of genes have greatly improved our understanding of deep animal relationships. However, limited genomic resources spanning molluscan diversity has prevented use of a phylogenomic approach. Here we use transcriptome and genome data from all major lineages (except Monoplacophora) and recover a well-supported topology for Mollusca. Our results strongly support the Aculifera hypothesis placing Polyplacophora (chitons) in a clade with a monophyletic Aplacophora (worm-like molluscs). Additionally, within Conchifera, a sister-taxon relationship between Gastropoda and Bivalvia is supported. This grouping has received little consideration and contains most (>95%) molluscan species. Thus we propose the node-based name *Pleistomollusca*. In light of these results, we examined the evolution of morphological characters and found support for advanced cephalization and shells as possibly having multiple origins within Mollusca."



The phylogram can be simplified to:

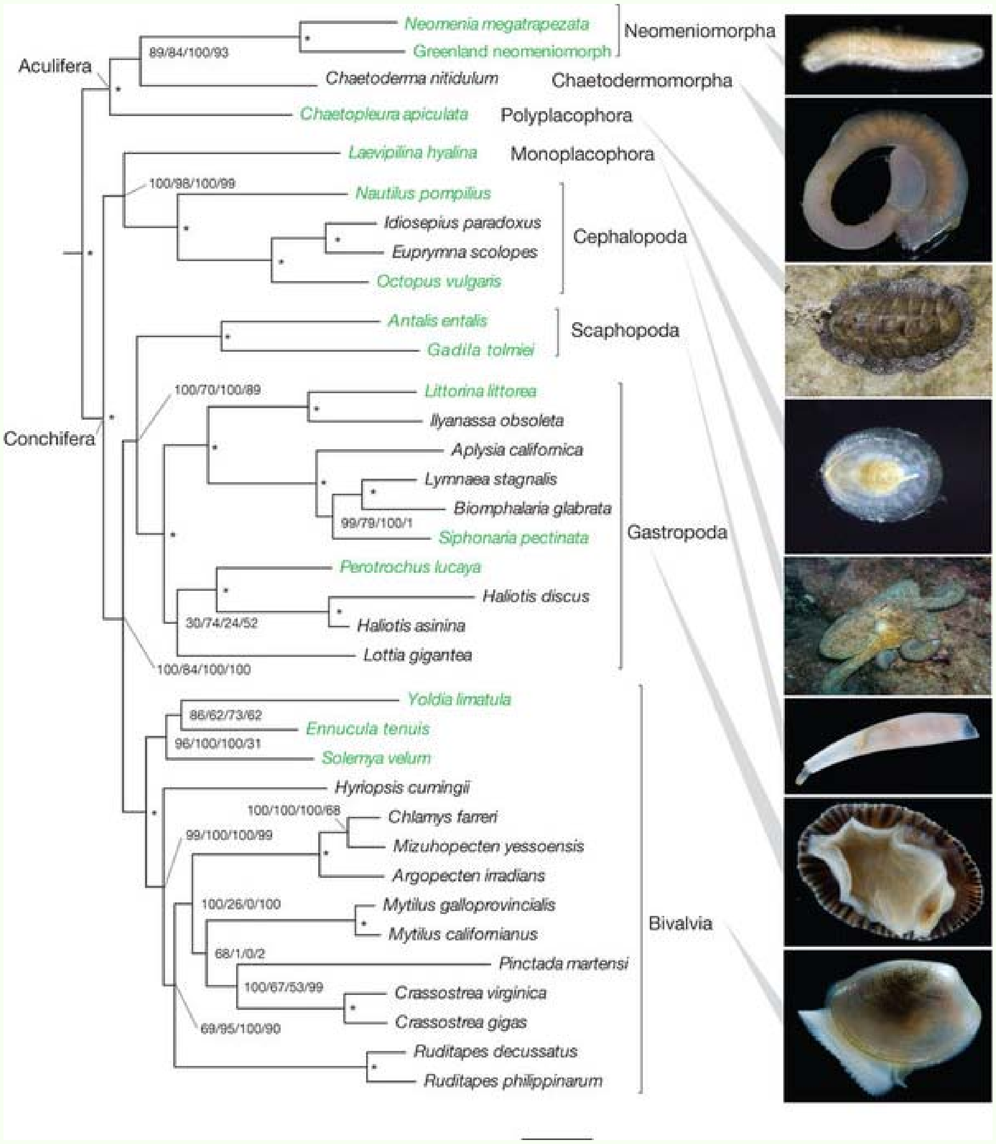
Both this phylogeny and the following support both the Aculifera (aplacocophara + polyplacophora) and the Conchifera. Both place the cephalopods in a basal position, and a similar result was recovered by Giribet et al 2006. The implication being that the advanced nervous system found in both cephalopods and gastropods evolved by convergence, as did similiar morphological features between cephalopods and scaphopods. Smith et al 2011 (below) make cephalopods and monoplacophorans sister taxa, which would support Cambrian fossils like *Knightoconus*, *Hypseloconus*, and/or *Tanuella* as intermediate forms, and a "monoplacophoran" origin is proposed also on a total evidence approach using fossil and morphological as well as molecular findings by Kröger et al 2011. Rather more surprising is that both affirm a clade consisting of bivalves, gastropods, and scaphopods, as either scaphopoda + (gastropoda + bivalvia) (Kocot et al 2011, also found by Vinther et al 2011), or bivalvia + (gastropoda + scaphopoda)



Deep molluscan phylogeny as inferred by Kocot et al 2011. Black circles represent nodes with bs = 100 and pp = 1.00. Gray circles represent nodes with bs = 100 and pp = 0.98.

(Smith et al 2011). It's hard to get a more opposite result to both morphology (which even in recent cladistic analysis (Simone 2009), paleontology, and ecological functionalism, all of which both favour the Diasoma-Cyrtosoma hypothesis. With such strong inconguuancy between morphoilogy and molocules the possibility of sequencing artifacts such as long chain attraction (as seems to be the case when turtles are resoved as (very unlikely) archosaurs) makes more sense to us than the number of reversals and convergences required to force morphology into a molecular tree. Of course this is the old problem of which methodology carries the more reliable phylogenetic signal. Here we need to look at fossils of transitional forms, morphology, ecology, and evo-devo development as well as molocules.. Regarding fossil groups, Rostroconchia might be a candidate for a transitional group between bivalves and scaphopods, although where gastropods fit is anybody's guess. MAK120504

From Smith et al 2011 (abstract below) and phylogram (*right*):



> "Molluscs (snails, octopuses, clams and their relatives) have a great disparity of body plans and, among the animals, only arthropods surpass them in species number. This diversity has made Mollusca one of the best-studied groups of animals, yet their evolutionary relationships remain poorly resolved. Open questions have important implications for the origin of Mollusca and for morphological evolution within the group. These questions include whether the shell-less, vermiform aplacophoran molluscs diverged before the origin of the shelled molluscs (Conchifera) or lost their shells secondarily. Monoplacophorans were not included in molecular studies until recently, when it was proposed that they constitute a clade named Serialia together with Polyplacophora (chitons), reflecting the serial repetition of body organs in both groups. Attempts to understand the early evolution of molluscs become even more complex when considering the large diversity of Cambrian fossils. These can have multiple dorsal shell plates and sclerites or can be shell-less but with a typical molluscan radula and serially repeated gills. To better resolve the relationships among molluscs, we generated transcriptome

> data for 15 species that, in combination with existing data, represent for the first time all major molluscan groups. We analysed multiple data sets containing up to 216,402 sites and 1,185 gene regions using multiple models and methods. Our results support the clade Aculifera, containing the three molluscan groups with spicules but without true shells, and they support the monophyly of Conchifera. Monoplacophora is not the sister group to other Conchifera but to Cephalopoda. Strong support is found for a clade that comprises Scaphopoda (tusk shells), Gastropoda and Bivalvia, with most analyses placing Scaphopoda and Gastropoda as sister groups. This well-resolved tree will constitute a framework for further studies of mollusc evolution, development and anatomy."

A consensus phylogeny, incorporating fossil forms, might be something like the following diagram by Telford & Budd (2011 (left)

There is actually some paleontological support for this new phylogeny as regards the Conchifera (right side of diagram), for example some high-shelled monoplacophorams ap[pear to be transitional or on the road to nautiloids (early shelled cephalopods) (Yochelson et al 1973, Webers & Yochelson 1989, Kröger et al 2011), whilst scaphopods, bivalves, and gastropods can all be derived from infaunal and epifaunal Helcionellids.

More problematic is the monophyletic Aculifera (left side of diagram). Despite both molecular and and paleontological-statistical cladistic data (Sigwart & Sutton 2007, Vinther et al 2011), there are no aculiferan synapomorphies, other than plesiomorphic halwaxiid (stem molluscan or basal spiralian) characteristics such as spicules and multiple dorsal shell plates. A monophyletic aculifera also leaves the ancestry of the Conchifera hanging in the air, as there are no other molluscan forms intermediate between the halwaxiids and crown group conchiferans. Along with some uncertainty regarding the status of the most primitive extant aculifera such as the worm-like solenogastres, and neontological morphology which strongly supports a paraphyletic aculifera, there is the possibility of molecular phylogeny showing a "false monophyly", as with the morphologically exceedingly unlikely cyclostomata clade of lampreys+ hagfish. A paraphyletic aculifera hypothesis is weakened by the fact that no transitional forms bewteen aculiferans and conchifera are known, although Giribet et al (2006)'s much disputed (on morphological grounds) Serialia could bridge the gap, if it is a paraphyletic grade rather than a monophyletic clade. It is quite possible also that the Aculiferan-Conchiferan split occurred very early, and that some soft-bodied forms like the annelid- and aplacophora-like *Acaenoplax* may represent a late (Silurian) survivor stem lineage ancetsral to both. Alternatively the pine-cone like Turrilepadids may be intermediate forms between the spiny and armoured halwaxiids and the molluscs in general. Initial cladistic analysis (Sigwart & Sutton 2007) show the turrilepadids to be stem-aplacophora, although this could change with further analyses and new material. For now we have tentatively assumed a paraphyletic aculifera leading to a monophyletic conchifera MAK120607

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Mollusca Glossary

Abbreviated Dendrogram

```
SPIRALIA
|--BRACHIOPODA
`--+--ANNELIDA
   |
   `--MOLLUSCA
      |--Aculifera
      |  |==Mattheviidae
      |  |   `--Aplacophora
      |  `-- Polyplacophora
      `--Conchifera
         |==Tryblidiida (Monoplacophora)
         |  `--Cephalopoda
         `==Helcionelloida
              |==Rostroconchia
              |  `-- Scaphopoda
              |--Bivalvia
              `--Gastropoda
```

Overview
Mollusca
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Adapical: Toward shell apex along axis or slightly oblique to it.

Adductor muscle(s): Anterior and posterior muscles that close a bivalve shell. In a bivalve, the muscle, either one or two, connecting valves and drawing them together.

anistrophic - a shell which is spirally coiled and is asymmetrical.

Annulated: Marked with rings.

Annulation or Annular ring: A growth increment in a tubular shell marked by regular constrictions (e.g., caecum).

Anterior an-te'ri-or (L ante=before) situated in front, in lower animals relatively nearer the head; At or towards the front or head end of a shell.

Anterior extremity or margin: Front or head end of animal or shell. In gastropod shells it is the front or head end of the animal, i.e. the opposite end of the apex of the shell; in bivalves the anterior margin is on the opposite side of the ligament, i.e. where the foot protrudes.

Aperture ap'er-ture (L apertures=an opening) The major opening of a univalve shell (gastropod, paragastropod, cephalopod, etc).

Apical: pertaining to the apex.

Apical whorls: Those whorls near the apex.

Apex, Apexes or Apices a'pex (L apex=the tip, summit) the tip of the spire of a gastropod and generally consists of the embryonic shell. First-formed tip of the shell. The beginning or summit of the shell. The beginning or summit or the gastropod spire. The top or earliest formed part of shell-tip of the protoconch in univalves-the umbos, beaks or prodissoconch in bivalves. In gastropods, the tip of the spire; in tusk shells, the small, open hind end.

Apical: At the apex, point or tip.

Aragonite: A mineral composed, like calcite, of calcium carbonate, but differing from calcite in certain characters of crystallization, density, and cleavage.

Articulated ar-tic'u-lated (L articulatus=jointed) the union forming a joint as the interlocking teeth of the hinge plate in bivalves

Articulamentum: Internal layer of a chiton shell. In chitons, the middle shell layer.

Asymmetrical as-ym-met'ri-cal (Gr a=priv.; syn=with; metron=measure) not even on both sides of an axis, bilaterally uneven, lack of symmetry

Attachment scar: Any impression left on a molluscan shell by the attachment of a soft part (e.g., mantle, muscle, or foot).

Axial: Pertaining to or more or less parallel to the axis of coiling.

Axial sculpture: Sculpture running parallel to the axis of coiling.

Axis: An imaginary line through the apex of a gastropod shell, about which the whorls are coiled.

Band: A strip of shell material differentiated by color or construction from the shell on either side of it.

Banding: Color marking in continuous stripes.

Bead: A small, more or less hemispherical protuberance resembling a bead. Beads are smaller than nodules.

Beaded: Sculptured so as to resemble beads, or strings of beads.

Bilateral symmetry, bilaterally symmetrical - having the right and left sides symmetrical

Bivalve bi-valve (L bi=two; valva=door) any mollusc having two valves or shells that are hinged together, as in mussels and clams. more

Body whorl: The most recently formed whorl of a spiral shell (generally gastropod but could refer to paragastropod or spiral tergmyan - in cephalopoda the term "living chamber" is more usually used), terminating in the aperture.

Branchiae(Gr Branchia=gills) gills; respiratory organs for breathing the oxygen dissolved in water.

Branchial (GR branchia=gills) The ventral or inhalant aperture. Used to take in food particles and oxygen and to release fertilized eggs.

Buccal buc'cal (L bucca=the cheek) pertaining to the mouth or cheek

Buccal mass a bulging; tongue-like object, made up of cartilage and muscle, which supports the radula

Buttress: A shell-strengthening structure--e.g., a supporting laminar costa in gastropods, or a support for part of the hinge in bivalves.

Calcareous cal-ca're-ous (L calyx=lime) consisting of, containing, or by the nature of limestone or calcium carbonate; a shelly substance.

Cephalic ceph-al'ic (Gr Kephale=head) of, pertaining to, on, in, or near the head

Calcified: With the conchiolin matrix partially or entirely reinforced by calcium carbonate intercalations.

Cephalopoda Ceph-a-lop'o-da (Gr Kaphale=head; pous=foot) One of the seven classes of molluscs. (Squids, octopus, Argonaut, Spirula.) **more**

Ceras cer'as (Gr Keras=horn) a horn or horn like appendage located on nudibranchs

Chambered cham'bered (Gr Kamara=anything with an arched cover) havingdivisions across the hollow of the shell, separating or dividing the same into chambers. (as in the Nautilus)

Chiton chi'ton (Gr Chiton=tunic) the coat-of-mail shells (Polyplacophora) . They possess a shell made up of eight shell plates. **more**

Cilium (plural Cilia) (L cilium=eyelid) A hair-like extension from the cell surface and capable of rhythmic movement. Used to designate the filaments on the mantle, in the gills, etc.

Coelom coe'lom (Gr Koilos=a hollow) body cavity, that space between the viscera and the body wall.

Columella col-u-mel'la (L columen=column) The thickened axial pillar around which the whorls of univalves are built.

Comarginal parallel with the margin

Compressed - high and narrow in cross-section, flattened laterally

Conchiolin con-chi'ol-in (L concha=shell) proteinaceous organic compound forming the periostracum of a shell, and also forms the organic matrix for calcareous parts of the shell.

Conchologist: One who collects shells; a student of conchology.

Conchology con-chol'o-gy (L concha=shell) The study of marine, fresh-water and land-shells; the arrangement and description of molluscs based upon a study of the hard parts only. Now generally replaced by Malacology..

Convolute: With last whorl completely concealing the earlier ones.

Cord(s): Coarse, rounded spiral or transverse linear sculpture on the shell surface; smaller than costae.

Cordate: Heart shaped.

Corneous: Consisting of horn, of a non-calcareous hornlike texture, as the opercula of some mollusks, such as the Neogastropod Busycon.

Corrugated: Folded or ridged; broadly and heavily sculptured.

Costa (pl. costae): Large, cordlike ridge that runs longitudinally, spirally, or concentrically on a shell rib. Line of ornament similar to, but of greater prominence than, a cord.

Costate: Rib-like sculpture, which is strongly ridged.

Cotype: One of several specimens collectively designated type; no longer used. See Holotype and Paratype.

Crassate: Coarse and solid.

Crenate, Crenulate or Crenulated: Finely notched, scalloped, wrinkled or delicately corrugated around the margin. Describing edge of the inner margins of some bivalve shells, or the outer lip margin of gastropod shells.

Crenules: Small notches or beads.

Crop (AS cropp=craw) a widened part of the esophagus where food may be temporarily stored before being passed on to the stomach

Ctenidium cten-id'I-um (Gr Kteis=comb) a gill-comb. Molluscan gill ; one of the respiratory organs found in molluscs. Plural is ctenidia

Cusp: Point of a tooth. A prominence, or point; temporary ridges of sand perpendicular to the shoreline.

Cuticle: An outer layer of cells; the precursor of the calcified shell. See Epidermis.

Decussate or Decussated: Sculpture crossings at acute angles. Having a latticed surface ornamentation formed by the intersection of fine ribs, not necessarily at right angles. See also Cancellate.

Deltoidal: More or less triangular.

Dentate: Sculptured, with teeth or short ridges. Having conspicuous projections along a margin in gastropod shells. See Denticles.

Denticles: Small teeth. Small projections around the margin of a gastropod aperture or the margin of a bivalve valve, especially near the hinge. (Not to be confused with true interlocking hinge teeth.)

Denticulate(d): Sculptured with small nodules or points. Having denticles. Toothed.

Dentition: Tooth structure: referring in bivalves to the hinge teeth, in gastropods usually to the elements of the radula.

Depressed: Low in proportion to diameter.

Detritus de-tri'tus (L detritus=a rubbing away) a mass of disintegrated material composed of bits of sea weed and other organic wastes found on the ocean floor

Deviate de'vi-ate (L de=from; via=away) To turn aside from the straight or regular coarse.

Dextral dex'tral (L dexter=to the right) Having the aperture on the right side of the shell when the apex is upwards and the aperture is facing you. The whorls spiral in a clock-wise manner.

Dioecious di-oe'cious (Gr Di=two; oikos=house) having the male and female present in different individuals. (an individual is either male or female but never both). Opposed to monoecious

Discoid or Discoidal: Disc-shaped; whorls coiled in one plane more or less compressed.

Distal dis'tal (L di=apart; sto=stand) relatively remote from the center of the body or point of attachment. Away from the center of origin, the farthest part from an object.

Dorsal dor'sal (L dorsum=the back) referring to the back edge or top of a bivalve, in the region of the hinge. The back of a gastropod remote from the aperture; The conical top surface of a limpet

Ectoderm - in triploblastic (three-layered) animals, this is the outer body layer. It forms the skin, nervous system, etc

Egg capsule: A protective structure enclosing an individual egg or a cluster of eggs.

Elevated: Raised up; high in proportion to diameter.

Elongate: Extended; considerably longer in one dimension than another.

Emarginate: With margin, or edge, of shell cut into by a notch or notches or gently indented.

Endogastric - coiled in a ventral or posterior direction. The opposite of Exogastric. Helcionelloids, early cephalopods (*Plectronoceras*, etc) and gastropods and all endogastrically coiled, although the latter developed from exogastric ancestors by means of torsion. **illustration**.

Epidermis: The outermost layer of the molluscan body, not associated with the shell; cuticle; integument or skin. (Often erroneously applied to the periostracum, the outer layer of the shell.)

Epifauna: Animals that normally live exposed, above the substratum surface; may be with or without attachment.

Esophagus e-soph'a-gus (Gr Oisophagos= the gullet) A membranous tube or canal through which masticated food or drink passes from the pharynx to the stomach

Exhalent siphon a short outlet formed of a fold of mantle through which water and other wastes are expelled.

Exogastric - coiled in a dorsal or anterior direction. The most primitive conchifran molluscs are exogastric.

Flange: An erect, projecting flattened ridge.

Foliaceous: Leaf-like, flattened, projecting like tiles.

Foot The muscular locomotor organ, undersurface of the body of a mollusc upon which the animal rests or moves. In bivalves, the contraction and expansion of this organ is used in the burrowing, locomotion, or for anchoring the animal. In the cephalopods, it is represented by the siphon and possibly the tentacles. The presence of a creeping or muscular foot is one of the characteristics that distinguish molluscs from other organisms.

Frilled: With a series of crowded, fine, wavy or pleated, sharp, often scaly ridges.

Gaping: Incapable of closing completely.

Gastropoda gas'trop'o-da (Gr Gaster-stomach; pous=foot) A class of molluscs. Scientific term for molluscs which have undergone torsion. The name refers to the fact that these creatures seem to creep upon their bellies. In fact in gastropods the stomach is situated well above the region of the foot. **more**

Gill (ME gile=a gill) or Ctenidium. A large sheet-like organ used for breathing the air dissolved in the water. In bivalves they also play the role of food collecting. The respiratory organ of molluscs.

Girdle gir'dle (AS gyrdel=a girdle) A flexible, leathery, muscular integument holding the valves of chitons in place. It is often ornamented with scales, spicules, or hairy processes.

Globose: Roughly spherical in outline.

Globular: Globe or sphere-shaped, like a ball.

Gonad gon'ad (Gr Gonos=seed) A generative tissue which eventually becomes a testis or ovary. **Gonoduct**, an oviduct or seminal duct.

Granular: Bearing granules as surface sculpture.

Granulate, Granulated or Granulose: Finely beaded or noduled. Having a rough surface of grainlike elevations.

Granule: A pustular surface structure.

Groove: An elongate and fairly uniform depression in the shell or soft parts of a mollusk.

Growth line(s): Impressed lines on the shell-surface due to growth-stages and rest periods.

Growth stages: Exaggerated growth lines indicating a cessation of growth.

Head: In general, the area of a molluscan body that bears the sense organs and the mouth (or proboscis). A usually distinct structure located at the animal's front end, containing the mouth, eyes, and sensory tentacles; absent in bivalves, poorly defined in chitons.

Haemolymph he'mo-lymph (Gr haima=blood) Molluscan blood

Helical: Spirally coiled.

Hermaphrodite her-maph'ro-dite (Gr Myth=Hermaphrodites, having a fabled son of Hermes and Aphrodite) Having the sexes united in the same individual The animal is both male and female.

Holotype hol'o-type (Gr Holos=whole = type) The original type. The single specimen upon which a species is based

Impressed: Indented. Pushed down, either as a line or an area.

Incised: Sculptured with one or more sharply cut grooves.

Incremental lines: Faint concentric growth lines.

Incrustation: An irregular deposit on the shell surface.

Incurved: Term used to indicate that a structure curves in upon itself, as do the umbones of certain bivalves, or the spines or lamellae of certain bivalves and gastropods.

Infauna, infaunal: Sessile and mobile animals that spend part or all of their lives buried beneath the substratum. Many bivalves are infaunal. Compare with semi-infaunal

Inflated: Applied to rotund shells of thin structure; swollen, increased unduly, distended.

Inflected or Inflexed: Turned inward, in the same direction.

Inhalant siphon a tube like fold of the mantle along which water, containing oxygen and food particles is drawn into the mantle cavity.

Intercostal: Placed or occurring between the ribs.

Intermediate ribs: Secondary sculpture, smaller than the primary ribs.

Involute: In gastropods (e.g., cypraea), coiling so that later whorls (or just the final whorl) envelop earlier whorls, such that the height of the aperture is the greatest vertical dimension.

Iridescent: Colors resulting from light refraction, not pigmentation.

Iteration, Iterative morphogenesis. In computer science, performing a repeated mathematical operation on a resulting value. In this context the term is used to denote processes that result in both metameric segments and repeated ectodermal skeletal structures.

Labial Palps la'bi-al palps (L. labium=lip palpare=to feel) Paired ciliated triangular flaps on either side of the mouth in bivalves.

Lamellar gills la-mel'lar gills (L. lamella=small plate) Enlarged, flattened plate-like gills (ctenidia) which form the feeding organs of most bivalves.

Lamellibranchia: Alternative name for Bivalvia; Bivalvia preferred.

Larva: The youngest stage of a mollusk after it hatches from the egg.

Larval shell: Shell of a molluscan larva before it undergoes metamorphosis, usually set off by a change of sculpture.

Lateral lat'er-al (L latus=the side0 pertaining to the side.

Lateral teeth; interlocking teeth of bivalves, not functioning as a hinge but serving to prevent valves from sliding upon each other when closed.

Length: In bivalves, the greatest horizontal dimension parallel to a line bisecting the adductor scars; in gastropods and scaphopods, the same dimension as height; in chitons, the greatest dimension parallel to axis of symmetry; in cephalopods, variously defined, but generally taken as the greatest dimension of the animal when the arms are stretched out parallel to their full extent.

Malacologist: One who studies the mollusc animal along with the shell.

Malacology mal-a-col'ogy (Gr malos=soft-bodied logia=to speak) The study of molluscs (clams and snail) based on soft anatomy. The branch of zoology that deals with molluscs, the animal within the shell.

Malacozoology: The study of living mollusks in relation to their animate and inanimate environment.

Mantle man’tle (L mantellum=a cloak, mantle) A soft, fleshy sheet of tissue that surrounds the mollusk's body and lines the inner surface of the shell. It secretes the materials that form the shell from the marginal glands and provides the periostracum. The presence of a mantle is one of the characteristics that distinguish molluscs from other organisms.

Mantle cavity: The space between the mantle and the visceral mass.

Mantle line: The line on the dorsal surface of a cowry shell and some bellerophontids where the mantle lobes meet.

Margin: Extreme edge of valve of bivalve shell; also the thickened periphery of base of some gastropods, notably cowries; sometimes used as equivalent to edge.

Median: Along the central line or axis.

Metamery, Metameric - having a series of repeated similar body segments - e.g. an annelid or arthropod. See also Pseudometamery

Muscle scar: Slight depression on the inner surface of the valve of a bivalve shell where a muscle is attached; in limpets, the scar left by the margin of the mantle and the foot retractor muscles. See also Accessory Scar; Adductor scar.

Nacre na’cre (Fr nacre=mothe-of-pearl) The pearly or iridescent substance which lines the interior of some molluscs shells.

Nacreous: With a layer of nacre, or mother-of-pearl.

Nodule: A rounded protuberance on the shell sculpture; larger than a bead.

Nodose, Nodulose or Nodular: Bearing rounded protuberances on the shell; sculptured with small tubercles, knobs, nodes or projections.

Nephridium ne-phrid’I-um (Gr nephros= a kidney) one of the tubular renal organs of the molluscs. **Nephridiopore**; the duct through which liquid wastes drain from the nephridium.

Operculum o-per’cu-lum (L operire=to close or shut) A horny or shelly (calcareous) plate attached dorsally to the foot serving to close the aperture, wholly or partially, when the animal withdraws into its shell. A chitinous or calcareous plate present in many molluscs.

Operculate; having an operculum

Opisthogyrate: In bivalves, having the beaks pointed backward, or posteriorly; opposite of prosogyrate.

Orbicular: Circular or rounded. Order: A group of related superfamilies.

Ornament: Surface sculpture standing out in relief on shell surface.

Osphradium os-phr’di-um (Gr Osphraddion=strong scent) An olfactory organ of some molluscs. A collection of elongated sensory cells over each gill.

Palps (plural palpi) (L palpare=to feel) Ciliated structures that surround the mouth. Food is sorted here and moved towards the mouth.

Pelagic pe-lag’ic (Gr Pelagos=the open sea) Pertaining to or living in the open sea far from land.

Pelecypoda pel-e-cyp’oda (Gr Pelekys=axe; pous=foot) Another term for Bivalves. Molluscs bearing a two valved shell that is hinged along one edge.

Periostracum per-I-os'tra-cum (Gr peri=around; ostracukon=shell) The outer skin or horny covering on the exterior of many shells. May be thin and transparent or thick, fibrous or hairy.

Plait: Spiral fold or ridge on the columella. Plica.

Planar - Of, relating to, or situated in a plane; flat, a planar surface.

Planispiral: Coiled in a single plane. Bellerophontiform and cephalopod shells are mostly planispiral

Planktotrophic: Refers to planktonic larval development where the larvae feeds on micro-organisms and development time in the plankton is long.

Plica: (plural plicae) Fold or ridge on the columella, a less conspicuous feature than columella fold but the two terms are more or less interchangeable.

Plicate: Folded or twisted or bearing plaits. Folded or plaited. Bearing plicae; also occasionally used here as equivalent to crenulate.

Plication(s): A raised ridge, fold, or plait, especially on the columella of a gastropod shell.

Plicate: Folded or twisted; having plicae.

Porcellaineous: Polished; surface and texture as in porcelain.

Posterior: The rear or tail end of an animal.

Propodium pro-po'di-um (Gr Pro=before; pous=foot) The foremost division of the foot of a gastropod used to push aside sediment as the animal crawls.

Protoconch pro'to-conch (Gr Proto=first; konche=shell) The embryonic shell of a univalve. It is present in the adult as the apical or nuclear whorls and often demarcated from the teleoconch whorls by a change of sculpture, design, texture or colour. The rudimentary or embryonic shell of a bivalve is called a **Prodissoconch**.

Pseudometamery - having multiple body organs, repeated in a metameruic fashion, but the organism as a whole is not metameric - e.g. Trybliida, Polyplacophora. There may be a gradation between pseudometamery and full metamery. Sometimes pseudometamery and metamery are taken to mean the same thing - e.g. in discussions of primitive molluscs.

Radial lines: Radiating in relatively unbroken lines from the beaks of bivalves, the apex of gastropods, or the mucro of chitons, as contrasted with concentric.

Radiating: Spreading in various directions

Radula rad'u-la (Lrado=to scrape or scratch) A rasp-like organ, odontophore or lingual ribbon of armed with tooth-like processes, found in nearly all molluscs except the bivalves. This tough chitinous ribbon of teeth obtains food particles by a rasping or licking action. The presence of a radula is one of the characteristics that distinguish molluscs from other organisms.

Reticulate: Lines, riblets, threads or grooves crossing each other like a net.

Rib: An elongate sculptural element of a shell, raised above the surrounding surface. A fine rib is a riblet, and a very fine rib is a thread.

Riblet: A small rib, but coarser than a thread.

Rugae folds; wrinkles; ridges in the ornament of a shell

Scaphopoda sca-phop'o-da (Gr Scaphe=boat; podos=foot) Tusk or tooth shells this class of molluscs possess an one-piece tapering, curved shell open at both ends and an elongated foot adapted for burrowing. more

Sculpture: the decoration (in terms of ridges, ribs, striae, etc) on the surface of a shell; a pattern of raised or depressed markings on the shell's surface. Synonymous with ornament.

Selenizone: Spiral band of crescentic growth lines, associated with marginal slit or foramen in certain univalves.

Semi-infaunal - lying partially buried in sediment, sand or mud. Some bivalves are semi-infaunal. Compare with infaunal

Shell (AS scell=shell) A hard rigid, calcareous or chitinous structure encasing an animal, or covering some part of it. Some molluscs have an internal shell.

Sinistral sin'is-tral (L sinister=left) Having the whorls of a spiral shell turning towards the left when a shell is held with its apex pointed up and its aperture facing the viewer. This is a counter-clockwise whorl.

Sinus si'nus (L sinus=a curve) A depression, bend, embayment; a recess or indentation as in the pallial line of a bivalve or gastropod.

Siphon si'phon (Gr Siphon=siphon) A prolongation or fold of the mantle conveying water into or out of the mantle cavity of most molluscs.

Siphonal Canal, siphonal notch A tube-like extension or notch-like infolding of the lip of the aperture in a gastropod shell, often continuous with columella, also known as an anterior canal, through which the inhalant (anterior) siphon is extended.

Siphuncle si'phun-cle (L siphunculus=a little tube) The small tube connecting the chambers in a nautilus shell.

Slit (AS slite=slit0 A shallow or relatively long incision in the outer margin of the aperture of a gastropod.

Spicule spic'ule (L spiculum=a dart) A small, slender, hard body, sharp-pointed, often needle-like as the spiculous fringe found on the girdle of chitons.

Spiral sculpture: Sculpture following the helical growth of a gastropod shell.

Spire: All whorls of a spiral shell exclusive of the body whorl.

Stria: (Pl. striae). Narrow and shallow incised groove.

Striate: Marked with striae.

Sub-apical surface: the surface of a shell on the *inside* of a spiral.

Subcentral: just beneath the center

Supra-apical surface: the surface of a shell on the *outside* of a spiral.

Suture: The continuous spiral line of junction of whorls of a gastropod shell. The septal connecting in cephalopods

Symmetrical sym-met'ric-al (Gr syn=with; metron=measure) Equal-sided, well balanced, having similar parts arranged in regular reverse order on both sides.

Teleoconch: All the whorls of a gastropod shell after the protoconch.

Thread: A very fine sculptural element of a shell, raised above the surrounding surface. Finer than a rib.

Trema (p. *tremata*) perforation of a shell, generally formed by periodic closure of a slit, but occurring also at the apex of some fissurulid limpets

Trematose - characterised by trema

Trochoid or Trochoidal: Like an inverted spinning top, or like the shell of a Trochus having a pointed spire, flat sides and flat base.

Truncate: Abruptly cut off; applied to the square-ended appearance of certain bivalve shells, and to the abrupt termination of the columella in some gastropod shells such as Planaxis.

Tubercle(s): Elevated knob-like projections or protrusion; larger than pustule.

Truncate: Cut off at the end, blunt.

Umbilicate: Navel-like; with depressed cavity. Having an umbilicus.

Undulate: Having a wavy surface.

Univalve: A mollusk consisting of a single spirally coiled shell.

Untorted - a mollusc, e.g. a gastropod predecessor, that has not undergone torsion

Valve (L valva=a leaf of a door) One of the separate portions of a shell of a mollusc. In bivalves, one of the two portions into which the shell is divided, the two valves usually joined by a hinge. In chitons, one of the eight plates comprising the shell. hence *Univalve*; one a single piece shell *Bivalve*; a two-pieced shell. *Multivalve*: more than two shell plates as in the chitons.

Veliger vel'I-ger (L veliger=snail-bearing) a larval mollusc in the stage of development where it has developed ciliated swimming membrane or membranes.

Velum: Ciliated mantle flap by which a molluscan larva swims.

Ventral ven'tral (L venter=the belly) Of, pertaining to, or situated on, the lower side of a dorsoventral organism; on the apertural surface of a gastropod shell; the edge remote from the hinge in a bivalve; the ventral margin is opposite the umbones. Opposite to dorsal.

Vermiform: Like a worm in shape.

Whorl: A single, complete turn of 360° in the spiral growth of a gastropod shell.

Abbreviations

(from Man and Mollusc Glossary)

AS = Anglo-Saxon
Fr = French
Gr = Greek
L = Latin

Links

Glossary/Mollusks - a very comprehensive glossary; Man and Mollusc Glossary - includes derivation of original word

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page by M. Alan Kazlev, checked ATW050713
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Mollusca References

Abbreviated Dendrogram

```
SPIRALIA
|--BRACHIOPODA
`--+--ANNELIDA
   |
   `--MOLLUSCA
      |--Aculifera
      |  |==Mattheviidae
      |  |--Aplacophora
      |  `-- Polyplacophora
      `--Conchifera
         |==Tryblidiida (Monoplacophora)
         |  `--Cephalopoda
         `==Helcionelloida
              |==Rostroconchia
              |  `-- Scaphopoda
              |--Bivalvia
              `--Gastropoda
```

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A possible scenario of molluscan evolution;

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page by M. Alan Kazlev, checked ATW050713
page uploaded 28 December 2002, last modified MAK120604

Aculifera

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
|  |==Mattheviidae
|  |--Phthipodochiton
|  `--+==Heloplacidae   (Aplacophora)
|     |  |--Solenogastres
|     |  `--Caudofoveata
|     `--Polyplacophora
`--CONCHIFERA
```

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Two specimens of Simrothiellidae sp. (Aplacophora: Solenogastres: Cavibelonia) in vivo from North Fiji Back-Arc Basin, site White Lady; cruise TUIM06MV (June 2005, MBARI). Strange as it seems, these shell-less worm-like creatures are actually molluscs.
Photo by Denisia 18 and ChEss - Biogeography of Deep-Water Chemosynthetic Ecosystems. Publisher: © Chris Allen, Photographer © G. Rouse., Creative Commons Non-Commercial Attribution via Encyclopedia of Life.

This section introduces the Aculifera, which may or may not be a monophyletic clade, and covers the really primitive Mollusca, either worm-like or with shells and plates, or Paleozoic forms resembling modern chitons. Not included are all those creatures we think of as molluscs, most of which belong to the Conchifera or shell-bearers, a huge group that includes all the advanced mollusks: Bivalvia, Cephalopoda, and Gastropoda along with their less known relatives and Paleozoic ancestors. Also the chitons are aculiferan, but deserve their own unit.

The molluscan way of life is ancient. Some elements of the molluscan body plan go as far back as the beginnings of the Bilateria. So, for example, *Kimberella*, an Ediacaran animal, was quite mollusc-like. In fact, it may even have had a scraping organ analogous to a radula. Whether it actually was related to molluscs is more difficult to determine. *Xenoturbella*, an extremely primitive living animal, is also mollusc-like, although it is probably a deuterostome. As with most invertebrate groups, Mollusca lacks a reasonable phylogenetic definition, so it is somewhat hard to say where the actual "Phylum Mollusca" begins. As applied in the literature, Mollusca probably corresponds quite closely to the crown group of all living "mollusks," *i.e.* Solenogastres + garden snails.

Our coverage of the vast diversity of basal molluscs in this and other units is fairly limited. As the cladogram above indicates, the phylogeny is still somewhat controversial (and hence mostly low resolution here). There are also a great many holes. We do have pages on the Solenogastres and the worm-like Caudofoveata, as well as, in following pages, the chitons and some early shelled mollusks, along with the Rostroconchia. Unfortunately, since most early mollusks lacked shells, the fossil record is also quite sparse. ATW, MAK120607

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Aculifera

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA  (paraphyletic)
|   |==Mattheviidae
|   |--Septemochiton
|   |--Phthipodochiton
|   `--+==Heloplacidae
|      |  |--Solenogastres    (Aplacophora)
|      |  `--Caudofoveata
|      `--Polyplacophora
`--CONCHIFERA
```

Overview
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    Are the Aculifera paraphyletic?
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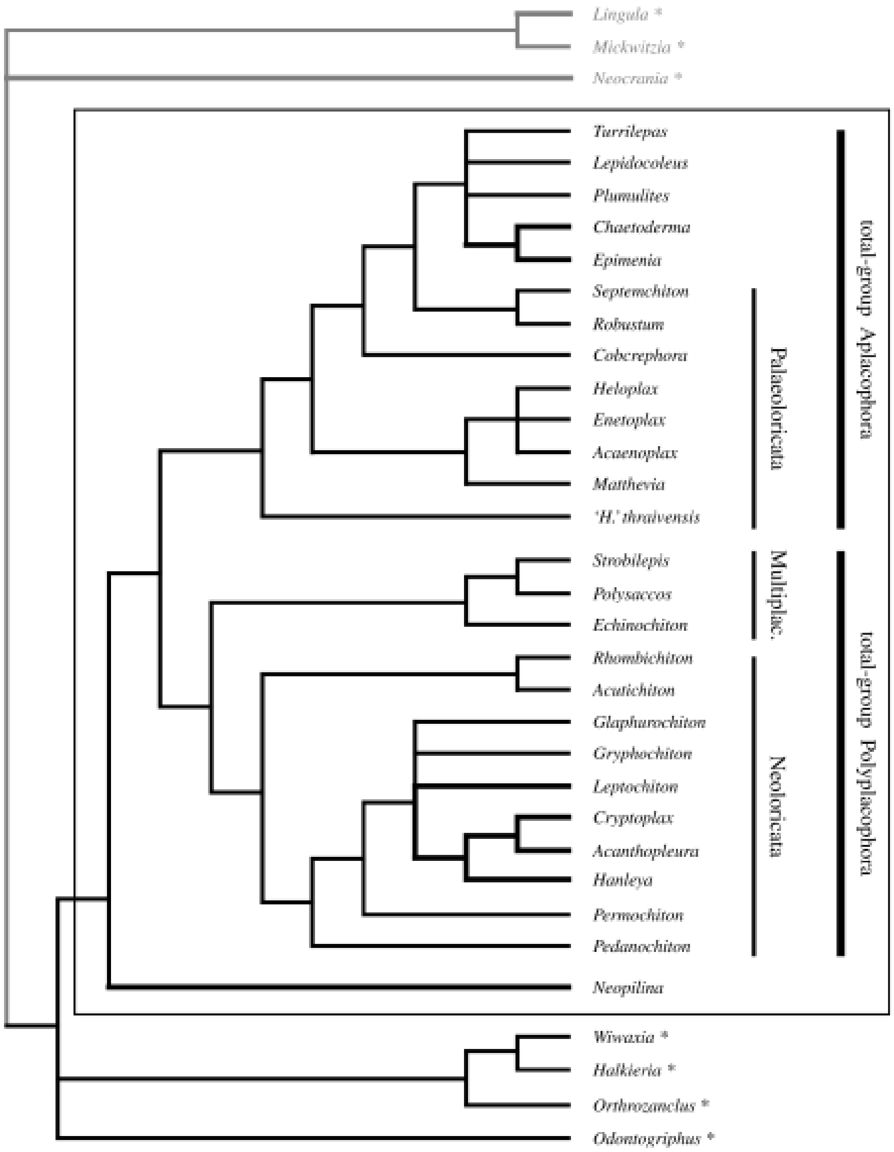
1. Aculifera
2. *Phthipodochiton*
3. Mattheviidae
4. *Septemochiton*

The Aculifera hypothesis

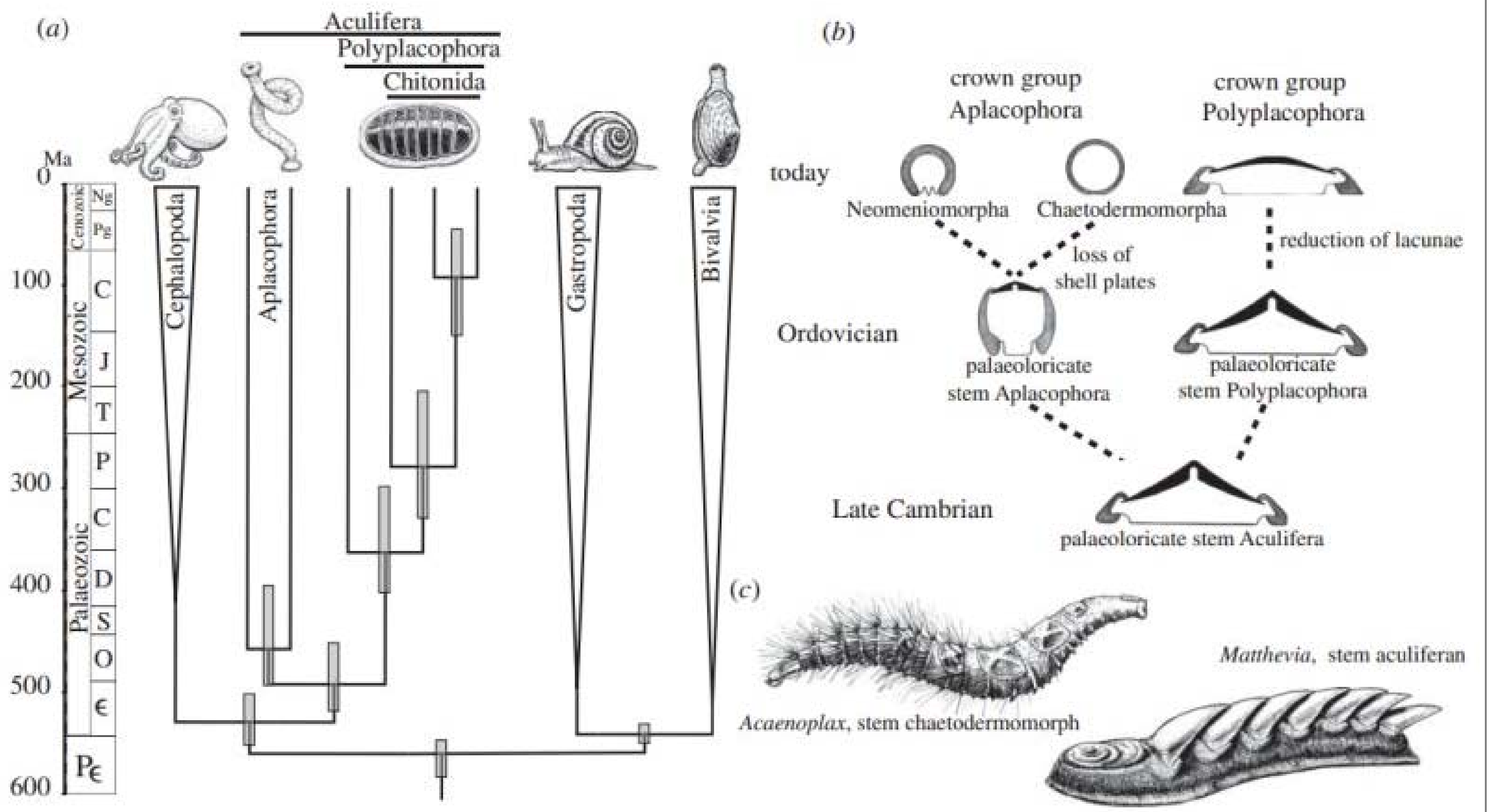
The name Aculifera is given to a clade of molluscs recovered through molecular phylogeny and some paleontological analyses (Sigwart & Sutton 2007 Kocot et al 2011, Smith et al 2011, Vinther et al 2011). It includes all molluscs that either primitively lack a shell (as opposed to having secondarily lost their shell) (aplacophora) or have a series of plates instead of a single shell (polyplacophora). These were originally called Amphineura, a class that was rejected be cause there are no morphological features that unite them to the exclusion of other molluscs. The group was restored, but under



Strict consensus tree from parsimony analyses showing inferred relationships among Aculifera and related taxa based on 101 most-parsimonious trees generated when brachiopod out-group characters were coded according to the brachiopod-fold hypothesis (Cohen et al. 2003). Lines in bold indicate living taxa; brachiopod (out-group) taxa are in grey; additional fossil outgroup taxa are indicated by asterisks. 'Polyplacophoran' groups Neoloricata, Palaeoloricata and Multiplacophora (Multiplac.) are labelled; molluscan crown group is indicated by the surrounding box. - cladogram and caption from Sigwart & Sutton 2007 fig 3. *Note*, *Turrilepas Lepidocoleus*, and *Plumulites* (shown at the upper left) are now known to be armoured annelids. However their close similarity with Paleozoic aculifera shows how closely related the two phyla are at thuis level (Vinther et al 2008 , Vinther & Briggs 2009)

a different name, following some morphological studies, but was never popular until being recovered by recent molecular and cladistic analyses. As currently defined, the Aculifera includes the eight-plated Polyplacophora (chitons) as well as the shellless and either primitive or degenerate Caudofoveata (=Chaetodermomorpha) and Solenogastres (=Neomeniomorpha), along with their fossil relatives. In terms of taxonomic rank, Aculifera is one of the two subphyla of the molluscs, the other being the Conchifera (shell-bearers), which includes the majority of molluscs. The cladogram on the right provides one possible phylogeny, and assumes a monophyletic aculifera and mollusca, which emerges from a paraphyletic halwaxiida and brachiopoda.

A similar phylogeny, shown below, is provided by the sketch of early molluscan evolution by Dr Jakob Vinther and co-workers. In this cladistic diagram, once again, aplacophorans emerge through the secondary loss of shell (and perhaps also the foot) from a paraphyletic assemblage of "paleoloricates". Illustrated are two early Paleozoic genera, the bizarre worm-like *Acaenoplax*, which seems to possess a combination of aplacophoran and chiton attribites, and the very basal spiny plated Cambrian form *Matthevia*



Aculiferan and molluscan evolution. (a) Timetree of aculiferans assessed with Bayesian relaxed molecular divergence estimation). Grey bars are 95% credibility intervals. (b) Morphological transitions in aculiferan evolution in relation to the foot, shell and mantle, based on molecular evidence presented herein and partly on previous morphological cladistic hypotheses [19,22]. The ancestral aculiferan was a form with a broad ciliary foot and a shell with lacunae (Paleoloricate). The molecular clock analysis and the fossil record indicate that in the Ordovician, the Aculifera had diverged into a stem group aplacophoran with a reduced foot and a laterally compressed body; fossil evidence demonstrates that this form was of palaeoloricate morphology with lacunae in the shell plates. Stem group polyplacophorans also retained the plesiomorphic palaeoloricate condition at this time. The aplacophorans diverged early into the chaetodermomorphs and the neomeniomorphs. Chitons reduced the lacunae in the shells and developed a more dorsoventrally flattened aspect and a smoother dorsal surface. (c) Reconstructions of two important fossil forms: *Acaenoplax hayae* (an aplacophoran relative) and *Matthevia* (the earliest known stem group aculiferan with multiple overlapping plates). - Diagram and caption from Vinther et al 2011 fig 4

Unlike the mammalian molecular clock, with its non-existent Mid-Late Cretaceous and Mid Tertiary placental radiations , this seems to be an instance where the molecular clock supporerts stratigraphy and vice-versa. In keeping with the phylogeny in Vinther et al 2011, the above cladogram presents aculiferans and cephalopods as sister taxa. As there is no morphological or paleontological support for this molecular-only hypothesis, we have chosen instead the phylogeny of Kocot et al 2011, according to which cephalopods evolved from monoplacophora (and the two are hence sister taxa, as in the molecular phylogeny of Smith et al 2011

Fossil Record

If Early to Middle Cambrian Sachitids are aculiferan ((Vinther 2009).) then the group appears at the start of the Paleozoic, which makes sense given the similar antiquity of the conchifera (higher molluscs). It may even be that halkeriids are aculiferans (Vinther & Nielsen 2005). The implication is that there is an unbroken continuum from basal halwaxiids to molluscs proper, and that some halwaxiids are basla molluscs. and even basal aculifrean; although if teh aculifera are paraphyletic, as we believe, than that last phrase is redundant) In any case, these early molluscs and proto-mo;;uscs seme to have bene common and widespread during the early Cambrian.. By the Late Cambrian they had goven rise to an accentric assemblage of Mattheviids which represent the predominant Late Cambrian and Ordovician aculiferan type.

During the Silurian there was a radiation of heloplacids, which combined the characteristics of chitons and aplacophoran molluscs. Multiplated skeletons in paleoloricates and heloplacid aplacophorans represent either parallel evolution (Cherns 2007) or the plesiomorphic state of dorsal armour (Sigwart & Sutton 2007, Vinther et al 2011), or both, and is not overlapping, unlike true chitons. Peaks of aculiferan evolutionary diversity in early Ordovician, mid-Silurian and early Carboniferous times correspond to periods with development of low latitude carbonate shelves. True chitons (Neoloricates) appear in the Devonian , and have an additional shell layer that adds articulatory plates. However the fossil record of the group at this time remains poorly known (Cherns 2007)

Are the Aculifera paraphyletic?

A challenge with molluscan phylogeny, as with phylogeny in general, is finding an overall explanation that can accomodate the more often contrary and less often mutually supporting hypothesis from morphological, functional, developmental, paleontological, stratigraphic, cladistic, and molecular methodologies. Too often only one methodology is used (the tendency now is to rely mostly or solely on molecular data) and contrary hypotheses using other methodologies is rejected. For example Salvini-Plawen 1980 and elsewhere, and Haszprunar 2000 argue on morphological grounds that the aplacophoran groups and the polyplacophora represent a gradation of primitive types leading to the Conchifera or higher molluscs. But in the 2000s through to 10s , cladistic and molecular studies (Sigwart & Sutton 2007, Kocot et al 2011, Smith et al 2011, Vinther et al 2011) reject a paraphyletic aplacophora in favour of the Aculifera hypothesis. It is asusmed that the more recent papers are more correct, and that the earlier work is outdated. But this is a misleading premise, because very different methodologies are used in each case, each with different phylogenetic signals, and it is not possible to refute one methodology using a totally unrelated methodology (e.g. morphology-based cladistics cannot be disproved by molecular sequencing, and vice-versa). There is also no way of knowing when a new paradigm will emerge, or new evidence uncovered, causing a toal turn around. For example in the 1950s 60s and 70s, text books regularily referred to the Amphineura (=aplacophora + polyplacophora). Following the work of Salvini-Plawen and others, the Amphineura was rejected and replaced by two or three unrelated classes. Now the tendency is for the aplacophora and polyplacophora to be again grouped together in a single group, now called Aculifera, despite there being very little in morphological terms that these various groups have in common, other than plesiomorphic molluscan or spiralian characteristics, such as spicules and multiple dorsal shell plates, both features shared with halwaxiids but lost in conchifera.

Although both molecular and paleontological-statistical cladistic data (Sigwart & Sutton 2007, Vinther et al 2011) support the Aculifera hypothesis (see cladograms above), the problem with a monophyletic aculifera is that it leaves the ancestry of the Conchifera hanging in the air. Since we do not wish to multiply entities unnessarily (William of Occam), iit seems much more parsimonious to reject the ghost lineages and simply assume that the Aculifera - which are morphologically intermediate between halwaxiids and conchifera - are a paraphyletic group. Their apparently monophyletic status can be explained by the loss or transformation of the original aculiferan synapomorphies in their conchiferan descendents (the same applies to Cambrian arthropods (Walossek & Müller 1998 pp.186f). If the same happened in the genome as well as the gross morphology, molecular phylogeny would likelwise give a "false monophyly" result (as with the cyclostome jawless fish, which are morphological a paraphyletic or polyphyletic gradation (as conclusively shown by Janvier) but in molecular phylogeny uniformly appear as monophyletic).

On the other hand, if the aculifera predate and give rise to the conchifera, it is necessary to explain why the earliest known fossil aculiferans are no older than the Late Cambrian, whereas the Conchifera were already diverse and numerous by the Early Cambrian. So hybrid forms such as *Matthevia*, which seem to combine attributes of chitons and monoplacophora, rather than being ancestral to the monoplacophora, may have evolved from them. Or the features the two groups have in common may simply be shared ancestral traits. The lineage represented by the Silurian spiny worm-like *Acaenoplax* may also belong here, or it may be closer to crown group aplacophora. It is also quite possible that *Halkieria*-like animals were stem mollusca (or even aculiferan (Vinther & Nielsen 2005, Vinther 2009), although that would make the latter group paraphylertic), and that they were the ancestors both of Mattheviid type multiplacophorans and conchiferan monoplacophora, both of which can be considered transitional forms. MAK120613

Descriptions

Aculifera Hatscheck, 1891

Range: Fr ECambrian

Phylogeny: paraphyletic Halwaxiida/ basal Mollusca **:** Conchifera + * **:** paraphyletic Mattheviidae + *Phthipodochiton* + *Septemochiton* + (Heloplacidae + (Caudofoveata + Solenogastres)) + Polyplacophora

Characters: spicules, multiple dorsal paltes or spines, larval or adult metamerism

Comments: Two possible classifications of Aculifera as a subphylum: Aculifera includes the Aplacophora (Caudofoveata and Solenogastres) and Polyplacophora (chitons), with all other molluscs being included in subphylum Conchifera (shell-bearers) (Hatscheck in Blumrich, 1891; Scheltema, 1993) or it including only the Aplacophora, with the polyplacophora going in the subphylum Placophora, and the Conchifera as previously described (Stasek, 1972). Haszprunar 2000, and Glaubrecht, Maitas & Salvini-Plawen, 2005) all would support a phylogenetic relationship like Solenogastres + (Caudofoveata + (Polyplacophora + Conchifera)) making the Aplacophora (and therefore Aculifera) paraphyletic. (Gofas (nd). In contrast, Sigwart & Sutton 2007 Kocot et al 2011, Smith et al 2011, Vinther et al 2011 all support a monophyletic Aculifera. Because groupings of molluscan classes into clades is highly controversial (for a review of competing hypothesis see Steiner & Dreyer (2003) , the various molluscan classes are better treated as an unresolved polytomy (Gofas (nd)) or the Conchifera and the three aculiferan classes can be considered an unresolved quadotomy. The Solenogastres and Caudofoveata can be derived from Paleozoic Mattheviids or *Phthipodochiton* or similar (Sigwart & Sutton 2007). Supporting the validity of the aculifera is the discovery that extant Solenogastre and Caudofoveatan embryology exhibits a chiton-like 7 fold iteration on the dorsal surface in late stages of trochophore larvae, which is lost during metamorphosis (Vinther ref). It is also possible that the multiplate chiton condition may be a primitive molluscan characteristic (related to annelid segmentation) which was lost with monoplacophorans (basal conchifera). If aplacophora and polyplacophora diverged in the Early Ordovician (Vinther et al 2011) than the Aculiferaare a monophyletic clade, although taxa such as *Hemithecella* and *Matthevia* with monoplacophora-like features could still be late surviving stem groups whose ancestors must have evolved during the very earliest Cambrian and would no doubt be among some of the problematic small shelly forms or Halkeriid-like animals. MAK120608

Mattheviidae Walcott, 1885 : *Calceochiton, Chelodes, Eukteanochiton, Hemithecella, Matthevia, Robustum, Spicuchelodes* (ref: Paleobiology Database)

Higher taxa and partial synonyms: Matthevina Fisher 1962; Chelodina Runnegar et al. 1979; Paleoloricata Cherns 1998.

Range: Late Cambrian to Early Devonian

Phylogeny: Aculifera **:** *Phthipodochiton* + *Septemochiton* + (Heloplacidae + (Caudofoveata + Solenogastres)) + Polyplacophora + *

Characters: massive, elongate, non-overlapping valves, monoplacophoran-like shells and muscle scars. Paraphyletic assemblage

Comments: Either basal aculiferan, intermediate between aculifera and monoplacophora, or both.

Matthevia is a Cambrian mollusc, with repeated monoplacophoran-like shells projecting dorsally as vertical plates or spines. Originally it was proposed that chitons arose when these tall shells began to overlap (Runnegar & Pojeta 1974). Now that aculiferans rather than monoplacophorans seem to be the most primitive molluscs, it may be that instead these plates merged, or one developed at the expense of the others. There are distinct head, 'centre', and tail valves, which occur approximately in the ratio 1:5:1 — suggesting a seven-plated configuration Wikipedia, MAK120608

Hemithecella is a problematic multiplated late Cambrian and Early Ordovician genus, with muscle scars identical to a monoplacophorans, unlike the musculature of the chitons. It therefore cannot be included in the latter group (Stinchcomb & Darrough 1995, Pojeta et al 2010). Wikipedia

Vendrasco and Runnegar argue that mattheviids are polyplacophoran on the basis of shared valve characters such as including granules, an apical shelf, a thin anterior margin, bilateral symmetry, three valve types, and a shell layer perforated with canals. The mattheviids themselves constitute a gradation between classic forms such as *Matthevia variabilis* with non-overlapping, spiky valves, and more traditional paleozoic chitons such as *Chelodes* (Vendrasco & Runnegar 2004). MAK120607

Septemochiton

Range: Ordovician of Iowa

Phylogeny: Basal Aculifera

Comments: Originally sole species of monotypal Family Septemochitonidae and Suborder Septemchitonina. Seven rather than the usual eight valves; phylogenetic position uncertain; the cladogram by Sigwart & Sutton 2007 makes *Septemochiton* the sister taxon of the Mattheviid *Robustum*. Hoare & Pojeta 2006 define the Septemochitonida Bergenhayn, 1955 as "Paleoloricates with intermediate plates differentiated into central and lateral areas." and include a number of families and genera. They fgive the range as Ordovician to Devonian MAK120607

Phthipodochiton thraivensis (Reed, 1911)

Synonym: *Helminthochiton thraivensis* Reed, 1911

Horizon: Lady Burn Starfish Beds, Ordovician of Girvan, southwest Scotland

Phylogeny: Basal Aculifera

Comments: Worm-like body plan, lacks a true foot despite bearing polyplacophoran-like valves: a spicular girdle wraps entirely around the ventral surface of the animal, implying that a polyplacophoran like foot was absent, although traces of a narrow solenogastre-like median pedal groove is possiblly evident in the fossils (Sigwart & Sutton 2007, Sutton & Sigwart 2012). That means that these animals either had not yet acquired the creeping molluscan foot or had aleady secondarily lost it. The valves are typically palaeoloricate in aspect, but differ in detail from all other palaeoloricate genera, hence the new generic name Sutton & Sigwart 2012). Carnivorous, fed on crinoids (Donovan et al 2011); has an apparent mosaic of aplacophoran and polyplacophoran features, and shows that at least some other palaeoloricates possessed a worm-like "armoured aplacophoran" body plan, in contrast to the limpet-like body plan of extant Polyplacophora Sutton & Sigwart 2012); the latter may simply be an adapatation to a specialised tidal-zone ecological niche among this ancient group MAK120612.

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Aculifera: Caudofoveata

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
|  |==Mattheviidae
|  |--Phthipodochiton
|  `--+==Heloplacidae   (Aplacophora)
|     |  |--Solenogastres
|     |  `--Caudofoveata
|     `--Polyplacophora
`--CONCHIFERA
```

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1. Caudofoveata

Introduction

Chaetoderma canadense, St. Margaret's, Nova Scotia, Canada.
photo © R. Robertson (from The Aplacophora Home Page

The Caudofoveata are small, worm-like aberrant molluscs, ranging in length from 2 mm - 14 cm..They construct burrows in soft marine sediments which they inhabit head downwards. They ingest sediment, or may be selective carnivores or scavengers. Many typical molluscan characteristics are either absent or reduced. There is no shell, no foot, and the mantle covers the entire body. Lacking a foot, they move by peristaltic contractions (like other primitive burrowing metazoa). They are dioecious (male and female reproductive organs in separate individuals). The posterior body cavity (believed to represent the mantle cavity) houses a pair of gills (ctenidia). The integument (skin) contains layers of embedded calcareous spicules. Most specimens have been collected by dredging, and relatively little is known about them. About 70 described living species of this class.

The Caudofoveata and Solenogasters are generally combined to form the class Aplacophora, although this practice is becoming discontinued as the differences between these two small primitive groups become known. For example, unlike Solenogasters, chaetoderms lack a pedal groove.

Like the Solenogasters, Caudofoveata are of great phylogenetic interest, and their precise evolutionary relationships are still unclear. Salvini-Plawen 1980 sees them as the sister group to all other molluscs, being little changed from the first "Scutopoda" (original burrowing forms). Bergström suggests that they may be surviving members of the Procoelomata, the ancestral sclerite-bearing early Cambrian metazoa. However, cladistic work by Haszprunar (Haszprunar 2000) indicates that Solenogasters are the most underived forms, with chaetoderms derived from them and higher (shell-bearing) molluscs next.

Caudofoveata

Synonym: Chaetodermomorpha

Range: No fossil record

Phylogeny: Heloplacidae **:::** *

Comments: Included under the probably polyphyletic Aplacophora. No foot, but they do have an oral shield and gills. Unlike the solenogastres, they have separate sexes. (Jack R. Holt)

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Aculifera: Heloplacidae

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
|  |==Mattheviidae
|  |--Phthipodochiton
|  `--+==Heloplacidae   (Aplacophora)
|     |  |--Acaenoplax
|     |  |--Heloplax
|     |  `--+--Solenogastres
|     |     `--Caudofoveata
|     `--Polyplacophora
`--CONCHIFERA
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1. *Acaenoplax*
2. Heloplacidae
3. *Heloplax*

Descriptions

Heloplacidae Cherns, 2004 : *Acaenoplax, Arctoplax, Enetoplax, Heloplax*

Range: Silurian

Phylogeny: basal Mollusca = paraphyletic Aculifera **:** Heloplacidae + (Caudofoveata + Solenogastres) + (*Phthipodochiton* + Polyplacophora) + *Septemochiton* + Conchifera

Comments: Plated aplacophora, best represented by *Acaenoplax* (Cherns 2004, Sutton et al 2004) Wikipedia. Correspond to the Paleoloricates i part. They seem to have been common and diverse during the Silurian. The granular dorsal ornament is similar to that of extant chitons, and hence possibly linked with sensory cells (aesthetes). Three Silurian baltic (Gotland) genera share an unusual, holoperipheral growth style similar to that of plated aplacophorans such as *Acaenoplax*, and coexisted with paleoloricate chitons in shallow inshore carbonate shelf environments (Cherns 2007). Preliminary cladistic analysis shows the Heloplacids form a sister group to other Early Palaeozoic paleoloricates (Cherns 2007) although they can just as easily and perthaps more likely forma paraphyletic ancetsral assemblage (Sigwart & Sutton 2007, Vinther et al 2011).

Heloplax

Range: Silurian

Phylogeny: Paraphyletic Heloplacidae

Comments: worm-like mollusc, preserved in three dimensions in the Silurian Herefordshire lagerstatte; its disarticulated valves are known from other Silurian deposits.[1] It is very bizarre by modern standards; it bears serially repeated units, and has spines. It probably falls somewhere between the aplacophorans and polyplacophora; its valves were composed of aragonite (Sutton et al 2004) Wikipedia

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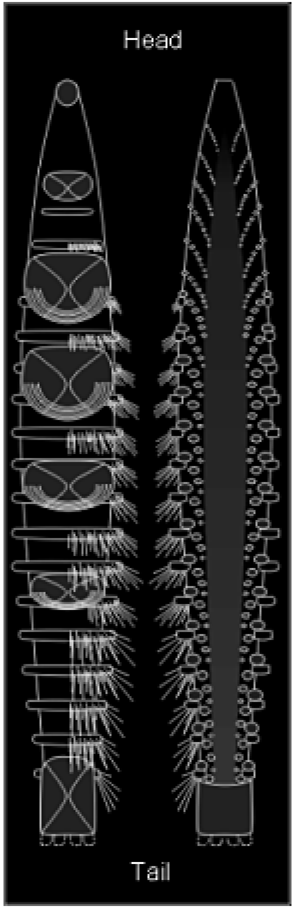
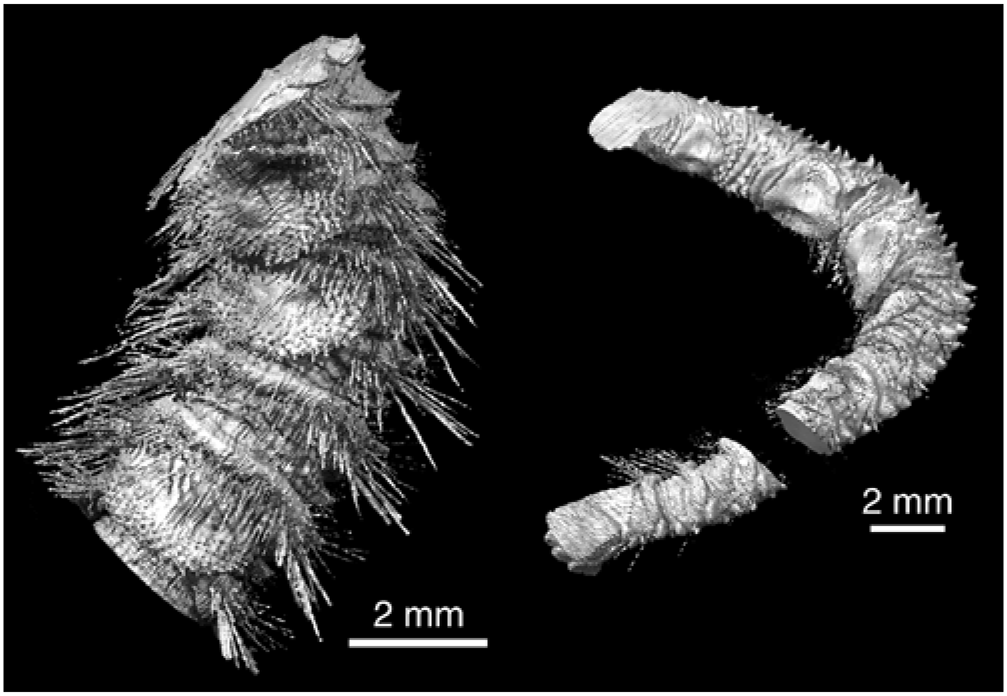


Idealized reconstruction of the Heloplacid *Acaenoplax hayae*Scale bar, 2 mm. - Sutton et al 2001 fig 3



Acaenoplax hayae, from Sutton et al 2001 fig 2 via Science Now

Acaenoplax hayae Sutton et al, 2001

Horizon: Herefordshire Lagerstatte (Wenlock, Silurian).

Phylogeny: Paraphyletic Heloplacidae

Comments: *Acaenoplax* is a worm-shaped mollusc a couple of centimetres long and half a centimetre wide, and comprises serially repeated units with seven or eight shells, and rings of 'spines'. The organism resembles a bristled worm, but bears a number of shells on its upper surface. The first shell is cap-like, whereas the others are saddle-shaped. The rearmost shell is almost rectangular, whereas the others are more circular, with spines on the rear surface of the third to sixth shells. The originally-aragonitic shells do not overlap. There are eighteen rows of spines projecting from ridges in the body surface, which encircle the body except for its bottom surface, which presumably bore a molluscan foot. Its straight gut was preserved in phosphate. (Sutton et al 2001, Sutton et al 2004) Wikipedia

Some of *Acaenoplax*'s characters are reminiscent of the polychaete worms, and the character combinations do not place it obviously in the stem of any modern mollusc group. It was it was originally interpreted as a polychaete, and (Steiner & Salvini-Plawen 2001 argue that it is an annelid rather than a mollusc, although this interpretation was refuted (Sutton et al 2001b), and the consensus opinion now is that *Acaenoplax* is an aculiferan mollusc (Cherns 2007, Sigwart & Sutton 2007, Vinther et al 2011, etc). MAK120607

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Palaeos		ACULIFERA
MOLLUSCA		SOLENOGASTRES

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Aculifera: Solenogastres

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
|  |==Mattheviidae
|  |--Phthipodochiton
|  `--+==Heloplacidae      (Aplacophora)
|     |  |--Solenogastres
|     |  `--Caudofoveata
|     `--Polyplacophora
`--CONCHIFERA
```

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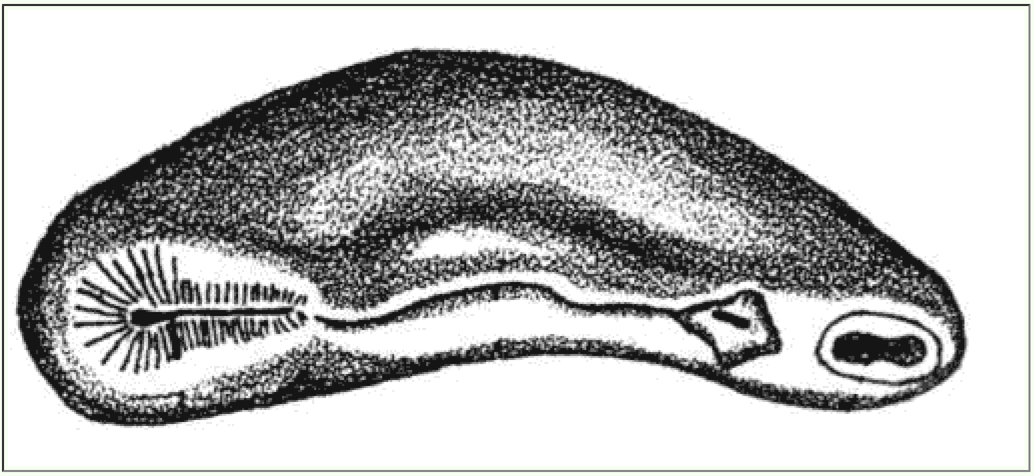
2. Solenogastres

Introduction



Neomenia, showing mouth (top), pedal groove, and cloaca. Image source

The Solenogastres are mostly small (less than 5 cm long] worm-like mollusks that live symbiotically (or feed upon) cnidarians. As with the Caudofoveata, many of the typical molluscan characters are absent. They have no shell, eyes, or tentacles. The mantle cavity is rudimentary, and instead of the standard molluscan flattened foot there is a pedal groove, which the animal uses to creep along the bottom. They are hermaphrodites and lack ctenidia (gills) in the mantle cavity. As with the Caudofoveata, the integument contains layers of embedded calcareous spicules, possibly a link to early Cambrian coelomates. The worm-shaped body is derived from the inrolling of the mantle margins.

unknown: possibly from *Invertebrate Zoology* by Edward E. Ruppert and Robert D. Barnes, reproduced at Man and Mollusc.

There are about 250 described species, probably with many more awaiting discovery. They are found primarily below 200 meters and are sometimes quite abundant in deep-sea epifauna or infauna. Many reside and feed upon cnidarians (hydroids and corals).

Despite being an important part of the deep-sea benthos, neomeniomorphs are poorly known, mainly because the difficulty of studying creatures that live in very deep water.

The Solenogastres have in the past been combined with the Caudofoveata to form the class Aplacophora. In some classifications the terms Aplacophora and Solenogastres seem to be synonymous. However the tendency now is to see them as distinct classes of mollusks.

Evolutionary Relationships

Whilst adult physiology may differ greatly between different groups of organisms, embryonic ontogeny may show evolutionary relationships, a fact discovered by the Darwinian philosopher Ernst Haeckel in the 19th century. Here larval ontology indicates the relation between Solengastres and Polyplacophora on the one hand, and sclerite-bearing "molluscomorphs" on the other. Salvini-Plawen 1980 provides an illustration (*below*) showing the similarity between larval forms of each class.

Differentiation of the mantle cover in just metamorphosed *Nematomenia banyulensis* (Solengastres - A and B) and *Middendorffia caprearum* (Polyplacophora - C and D). **Pl** shell plates in formation through the coalescence of the scaly bodies **Sp** arranged in seven transverse rows. Caption and figure from Salvini-Plawen 1980 p.252

Similarly, a recent discovery of a neomenioid postlarva (Scheltema & Ivanov, 2002) shows it has six iterated, transverse groups of spicules and seven regions devoid of spicules. These resemble the shell fields in developing polyplacophorans, and spicule arrangement is compared to sclerite arrangement on the Cambrian fossils *Wiwaxia corrugata* and *Halkieria evangelista* and to the spines and shell plates of the Silurian *Acaenoplax hayae*. Such iterative morphogenesis was probably a common theme in earliest Cambrian halwaxiid animals and shows how these groups are related

It is still unclear to what extent the Solenogastres and Caudofoveata are specialized and to what extent they are primitive, even "living fossils". Both these groups have been hypothesized to be ancient, pre-Tethyan deep-sea forms, perhaps relics of the original Cambrian metazoan radiation (Dzik (1993), in contrast, suggests they developed from aberrant chitons like the Silurian *Carnicoelus gazdzickii* (*id.* at p.368, fig.12), but there is no evidence a shell was ever present. Barnes (1980). Salvini-Plawen (1980) sees Solenogastres as the sister group to all shelled mollusks (Testaria), while a cladistic study by Haszprunar (2000) indicates that Solenogasters are even more underived than Caudofoveata.

Descriptions

Aplacophora

Range: No fossil record

Phylogeny: either paraphyletic or polyphyletic, not a clade as currently defined, evolved from Paleozoic Heloplacidae

Comments: laterally-compressed marine worm-like shellless molluscs. Some burrow in the mud or live in interstitial spaces. Many aplacophorans live among corals and feed on them. Mantle covers almost all of the body except for a ventral groove, secretes several layers of calcareous bodies. They have a preoral sense organ and a subterminal ventral mouth. They do not have ctenidia, but sometimes do have secondary gills. There are no specialized excretory organs. Some of the aplacophorans do not have a radula. They have ganglia that are fused with both ventral and dorsolateral longitudinal nerve cords. - Jack R. Holt

Links the Aplacophora Home Page - the only site dedicated to these two little-known molluscan groups, the Caudofoveata and Solenogastres; Aplacophoran good coverage; Two Aplacophoran Subclasses - short intro and illustration; The Class Neomeniomorpha and The Class Chaetodermomorpha - short intro; checked ATW050731

Solenogastres

Synonym: Neomeniomorpha

Range: No known fossil record

Phylogeny: Heloplacidae **:::** *

Comments: Included with the Caudofoveata under the paraphyletic or, in view of current phylogenies, probably polyphyletic Aplacophora. No gills, foot is present but highly reduced; hermaphroditic (Jack R. Holt)

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Aculifera: Dendrogram

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
|  |==Mattheviidae
|  |--Phthipodochiton
|  `--+==Heloplacidae   (Aplacophora)
|     |  |--Solenogastres
|     |  `--Caudofoveata
|     `--Polyplacophora
`--CONCHIFERA
```

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```
MOLLUSCA
|--ACULIFERA
|  |==Mattheviidae
|  |--Septemochiton
|  |--Phthipodochiton
|  `--+==Heloplacidae   (Aplacophora)
|     |  |--Acaenoplax
|     |  |--Heloplax
|     |  `--+--Solenogastres
|     |     `--Caudofoveata
|     |  |--Solenogastres
|     |  `--Caudofoveata
|     `--Polyplacophora
`--CONCHIFERA
```

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Aculifera: References

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
   |==Mattheviidae
   |--Phthipodochiton
   `--+==Heloplacidae   (Aplacophora)
|     |  |--Solenogastres
|     |  `--Caudofoveata
|     `--Polyplacophora
`--CONCHIFERA
```

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Aculifera - Fossil Record, Heloplacidae

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Gastropoda

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA  (crown group)
            |==Eogastropoda  (paraphyletic or
polyphyletic)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
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A selection of gastropods exposed by the tide cling to rocks in the intertidal littoral zone. A strong defensive shell, whether coile dor uncoiled, is one of the secrets of gastropod success.
Photo by Sherry Ballard, © 1999 California Academy of Sciences Creative Commons Non-Commercial Attribution Share Alike via Encylopedia of Life.

The most diverse and speciose of the molluscan classes, the gastropods appear in the late Cambrian, and by the Ordovician and Silurian had radiated into a number of lineages, although they were not to achieve their present levels of diversity until the late Mesozoic. Instantly recognised by their helical, spiral shell, an object as protective of the soft animal as it is beautiful in form, although some types have a simple cap like shell, and others - the slugs - lost their shell altogether. More distinctive from a phylogenetic point of view (i.e. a synapomorphy or shared defining feature) and the key to their evolutionary success, is the larval developmental process of torsion where the body rotates and the gut becomes U-shaped, thus avoiding fouling (a problem when the anus is positione dover the inlet siphon. But again, there are no rules with gastropods, as in some specilaised groups torsion is reduced or lost.

For the most part highly mobile animals, with a wide flat foot, gastropods are the only molluscs to have conquered dry land. Here their shell serves a s adefense against dessication, an ever present problem facing all terrestrial life. Some terrestrial forms however make do without a shell, instead relying on most environments.

Gastropods have the second-most highly developed nervous system among molluscs, exceeeded only by the cephalopods. Like the cephalopods, they have a head with eyes and tentacles, although in the case of gastropods these have a sensory rather than a raptorial role. Indeed the morphological parallels between gastropods and cephalopods are so close that it was thought until recently that the two groups are closely related and share a common ancestor. Molecular phylogeny however does not support this hypothesis, and it seems instead that the similarities are convergences, parallel evolution, resulting perhaps from a similar active lifestyle. MAK120621

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            |   |?--Euomphaloidea
            |   `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
```

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Introduction

The Latest Cambrian (Late Dolgellian Age) and Earliest Ordovician (Early Tremadoc saw a tremendous radiation of early gastropods. During this period the gastropods, like the cephalopods, underwent a tremendous evolutionary radiation. From one or two planispiral types, represented by a Tropidodiscid ancestor, there developed several distinct taxa, including high spired, lower spired, planispiral, and hyperstrophic types. These could be grouped in three main clades: Eogastropoda, Orthogastropoda, and the extinct Bellerophontoidea. By the earliest Ordovician the three main clades of gastropods had already established themselves and were continuing to diversify into a range of different morphotypes and lifestyles.

The Palaeozoic Pleurotomariacea - A

misinterpretation?

The "Pleurotomariacea" or slit shells and their relatives have traditionally [Knight, et al., 1960] been considered among the earliest and most primitive of the gastropods, first appearing in the Furongian.

Dr Peter Wagner however [Wagner 1999] has used cladistic methodology to try to determine the phylogeny of early Palaeozoic gastropods, and his findings indicate that the Early Paleozoic Pleurotomarioids are actually a polyphyletic assemblage. A diverse assemblage of forms that have traditionally been placed in the "Pleurotomariacea" actually belong among the Euomphalida and the Murchisoniida.

Gastropoda: = Crown Group Definition of Gastropoda, here defined as the LCA (Latest Common Ancestor) of all extant gastropods)

Stratigraphic Range: Latest Cambrian [Late Dolgellian] to Recent

Phylogeny: Unnamed Node **:** Strepsodiscus + Tropidodiscidae + **:** *Schizopea* + Euconiidae + Eogastropoda + Unnamed Node

Characteristics: **$** larval operculum; **$** cephalic and epipodial tentacles; **$** post-torsional right gonad only; **$** radular cartilages not hollow; **$** oesophagus showing torsion; **$** hypoathroid nervous system (adjacent pleural and pedal ganglia) [all from Haszprunar 1988 p.9]; Anisotrophic (helically coiled) shell; body asymmetry. Some of these characters may also pertain to "Gastropodiformes" in general.

Links: see Links section

Schizopea: *Schizopea typica* (= Ophiletinae in part (paraphyletic))

Stratigraphic Range: Furongian (Late Dolgellian Age) to Early Ordovician (Early Tremadoc

Geographic Distribution: Laurentia [= N. Am - Knight, *et al.*, 1960 p. *I*200]

Phylogeny: Gastropoda **:** *Schizopea* + Euconiidae + Eogastropoda + Unnamed Node

Characteristics: spire low, widely phaneromphalus, sutures deep, sinus culminating at blunt anggulation that forms the periphery [Knight, et al., 1960 p. I200]

Notes: Knight, et al., 1960 includes this genus under the subfamily Ophiletinae of the family Raphistomatidae and superfamily Pleurotomariacea. But cladistic analysis by Wagner 1999 indicates that the species *Schizopea typica* is actually a member of an unresolved tetrachotomy that includes the most basal helically-coiled gastropods. It may be that related species may also belong in this clade

Schizopea

Schizopea typica
diameter about 4 cm
Late Dolgellian to Early Tremadoc of Laurentia
(Tremadoc of Missouri)

image © xxxx Knight, et al., 1960 p.*I*200

"Euconiidae": *Euconia etna*, *Jarlopsis conicus*, *Rhombella umbilicata* (= Ophiletinae in part (paraphyletic))

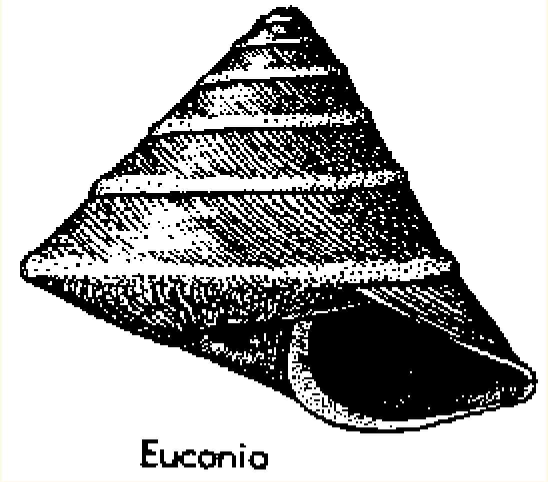
Stratigraphic Range: Early Ordovician (Early Tremadoc to Floian)

Geographic Distribution: Laurentia [= N. Am - Knight, *et al.*, 1960 p. *I*200]

Phylogeny: Gastropoda **:** *Schizopea* + "Euconiidae" + Eogastropoda + Unnamed Node

Characteristics: conical trochiform shell, sutures shallow, sinus culminating at angular periphery just above upper suture [Knight, et al., 1960 p. I 200]

Notes: Knight, et al., 1960 includes *Euconia* under the subfamily Ophiletinae of the family Raphistomatidae and superfamily Pleurotomariacea. But cladistic analysis by Wagner 1999 places this genus as part of off-shoots an unresolved tetrachotomy that includes the most basal helically-coiled gastropods. I have informally coined the family name "Euconiidae" to distinguish this clade from other early gastropods



Euconia etna
diameter about 3 cm
Early Ordovician of Laurentia
(Newfoundland)

image © xxxx Knight, et al., 1960 p.*I*200

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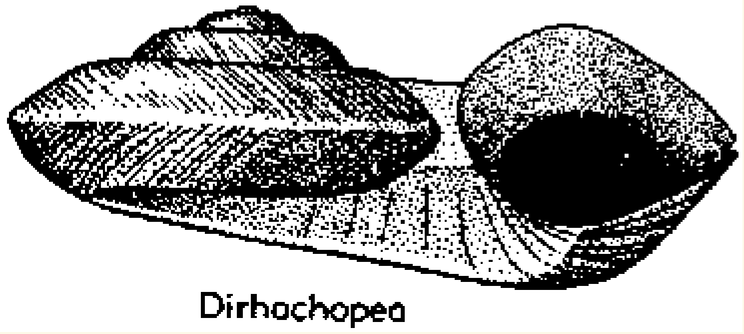
unnamed node: (= Ophiletinae in part (paraphyletic))

Stratigraphic Range: Furongian (Late Dolgellian Age) to Early Ordovician (Late Tremadoc

Phylogeny: Gastropoda **:** Schizopea + Euconiidae + Eogastropoda + Unnamed Node **:** *Dirhachopea normalis* + *Gasconadia putilla* + (*Dirhachopea subrotunda* + "Sinuopeidae")

Notes: node 4 on diagram based on Wagner 1999



Dirhachopea normalis
diameter about 3 cm
Late Dolgellian of Laurentia (Missouri)

image © xxxx Knight, et al., 1960 p.*I*200

"Sinuopeidae": *Sinuopea basiplanata*, *Taenospira emminencis*, *Sinuopea sweeti*, *Taeniospira st. clairi* (= Sinuopeinae and Eotomariinae in part (paraphyletic))

Stratigraphic Range: Furongian (Late Dolgellian Age) to Early Ordovician (Late Tremadoc

Geographic Distribution: Laurentia [= N. Am - Knight, *et al.*, 1960 p. *I*198, 203]

Phylogeny: Unnamed Node **:** *Dirhachopea subrotunda* + Sinuopeidae **:** Bellerophontoidea + Orthogastropoda

Characteristics: Turbinoform, sinus wide, with or without slit

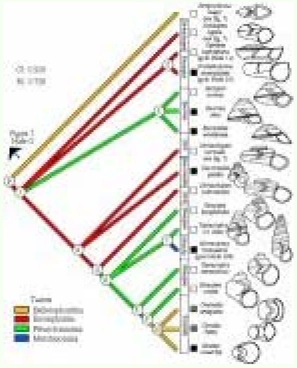
Sinuopea sweeti
height about 3 cm
Late Dolgellian of Laurentia (Wisconsin)

image © McGraw Hill Book Company, from Moore, *et al.* 1952, p.291

Notes: This is a paraphyletic grouping. Knight, et al., 1960 includes *Sinuopea* in the subfamily Sinuopeinae (Furongian to Late Silurian) of the family Sinuopeidae (Furongian to Middle Permian) in the superfamily Pleurotomariacea, and *Taenospira* as the earliest member of the tribe Ptychomphalides (Furongian to Early

Jurassic) of the subfamily Eotomariinae of the family Eotomariidae (also Furongian to Early Jurassic). But cladistic analysis by Wagner 1999 indicates that these forms are basal members of the clade that includes both the Murchisoniida and the Bellerophontoidea. It may be that some other members of the Sinuopeinae and Eotomariinae may also belong here, extending the stratigraphic range of this assemblage

Interpretations of Early Gastropod Evolution



early gastropod relationships
image © Peter Wagner

The diagram (click the thumbnail for larger image) shows the suggested relationships among late Dolgellian and Early Tremadocian (latest Cambrian and earliest Ordovician) gastropods, according to cladistic analysis [Wagner 1999], which is the one adopted here. The colors in the diagram refer to taxonomic assignments based on Knight, et al., 1960, the rather dated *Treatise of Invertebrate Paleontology*. Taxa previously considered Pleurotomariacea (green) are actually more closely related to the Euomphaloidea (red) or Murchisoniida (blue). Even the torted Bellerophontiforms (orange) are here shown to diphyletic (*Streptodiscus*. For the sake of convenience the Order Bellerophontoidea is here defined as a monophyletic crade that begins at node 10.

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Gastropoda

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            |   `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
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Introduction

Gastropods, the group of mollusks that include the terrestrial snails and slugs and the marine limpets, periwinkles, abalones, whelks, and their relatives, are the largest and most varied class of mollusks, with more than 75,000 extant species in addition to 15,000 fossil forms that are known.

These successful animals are the only class of mollusks to occupy both marine, fresh-water, and terrestrial environments. In the sea, most species are epibenthic, crawling on the surface, but there are some swimming forms as well (some types of Opisthobranchia). Although many gastropods are herbivorous grazers, several groups are active carnivores able to drill through the shell of their victim, or in the case of predatory forms like the Conidae (Neogastropoda) cases swallow it whole through a proboscis.

Most of the gastropods are classified on the characteristics the gill structures and other soft-bodied features. Few distinguishing characters of the shell are used in classification as many are the result of convergent evolution. Although the differences in the shell form may be difficult to recognize, different morphologic groups can generally can be differentiated on characteristics of ornamentation, shell shape, and aperture. The shell of many gastropods can either be external or, less commonly, internal. The difference can often be deduced by the luster of shell material and the presence of other features such as deviations of a structural shell form.

Gastropods are also sometimes known in older books as "Univalves", because they possess a single shell (in contrast to bivalves with two, and chitons with eight). The shell varies greatly from high- and low- spired helical coiled (snail-like) shells, planispirals (coiled in one plane) found in some Paleozoic marine and modern freshwater types, to cap-like limpets. There are many kinds of land slugs and marine sea-slugs which have lost their shell altogether, or have a small internal or vestigial shells beneath the mantle.

The head is well developed (only cephalopods have a more strongly developed head) with a mouth, tentacles, eyes, and other sense organs. In some advanced marine gastropods there is a tube-like structure - a proboscis - with which the animal can capture its prey. The head is more or less continuous with an elongate body. The digestive, reproductive, and other organs are coiled in a spiral which is enclosed in, and is protected by, the shell.

There is usually a muscular foot running the entire length of the ventral (lower) surface of the body. The animal creeps along the flat sole-like lower surface by small waves of muscular contraction, lubricated by slime from mucous glands.

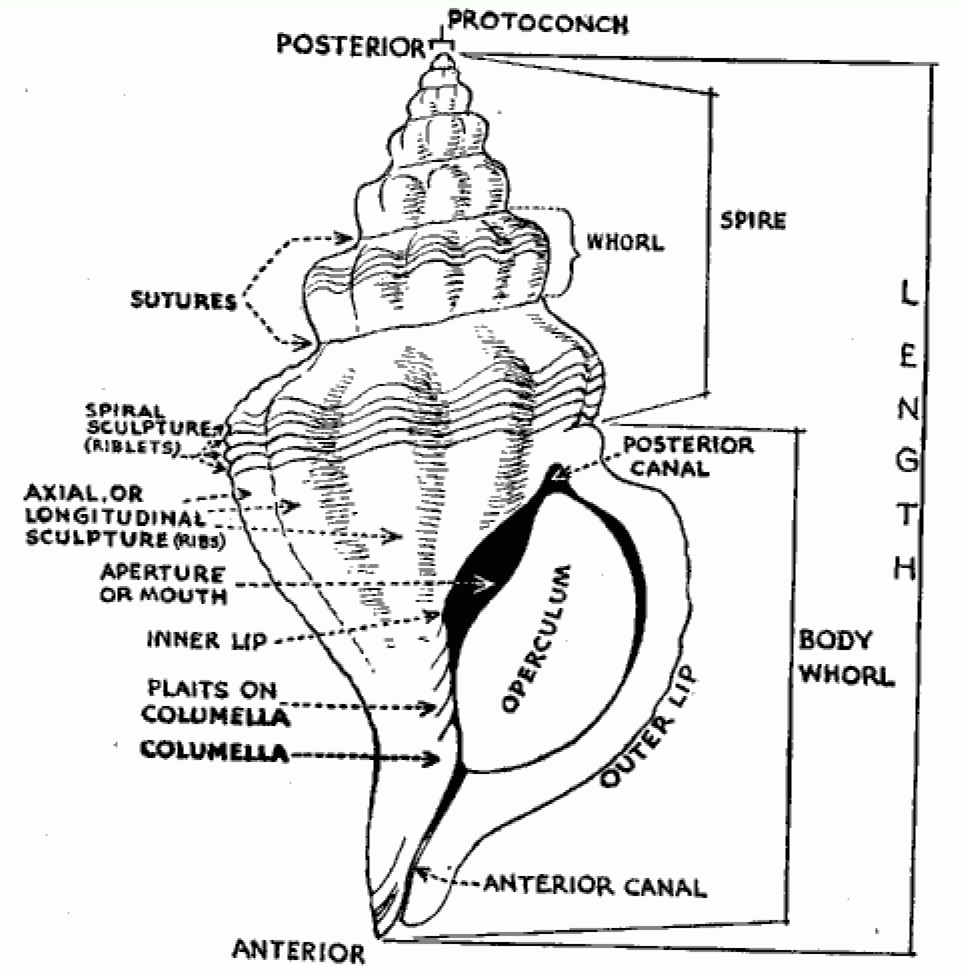
The entire body (or head-foot) may be withdrawn into the last (largest or body) whorl of the shell by retractor muscles and in many marine and some land snails the opening may be closed with a horny or calcareous plug or door called an operculum, which is attached to the posterior dorsal surface of the body. This blocks the opening and protects the animal from predators or other dangers.

This ability to withdraw inside their shells and thus escape predators gave gastropods a great advantage, and they have been incredibly successful since their appearance in the Latest Cambrian right through to the present day.

The Gastropod Shell

Geometrically, the typical gastropod shell is a cone coiled round a central axis as a spiral. The reason the shell is coiled is simple - a high uncoiled shell would be impossible to carry because of its high center of gravity. therefore the shell is coiled and usually tilted. Most shells coil to right (dextral), although a few coil to left (sinistral), and there are even Palaeozoic types (some Euomphalida, especially macluritids) where the spire was "upside down" (hyperstrophic)

The following diagram shows the various parts of the gastropod shell.



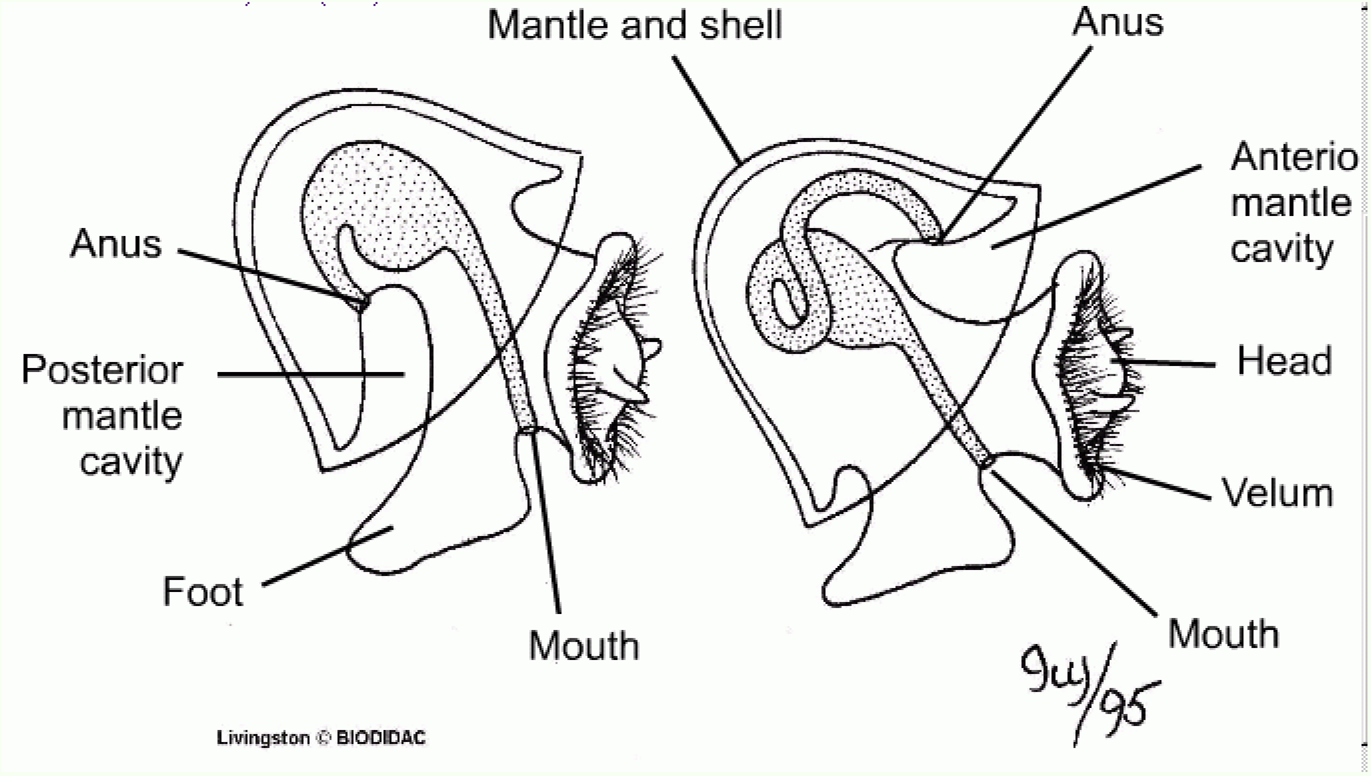
drawing © xxxx by G. J. Browning from *Marine Molluscs of Victoria*

The central axis of coiling is called the *columella* and at the anterior end of the shell forms the inner lip of the mouth opening, called the aperture. In neogastropods it may be drawn out to form with the anterior edge of the mouth a canal (anterior canal) sheathing the proboscis. There is also in some species, a notch between the outer lip and the body-whorl, this is called the posterior canal, for the inhalant siphon. The shape of the spiral varies considerably, as does the form of the aperture. The outer lip may be thickened or sharp and may or may not be indented with "teeth". At the apex of the spiral is the embryonic shell called the *protoconch*; it often has a different form and ornament from the adult shell [Macpherson and Gabriel 1962 p.26]

Torsion

The single unique defining characteristic (or synapomorphy) of the gastropods is a process known as *torsion*. Even though not all gastropods are torted, those that are not have evolved from torted ancestors.

During the development of the planktonic larva, the visceral mass is horizontally twisted nearly 180° in a counterclockwise direction in relation to the lower part of the body. As a result, the mantle cavity, gills, anus, and two nephridopores are rotated from back to front, and are now located in the anterior position, above the head, and the body was no longer symmetrical.



Livingston © BIODIDAC

It is not quite clear why this first happened, more than five hundred million years ago. Walter Garstang in the 1920s proposed that it helps larval veliger pull its head inside its shell (and even wrote this as a poem: "Ballad of the Veliger or how the Gastropod got its Twist"!). Other explanations are that it helps the adult carry weight of shell, or it was an adult adaptation to protect the head and utilize the anterior water current.

Torsion obviously has benefits (including increased water current and allowing the animal to withdraw more deeply into the shell then would otherwise be possible), but it created a number of problems as well, the most serious of which was fouling. With the anus and nephridia in the front of the body, the animal would be dumping its waste on its head. This problem was solved by slit or cleft in the front of the shell, above the mantle cavity. pretorted protogastropods already had a slit in their shell. This faced backwards in the pretorted mollusk, so when the entire shell was rotated through 180° it was at the front, and there was a ready-made solution (a perfect example of pre-adaptation). Thus the inhalant current continued to come in over the head and gills, but instead of making a U-turn and passing out the same way, it flowed up and out through the slit in the shell, taking the waste with it. [Barnes 1980, from Rollins and Batten 1968]

Note that torsion does not imply coiling. The first gastropods evolved from untorted ancestors like *Crytolites* that still had a coiled shell.

Relationships and Evolutionary History

Gastropods have been a stable and constant component of the marine benthic ecosystems since the early Paleozoic. Unambiguous Gastropods first appear in the second half of the Furongian (Dolgellian Age), probably evolving from bellerophontiform "Tergomya" ("monoplacophora") like *Cyrtolites*. Earlier spiral shells attributed to the class, and dating to the early and middle Cambrian, are now considered to be non-molluscan (e.g. *Aldanella*) or non-gastropod (either Helcionellid, tergomyan, or Paragastropod) mollusk.

Like the Cephalopods that also appeared at this time, Gastropods radiated very quickly, but unlike the Cephalopods made it through the end Cambrian mass extinction event with few casualties. These very early (latest Cambrian and earliest Ordovician) forms can in a variety of shell types, including bellerophontiform, discoidal (planispiral), low-spired anistrophical (conventional helically coiled spiral) and hyperstrophic ("upside down" spiral - Macluritina) coiled forms, loosely coiled, and high spired types.

Working out the evolutionary relationships of creatures long-gone is not easy. All these very early forms used to be included under the now redundant taxon "Archaeogastropoda". Also, Dr Wagner's cladistic analysis [Wagner 1999] has shown that many forms previously considered Vetigastropod (Pleurotomarid) are actually members of either the Euomphalida (probably Eogastropoda) or the Murchisoniida (probably Orthogastropoda) [Wagner no date]. The bellerophontiform gastropods he considers to be bi-phyletic, with one group perhaps ancestral to, and another an off-shoot of, a very early paraphyletic assemblage called the Sinuopeidae (latest Cambrian to middle of the Early Ordovician). Of course, it is also possible that the Sinuopeids evolved from torted bellerophontiforms, which in turn developed from untorted bellerophontiforms.

By Carboniferous times gastropod faunas were diverse. Not only were there a large number of marine forms, but some lineages had adapted to fresh water, and the first terrestrial forms appeared. These however were unrelated to the pulmonates of the Mesozoic to recent eras.

Like most other organisms, the gastropods were affected by end-Permian mass extinction event, and a number of groups died out at this time. Many more however survived through to the Mesozoic. A number of new groups flourished at this time, including the Nerineidae - a family of high-spired Mesozoic mesogastropods - and - later in the Mesozoic - the various Neogastropod taxa. The Jurassic and Cretaceous also saw the appearance and radiation of the Pulmonates or fresh-water and terrestrial forms. But the real acme of gastropod evolution was reached in the Cenozoic, continuing until the present, with the great success of the long-siphoned neogastropods which dominate today's gastropod fauna. [Clarkson, 1979, pp.163-64]

Systematics

Gastropod systematics and phylogenetic understanding has undergone radical revision in the last few decades, and the old three-fold classification of Prosobranchia, Opisthobranchia, and Pulmonata, with the Prosobranchia divided into Archaeogastropoda, Mesogastropoda, and Neogastropoda, is no longer accepted by recent workers in this field, who have adopted a cladistic perspective based on more thorough recent research. The terms are however still found in older (and even fairly recent) books, and may still be used as generic categories - especially Linnaean categories. While there have been attempts to reconcile the current paradigm with the Linnaean hierarchy, such an approach is bound to fail, because these are two completely different methodologies. The following presents a cladistic summary:

```
Tropidodiscidae
          Sinuopeidae
                    Bellerophontoidea
                    Eogastropoda
                            "Euomphalida" (paraphyletic grade)
                            Patellogastropoda
                    Orthogastropoda
                           "Murchisoniida" (paraphyletic grade)
                              Neritopsomorpha
                              Vetigastropoda
                              Caenogastropoda
                              Allogastropoda
                                   Heterostrophia
                                    Opisthobranchia
                                    Pulmonata
```

Suggested revised Linnaean classification:

The following is suggested as a very tentative and provisional alternative to the traditional classification. In keeping with the convention of the *Treatise* authors of the volumes on Gastropoda and Cephalopoda, the suffix -*ina* is used for suborders, and -*ida* for orders.

```
Incertae Sedis (primitive forms - Prosobranchia / Archaeogastropoda in part)
                Order "Tropidodiscida" ("Bellerophontina" in part)
                Order Bellerophontida ("Bellerophontina" in part)
                Order Cocculinida (polyphyletic?, may be either Eogastropod or Orthogastropod)

Subclass Eogastropoda (primitive forms - Prosobranchia / Archaeogastropoda in part)
                Order Euomphalida
                Order "Platycerida" (normally a superfamily, see note)
                Order Patellogastropoda (Docoglossa)

Subclass Orthogastropoda (all other gastropods)

        Infraclass unnamed (Prosobranchia in part))
            Superorder unnamed (Archaeogastropoda in part)
```

- Order Murchisoniida
- Order Neritopsina
- Order Neomphalida
- Order Vetigastropoda

Superorder **Caenogastropoda**
  - Order Architaenoglossa
  - Order Neotaenioglossa
  - Order Neogastropoda

Infraclass **Allogastropoda**
  - Order Heterostrophia

Infraclass **Opisthobranchia**
  - Order Architectibranchia
  - Order Cephalaspidea
  - Order Anaspidea
  - Order Thecosomata
  - Order Gymnosomata
  - Order Sacoglossa
  - Order Umbraculomorpha

Infraclass **Pulmonata**
  - Order Systellommatophora
  - Order Basommatophora
  - "Order" Actophila (= Archaeopulmonata?)
  - Order Stylommatophora

note: the Platyceroidea are considered Trochid "Archaeogastropoda" (= Vetigastropoda) by Knight, et al., 1960 and the "Euomphalina" by Jeffery 2001 [following Wagner 1999] However they would seem to differ from ordinary Euomphalids as much as Patellogastropods do, so I have placed them in their own (Linnaean) Order.

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Eogastropoda

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA  (crown group)
            |==Eogastropoda  (paraphyletic or
polyphyletic?)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
```

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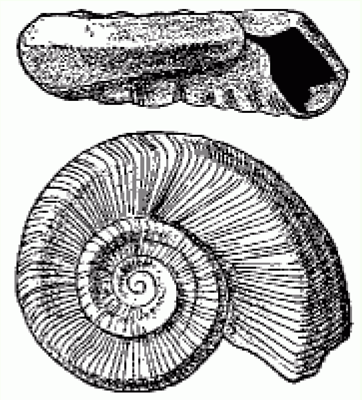
1. Eogastropodae

Introduction

Cellana tramoserica (Holten, 1802)
Patellogastropoda - Nacellina - Nacelloidea - Nacellidae

Patty Jansen - Capricornica Publications



Euomphalus pernodosus
Euomphaloidea - Euomphaloidea - Euomphalidae
diameter about 4 cm
Carboniferous (Late Moscovian) of western Euramerica

image © McGraw Hill Book Company, from Moore, *et al.* 1952, p.306

The clade Eogastropoda was defined by Ponder and Lindberg 1997 to distinguish the most primitive gastropods from their more derived cousins. This was based on the argument that the limpets (Patellacea/Patelloidea/Patellina), originally classified as "archaeogastropods" because of soft-part anatomy [Moore, *et al.* 1952, p.309], and considered specialized descendants of

Pleurotomariaceans, are actually a group of much more primitive survivors from the original gastropod radiation. There are a number of reasons for this. Limpets retain the same docoglossa-type radula as Polyplacophora and Scaphopoda, whereas other "archaeogastropods" have a rhipidoglossa type of radula [Golikov and Starobogatov 1975). They also have much more primitive eyes and other characteristics. Lindberg 1988, Haszprunar 1988, Ponder and Lindberg 1997, Sasaki 1998 and others all argue that the patelloids - now called Patellogastropoda or Doccoglossa - are the sister taxon of all other extant gastropods. Phylogenetic analyses of partial 18S rDNA sequences indicate that the Patellogastropoda comprises a robust clade with high statistical support [M. G. Harasewych, A. G. McArthur, A molecular phylogeny of the Patellogastropoda (Mollusca: Gastropoda)]

Because the Eogastropoda includes not only extant species but also many extinct (mostly Palaeozoic forms, e.g. *Euomphalus*, shown left) as well, most of which look nothing at all like modern limpets, and probably had very different habits as well, it can better be defined cladistically as a "stem group" taxon - i.e. all gastropods more similar to (say) *Patella* than to (say) *Helix*, rather than a "crown group" definition (the common ancestor of all extant limpets and its descendants). For more on cladistics and how this works see this page.

In the Linnaean framework, the Eogastropoda is a subclass, the counterpart of the Orthogastropoda (which includes all other gastropods). Possibly other extinct groups, like the Bellerophontoidea, might belong under their own subclass

Eogastropoda: *Patella* > *Helix*

Range: Latest Cambrian (Late Dolgellian Age) to Recent; Worldwide

Phylogeny: Gastropoda : Orthogastropoda + Eogastropoda : Euomphaloidea ::: Patellogastropoda

Characters: the following primitive soft-body characteristics of the Patellogastropoda may also apply to the earliest Eogastropoda: **$** the shallow mantle cavity; **$** ctenidium without skeletal rods; **$** paired excretory system; **$** simple eye type; **$** position of statocysts, (all from Haszprunar 1988 p.9], **$** primitive-type sperm morphology (Koike, 1985; Healy, 1988; 1996), **$** osphradium lacking true sensory cells; **$** double-layered jaw plate (shared by Patellogastropoda and Cephalopoda) Sasaki 1998, primitively, paired and equal ctenidia and other organs [Knight, et al., 1960], some body asymmetry in later forms.

Taxon Rank: Subclass [Jeffery 2001]

Comment: may be paraphyletic orf polyphyletic as originally defined. Nevertheless there is a similarity between euomphalid and contemporary patellogastropod protoconches.

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Gastropoda

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA   (crown group)
            |==Eogastropoda   (paraphyletic or
polyphyletic)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
```

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1. Euomphaloidea

Introduction

```
o Eogastropoda
`--o Ophiletidae
   |--+-- Macluritoidea
   |  |  ? --Omphalocirridae
   |  |--o Helicotomidae
   |  |  `--+--o Anomphalidae
   |  |      `--o Euomphalidae
   |  |         `--o Pseudophoridae
   |  |  ? --Omphalotrochidae
   |  `--o Lesueurillidae
   |  ? --Planitrochidae
   `--+-- "Lytospiridae"
      `--o Euomphaloidea (in part)
         `--o Raphistomatidae
            `--o Platyceratoidea
```

The Euomphalids (originally Euomphalacea or Euomphalina) are an important Paleozoic clade of low-spired to planispiral gastropods, some of which, like the macluritids, are hyperstrophic. They are very abundant in some Paleozoic formations and include useful index fossils. Moore, *et al.* (1952). Some lived lifestyles like modern gastropods, others it seems were sedentary filter-feeders.

```
         `--o Holopeideae
            `-- Platyceratidae
     ? --Metoptomatidae
         ? -- Patellogastropoda
             ? --Cocculiniformia
```

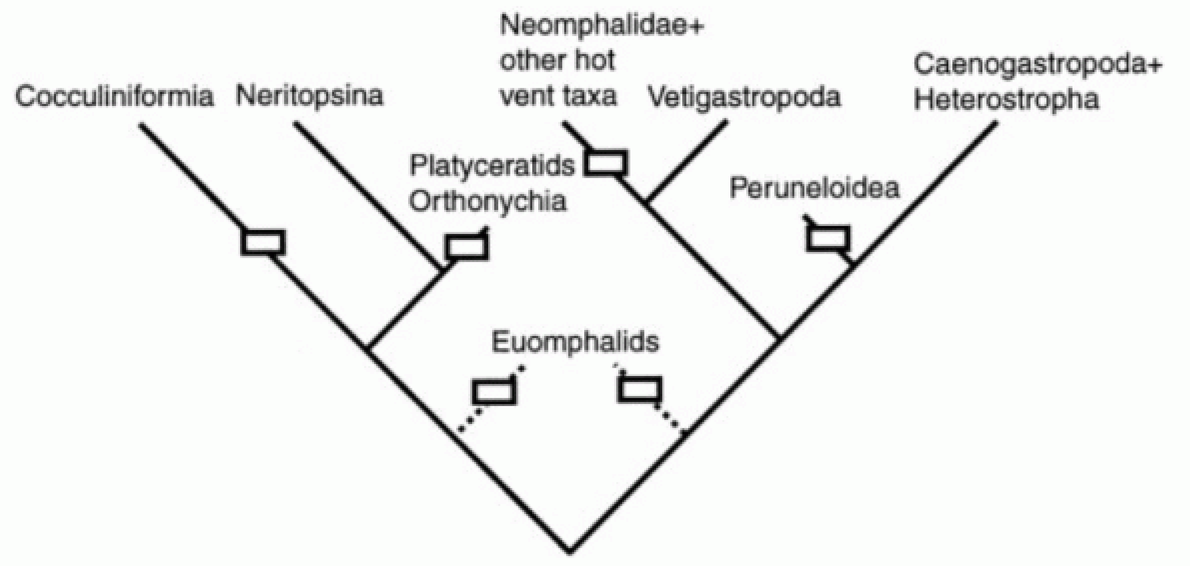
See also the **Euomphalida cladogram** page

The group was originally considered a superfamily of Archaeogastropoda, and according to Knight *et al*. (1954), evolved from macluritids, with which they seem to be clearly related. Linsley & Kier (1984) tentatively place them, along with the Macluritoidea, in the Paragastropoda. But Wagner (1999) derives both groups from ophiletids, although they seem to have diverged very early.

The group as originally defined had two peaks of development, one in the Devonian and another in the Triassic (finally dying out in the Cretaceous) , but these would seem to be actually two distinct stocks. Moore, *et al.* (1952). The Palaeozoic forms are true Euomphalids, whereas the Mesozoic taxa appear to be derived trochoids. Bandel (1988). Examination of shell mineralogy, larval shells, and teleoconchs (adult shells) confirm that the Euomphalacea/Euomphaloidea, like the Bellerophontoidea and other extinct taxa, are polyphyletic. Wagner (2001).

Not only are many species formerly considered Euomphalids not really related, but it seems that other forms that have previously been thought of as having different origins actually are. Studies also indicate that many Paleozoic Palaeotrochoidea (placed in the Trochina -- now included in the Vetigastropoda -- by Knight, *et al.*, 1960) are a polyphyletic assemblage related to the euomphaloids. Wagner (2001). Ponder and Lindberg (1996, 1997) suggest that palaeotrochoids and vet gastropod trochoids are only distantly related. According to Wagner (1999), both palaeotrochoids and traditionally placed euomphaloid planispiral taxa arose at least six times each in the Ordovician and Silurian, mostly within the same clade. Wagner (2001).

Recent study of the the protoconch of Carboniferous euomphalids in far greater detail by Nutzel (2002) reveals that the protoconch (larval shell) less than one planispiral whorl that is umbilicated or openly coiled, before a sudden transition to the teleoconch (adult shell). The euomphalid protoconch is umbilicate (openly coiled) and bilaterally symmetrical. Similar protoconchs are present in Recent species of the Cocculiniformia, the Neomphalidae and the Docoglossa (Patellogastropoda). This conforms a previously suggested close phylogenetic relationship between the euomphalids and extant limpets. The fact that several other Palaeozoic gastropod clades, unlike most modern gastropods, also have an openly coiled initial whorl is remarkable, and it is only the planispiral



Relationships of major extant gastropod clades are largely based on the 50% majority consensus tree of Ponder and Lindberg (1997). Since this does not include a comprehensive phylogenetic analysis, the fossil taxa are included here with reservations. Assignments are based on the resemblance of a few features (e.g. the Peruneloidea resemble caenogastropods in teleoconch shape and the platyceratids have an outer calcitic layer like many neritopsines). Two possible positions of the euomphalids are suggested. Although other possible arrangements might be as likely, it is clear that umbilicate or openly coiled protoconchs (indicated by rectangles) are present in different clades and connected with different teleoconch morphologies. - dendrogram and caption from Nutzel (2002).

shape of the euomphalid protoconch that distingusihes these gastropods. The relevance of the distinctive paleozoic protoconch for the phylogeny and the systematics of the Gastropoda is not yet clear. MAK120621

Euomphalida Dendrogram

The following dendrogram is copied from Mikko Haraamo pages

```
<== o EUOMPHALINA de Koninck, 1881
   |-- Prohelicotoma
   |-- Ophileta subraplana
   `--+-- Ophileta complanata
      `--+-- Lecanospira compacta
         |-- Lecanospira nereine
         `--+-- Barnesella ?lecanospiroides
            |--o Ecculiomphalus Portlock, 1843
            |  |-- Malayaspira rugosa
            |  `--+-- MACLURITOIDEA Fischer, 1885
            |     `--+-- Malayaspira hintzei
            |        |--+--+-- Russospira harrisae
            |        |  |  `-- Ecculiomphalus bucklandi
            |        |  `--o Helicotomidae Wenz, 1938
            |        |     |?- Linsleyella Rohr, 1980
            |        |     |-- Lophonema peccatonica Ulrich, in Purdue & Miser, 1916
            |        |     |--+-- Polehemia taneyensis
            |        |     |  `-- Walcottoma frydai
            |        |     `--+--+--o Ophiletina Ulrich & Scofield, 1897
            |        |        |  |  |-- Oriostoma bromidensis
            |        |        |  |  `--+-- O. sublaxa
            |        |        |  |     `-- O. angularis
            |        |        |  `--o Helicotoma Salter, 1859
            |        |        |     |-- H. tennesseensis
            |        |        |     |--+-- H. planulata
            |        |        |     |  `--+-- H. robinsoni
            |        |        |     |     `-- H. blodgetti
            |        |        |     `--o Palaeomphalus Koken, 1925
            |        |        |        |-- P. ?gradatus
            |        |        |        `-- Helicotoma? sp. [Girvan sp.]
            |        |        `--+--o Anomphalidae Wenz, 1938
            |        |           |  `--o Trochomphalus Koken, 1925
            |        |           |     |-- Trochomphalus ?dimidiatus
            |        |           |     `--+-- Straporillina sp. cf. S. circe (sensu Rohr, 1988)
            |        |           |        `--+-- Grantlandispira christei
            |        |           |           `--o Pycnomphalus Lindstr�m, 1884
            |        |           |              |-- P. acutus
            |        |           |              `--+-- P. obesus
            |        |           |                 `-- Turbocheilus immaturum
            |        |           `--o Euomphalidae de Koninck, 1881
            |        |              |?- Micromphalus Knight, 1945
            |        |              |--o Boucotspira Rohr, 1980
            |        |              |  |-- B. cariniferus [Euomphalopterus cariniferus]
            |        |              |  `-- B. ?ordovicicus [Euomphalopterus ?ordovicicus]
            |        |              |--o Euomphalopterus Roemer, 1876
            |        |              |  |-- E. subcarinatus
            |        |              |  |-- E. alatus
            |        |              |  `--+-- E. togatus
            |        |              |     `--+--+-- E. praetextus
            |        |              |        |  `-- E. undulans
            |        |              |        `--o Spinicharybdis Rohr & Packard, 1982
            |        |              |           |-- S. frenatus [Euomphalopterus frenatus]
            |        |              |           `-- S. wilsoni
            |        |              |--o Poleumita Clarke & Ruedemann, 1903
            |        |              |  |-- P. alata
            |        |              |  `--+-- P. discors
            |        |              |     |-- P. granulosa
            |        |              |     |-- Centrifugus planorbis Bronn, 1834
            |        |              |     |--o Nodonema Linsley, 1968
            |        |              |     |  |-- N. rugosa [Poleumita rugosa]
            |        |              |     |  `-- N. octavia [Poleumita octavia]
            |        |              |     `--+-- Euomphalus Sowerby, 1814
            |        |              |        `-- Straparollus de Montfort, 1810
            |        |              `--o Pseudophoridae Miller, 1889
            |        |                 |?- Elasmonema Fischer, 1885
            |        |                 |-- Streptotrochus lamellosus [Boucotspira [in partim]]
            |        |                 `--+-- Streptotrochus? visbeyensis [Boucotspira [in
partim]]
            |        |                    `--+--o Streptotrochus Perner, 1903
            |        |                       |  |-- S. incisus
            |        |                       |  `--+-- S. lundgreni
            |        |                       |     `-- Hystricoceras astraciformis Jahn, 1894
```

```
            |        |                       `--o Discordichilus Cossmann, 1918
            |        |                          |-- Streptotrochus sp. aff. S. incisus
            |        |                          `--+-- D. gotlandicus [Siluriphorus
gotlandicus]
            |        |                             |-- D. undulans [Siluriphorus undulans]
            |        |                             |--+--+-- D. dalli
            |        |                             |  |  `-- D. mollis
            |        |                             |  `--o Pseudotectus Perner, 1903
            |        |                             |     |-- P. kolmodoni [Discordichilus
kolmodoni]
            |        |                             |     `-- P. comes
            |        |                             `--o Pseudophorus Meek, 1873
            |        |                                |-- P. stuxbergi
            |        |                                `-- P. profundus
            |        `--o Lesueurillidae Wagner, 2002
            |           |-- "Lesueurilla" declivis
            |           |--o Eccyliopterus Remel�, 1888
            |           |  |-- E. regularis
            |           |  `--+-- E. ?princeps
            |           |     `--+-- E. alatus
            |           |        `-- E. owenanus
            |           `--+-- "Lesueurilla" prima
            |              |--o Lesueurilla Koken, 1898
            |              |  |-- "Eccyliopterus" louderbacki
            |              |  `--+-- Lesueurilla infundibula
            |              |     `-- "Eccyliopterus" beloitensis
            |              |--o Mestoronema Wagner, 2002
            |              |  |-- "Lesueurilla" marginalis
            |              |  `--+-- "Lesueurilla" scotica
            |              |     `-- "Lesueurilla" bipatellare
            |              `--o Pararaphistoma Vostokova, 1955
            |                 |-- Climacoraphistoma vaginati
            |                 |-- Climacoraphistoma damesi
            |                 `--+-- Pararaphistoma qualteriana
            |                    `-- Pararaphistoma schmidti
            `--o Asgardaspira Wagner, 2002
               |-- Barnesella measuresae
               `--+-- Lytospira yochelsoni
                  `--+--o Lytospira Koken, 1896
                     |  |-- L. angelini
                     |  `-- L. subrotunda
                     `--+--+-- Lytospira gerrula
                        |  `-- Lytospira ?norvegica
                        `--o EUOMPHALOIDEA de Koninck, 1881
                           `--o Raphistomatidae Koken, 1896
                              |-- Ceratopea canadensis
                              |-- Orospira bigranosa Butts, 1926
                              |--o Bridgeites Flower, 1968a
                              |  |-- B. planodorsalis
                              |  `--+-- B. supraconvexa
                              |     `-- B. ?disjuncta
                              `--+-- Ceratopea ?laurentia
                                 |--+-- Ceratopea pygmaea
                                 |  `-- Ceratopea unguis
                                 `--+-- Pararaphisoma lemoni
                                    `--+-- Helicotoma medffraensis Salter, 1859
                                       `--+--o Scalites Emmons, 1842
                                          |  |-- "Palaeomphalus" giganetus Koken, 1925
                                          |  `--+-- Scalites katoi
                                          |     `--+--+-- Raphistoma tellerensis
                                          |        |  `-- Raphistoma peracuta
                                          |        `--+-- Scalites angulatus
                                          |           `--o Raphistoma Hall, 1847
                                          |              |-- Raphistoma striata
                                          |              `-- Helicotoma gubanovi
                                          `--o Holopeidae Wenz, 1938
                                             |?- Umbospira Perner, 1903
                                             |--o Raphistomina Ulrich & Scofield, 1897
                                             |  |-- R. lapicida
                                             |  |-- R. aperta
                                             |  |-- R. fissurata
                                             |  `-- R. rugata
                                             `--+-- Pachystrophia devexa
                                                |--+-- Pachystrophia contigua
                                                |  `--o Holopea Hall, 1847
                                                |     |-- H. insignis
                                                |     |-- H. pyrene
                                                |     `--+-- H. rotunda
                                                |        `-- H. symmetrica
                                                `--+--o Sinutropis Perner, 1903
                                                   |  |-- Pachystrophia spiralis
                                                   |  |-- Sinutropis ?esthetica
                                                   |  `-- Euomphalus tubus
                                                   `--o Pachystrophia Perner, 1903
                                                      |-- P. gotlandica
                                                      `--+-- Lytospira triquestra
```

```
                                                   `-- Lytospira subuloides
```

Reference(s):

Wagner, P. J., 2002 [1995]: Phylogenetic relationships of the earliest anisostrophically coiled gastropods. --*Smithsonian Contributions to Paleobiology*: Vol. 88, pp. vi-152
[Author notes that scientific material of this article is based on his 1995 Ph.D. dissertation, which is partly outdated]

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note: in keeping with the convention of the *Treatise* authors of the volumes on Gastropoda and Cephalopoda, the suffix -*ina* is used for suborders, and -*ida* for orders. Since the Euomphalida are here considered of ordinal rank, the previous suffix -ina has been changed accordingly

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Macluritoidea

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA  (crown group)
            |==Eogastropoda  (paraphyletic or polyphyletic)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
```

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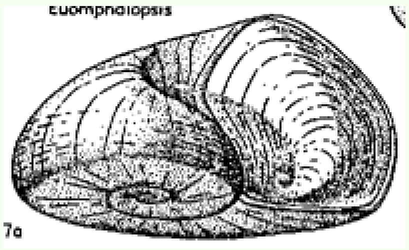
1. Macluritidae
2. Macluritoidea

Introduction

Earth History Resources - image South Dakota School of Mines and Technology - Museum of Geology

The Macluritids are a unique but short-lived group of extinct mollusks that include some excellent guide fossils in Ordovician rocks [Moore, *et al.* 1952, p.302]. They have been variously identified as archaeogastropods, paragastropods, and eogastropods; either ancestral to, or closely related to, the Euomphaloidea, and are limited entirely to the Ordovician, being most common in the early and early-middle part of the period.

Left Handed or Hyperstrophic?



Maclurites logani (Salter)
diameter about 10 cm
Sandbian, Late Ordovician of Laurentia
(Quebec)

image © xxxx Knight *et al*., 1960 p.***I***188

The Macluritid shell is very distinctive, and nothing at all like the shell of any extant gastropod. One side of the shell is nearly flat, and the opposite side is concave because of the wide umbilicus.

If the umbilicate side is directed downward and the flat side upward, this gives the impression the shell is sinistral or a left-handed spiral, because the aperture when held toward the observer is on the left.

The heavy calcareous operculum tells a different story. The operculum is often preserved as a fossil, both apart from the rest of the shell, and also fitting snugly in the aperture. While some opercula grow concentrically, in the case of *Maclurites* it is in a spiral. A spiral can be either left or right-handed, and can also be used to establish the direction of the coiling of the shell to which it belongs, regardless of shape. This is because it is opposite that of the rest of the shell. So the spiral of the operculum of a dextral (right-handed) snail is invariably counterclockwise, while that of a sinistral shell is the opposite. From the shape of Macluritid opercula, we know that Macluritids are dextral shells with a depressed (sunken or downward pointing) spire, not left-handed shells with a normal elevated one. The flat side is therefore (logically) the base of the shell [Moore, *et al.* 1952, p.302].

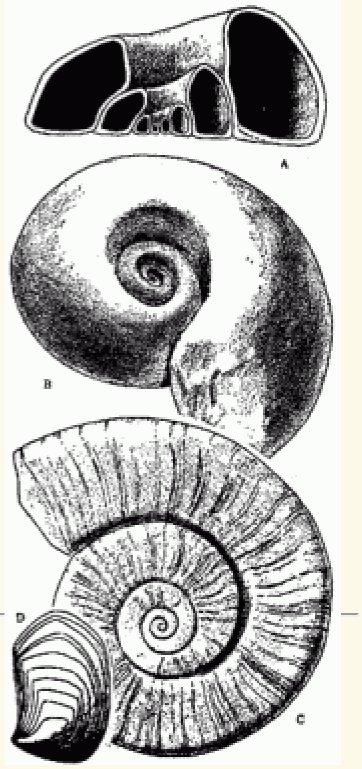
Lifestyle

The Macluritids were almost certainly sedentary, resting in quite water with the base on the seafloor, and living as suspension feeders sweeping up food particles with cilia (or possibly, although much less likely, mucus nets). This was clearly a very successful adaptation, as the group is very abundant in the Ordovician rocks.

This same lifestyle was also adopted independently by the Mimospirida and Euomphaloidea, and so the filter feeding habit continued throughout the Paleozoic (although the Macluritids themselves became extinct at the end of the Ordovician). But whereas the macluritids rested with their *right* (flat or base) side on the substrate so that the spire is down, the Mimospirid Clisospiridae rested their *left* side against the substrate so that the spire is upwards. [Linsley and Kier 1984]

Gastropods or Paragastropods?

The Macluritids were originally considered a superfamily of Archaeogastropods, and according to Knight *et al* 1954 gave rise to the Euomphaloidea, with which they are usually associated. However on the basis of shell form and inferred water flow patterns, Linsley and Kier 1984 proposed the Class Paragastropoda, including the Pelagiellida, the Mimospirida, the Macluritidae, and tentatively the Euomphaloidea, as untorted (and hence non-Gastropod) molluscs. Runnegar, 1983 suggested a similar phylogenetic scheme, according to which the Macluritoidea and other gastropods independently arose from untorted pelagiellids and subsequently acquired torsion independently. But flow-tank studies by Morris (1991) indicate that the shell morphology of *Maclurites* would encourage Bernoulli effects and thus facilitate suspension feeding, but only if it was a torted mollusk [Wagner 2001]. And cladistic analyses by Wagner 1999 relate the Macluritoidea to other euomphaloid gastropods. The protoconchs of macluritids, which could help resolve this question, are still unknown.



Maclurites magna LeSuer
showing cross-section (top), apical (upper) view, base view, and operculum
shell diameter about 7 cm
Chazy = Darriwilian Middle Ordovician of Laurentia

image © McGraw Hill Book Company, from Moore, *et al.* 1952, p.299,

Macluritoidea:

Stratigraphic Range: Ordovician

Phylogeny: ?Paragastropoda/Gastropoda/Eogastropoda Euomphalida **:** Macluritoidea

Characteristics: Rather large, **$** hyperstrophic shells with radial apertures. **$** Aperture rather elongated with angulation at upper surface that is presumed excurrent. **$** Base flattened or gently protruding. [Linsley and Kier 1984 p.251]

Taxon: Superfamily Macluritoidea Fischer, 1885

Macluritidae :

Stratigraphic Range: Ordovician

Phylogeny: see Macluritoidea

Characteristics: Same as Superfamily.

Taxon: Family Macluritidae Fischer, 1885

Genera included: - *Palliseria* Wilson, 1924; *Maclurites* Lesueur, 1818; *Macluritella* Kirk, 1927; *Teiichispira* Yochelson & Jones, 1958.

Notes: The superfamily Macluritoidea includes only the single family Macluritidae (the Onychochilidae are also included under the Macluritoidea by Knight, *et al.*, 1960 but are transferred to the Paragastropoda by Linsley and Kier 1984, Wagner 1999's outgroup analysis also supports the Onychochilidae placement). Less than a dozen genera are known, typified by *Maclurites*. Most of the shells are large, and all are planispiral or very low conispiral, being either tightly or loosely coiled.

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Unit Back | Clade Down: Vetigastropoda Neritimorpha, Caenogastropoda Heterobranchia | Glossary | Unit Next

Orthogastropoda

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA  (crown group)
            |==Eogastropoda  (paraphyletic or
polyphyletic)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
```

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1. Macluritidae
2. Macluritoidea

Introduction

Orthogastropoda:

Range: from the Late Carboniferous (Dolgellian)

Phylogeny: Gastropoda **:** Eogastropoda + * **:** Murchisoniida **:::** Neritopsida + Vetigastropoda + Cocculiniformia (may be polyphyletic?) + Apogastropoda

Characters: **$** Plexo(rhipido) glessate buccal apparatus; pin-hole eyes; **$** osphiadia with sensory cells; **$** statocysts ventrally situated (all from Haszprunar 1988 p.9],

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Patellogastropoda: the Limpets

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA  (crown group)
            |==Eogastropoda  (paraphyletic or
polyphyletic)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
```

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1. Patellogastropoda

Introduction

The true limpets (Patellogastropoda) are a familiar site to beachcombers and visitors to the seashore, clinging tenaciously to rocks in the intertidal zone in countless numbers, or in shallow rock pools. The shell is a simple cap shape, of which there is no sign of coiling even in the protoconch, and there is a reduction or even loss of gills among the various lineages. The mantle and shell overhang produce a

```
o Euomphaloidea
`-+- ??? Metoptomatidae
  `-o Patellogastropoda
    |--o Lepetopsina
    |  |--Lepetopsidae
    |  `--Neolepetopsidae
    |--o Patellina
    |  |--Patellidae
    |  `--"Scutellastriids"
    `--o Nacellina
       |-- Nacelloidea
```

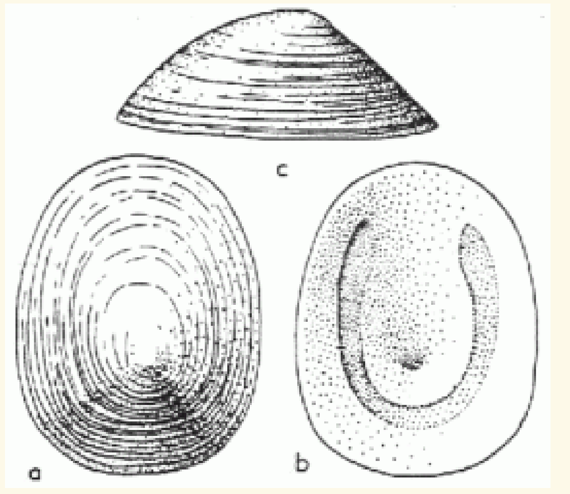
```
        `--o Acmacoidea
           |-- Lepetidae
           |-- Acmaeidae
           `-- Lottiidae
     ? Cocculiniformia
```

distinct groove on each side between the foot and the mantle edge. Barnes (1980).

Patellogastropoda seem to have evolved from Euomphalids, possibly as part of the general movement of life colonizing the littoral niche. Like the chitons, they are a primitive molluscan type that found refuge from predators in the harsh intertidal environment. If one includes the Metoptomatidae, then the group first appeared in the Middle Ordovician (Knight, *et al.*, 1960), otherwise the Patellogastropoda date back no further than the Middle Triassic, which is when several extant families seem to appear. The term "true limpets" is used here to distinguish these gastropods from several other unrelated lineages which also developed a limpet-shell morphology.

Descriptions

Metoptomatidae:



Lepetopsis levettei (White 1882)
height 1.2 cm; diameter 3 cm
Carboniferous (Vis�an of Western Euramerica (Indiana)

image © xxxx Knight, et al., 1960 p.***I***232

Stratigraphic Range: Middle Ordovician (Darriwilian) to Middle Permian (Knight, *et al.*, 1960)

Phylogeny: Euomphaloidea? **:::** Metoptomatidae **:::**??? Patellogastropoda

Characteristics: shell limpet-shaped or weakly endogastrically curved; horseshoe-shaped muscle scar with anterior opening not closed by pallial line, nature of inner shell layers and possibly coiled protoconch imperfectly known. Knight, *et al.*, (1960).

Taxon Rank: Family. Knight, *et al.*, (1960)

Notes: Golikov & Tarobogatov (1975) place the Metoptomatidae among the Helcionellida on the basis of conchological similarity. If so, this means that the Metoptomatids are the last surviving Helcionelloids, and not gastropods at all. However the single Metoptomatid muscle-scar is nothing like the multiple Trybliidid-like muscle scars known from the supposed Helcionellid *Scenella*. Knight, *et al.*, 1960 tentatively include the Metoptomatidae among the Patellina, and Jeffery (2001) follows suit. There is a gap of several tens of millions of years between the Middle Permian when the last Metoptomatids lived, and the Middle Triassic when the true limpets appear. If the Metoptomatidae are Patellogastropod ancestors then this is a paraphyletic group that would seem to have given rise to later forms at the end of Permian. It is just as likely however that this is a distantly related, or completely unrelated, taxon

---

Patellogastropoda:

Stratigraphic Range: Middle Triassic to Recent

Phylogeny: Euomphaloidea (or Metoptomatidae?) **:::** + ?Cocculiniformia + Patellogastropoda **:** + Lepetopsina + Patellina + Nacellina

Characteristics: $ lowest number of chromosomes (9 pairs) ; $ pallial gills, $ "wart-organ," $ rectum outside of pericardium, $ loss of gonoducts, style and gastric shield (Lindberg, 1988); $ Salivary glands compact with ducts; $ loss of right clenidium; $ hypobranchial glands reduced; $ osphradium of distinct type close to the "wart-organ"; (all from Haszprunar, 1988], ***note***: Some or all of these characters may also pertain to Eogastropoda as a whole; predominantly intertidal and shallow nearshore habitats, global, cap-shaped shell (Lindberg, 1988).

According to Sasaki (1998), the Patellogastropoda are characterized (including plesiomorphic primitive characters) by:

> 1) anteriorly pointed shell apex, 2) symmetrical protoconch, 3) shallow pallial cavity restricted to head region, 4) operculum absent in post-larval stage, 5) horseshoe-shaped shell muscle that is constricted into bundles and connected anteriorly by pallial muscle, 6) shell muscle penetrated by blood vessels from visceral sinus, 7) retractile pallial tentacles, 8) eyes within cephalic tentacles, 9) open eyes without vitreous body, 10) symmetrically paired osphradia of "wart-organ" type on pallial floor (absent in Lepetidae, Acmaeidae, and Neolepetopsidae), 11) ctenidium post-torsional left only (in Acmaeoi-dea), 12) ctenidium (if present) lacking skeletal rods, 13) hypobranchial gland absent, 14) secondary circumpallial gills (in Patelloidea and some lottiids), 15) single bilamellate, double-layered jaw, 16) anterior wings of jaw associated with inner lips, 17) posterior wings of jaw bound to odontophore, 18) licker well developed, 19) dorsal protractor muscles of odontophore present, 20) ventral approximator muscle of odon tophore cartilages two-layered, 21) transverse labial muscles present, 22) docoglossate (= stereoglossate) radula that is longitudinally inflexible on bending plane, 23) greatly reduced or completely lost central tooth, 24) lateral teeth with broad bases firmly fixed on basal plates (except Lepetidae and Neolepetopsidae), 25) mid-esophagus with lamellar folds, 26) simplification of stomach (loss of gastric shield and gastric caecum; reduction of sorting area), 27) single auricle, 28) rectum not passing through pericardium or ventricle, 29) muscular bulbous aorta within pericardium, 30) two unequal kidneys (smaller left and much larger right), 31) gonoduct extending from left side and connected to right kidney, 32) labial ganglia inter connected by labial commissure, and 33) statocysts on outer sides of pedal ganglia.

Taxon Rank: Order (Lindberg, 1988).

Links: Limpets (Marine Ecology Online Habitat Series); Molluscs - Limpets (Australian Seashores); Limpets (Australian Museum);

Lepetopsina:

Stratigraphic Range: no fossil record known

Phylogeny: Patellogastropoda **:** Metoptomatidae + Lepetopsina + Patellina + Nacellina

Taxon Rank: Suborder (Lindberg, 1988).

Characteristics: Deep-water forms

Patellina:

Stratigraphic Range: ? Jurassic or Early Cretaceous II (Albian) to Recent (Lindberg, 1988).

Phylogeny: Patellogastropoda **:** Lepetopsina + Patellina + Nacellina

Characteristics: $ Concentric and radial foliated shell structure; $ loss of prismatic outer layer, predominantly intertidal, tropical-temperate seas.

Patella vulgata
from Southwick beach, Sussex
© Andy Horton (photographer) and the British Marine Life Study Society [cropped from original image]

Taxon Rank: Suborder (Lindberg, 1988).

Contains: family Patelliidae

Notes: These limpets strikingly parallel the chitons, which are also adapted for life on rocky shores. In *Patella*, a widespread intertidal genus, secondary gills have formed as folds of the mantle, and project into the pallial groove along the side of the body. The ventilating current enters and leaves laterally in the vicinity of each gill. Barnes (1980).

Like chitons with which they share a very similar lifestyle, these shy animals move about slowly at night, grazing on algae and other microorganisms encrusting the rock surface

Links The Patella Site - all about the family Patellidae

Nacellina:

Stratigraphic Range: Middle Triassic to Recent (Knight, *et al.*, 1960).

Phylogeny: Patellogastropoda **:** Lepetopsina + Patellina + Nacellina **:** Nacelloidea + Acmacoidea

Characteristics: **$** Reduced terminal chromosome, **$** reduction of inner radular tooth field, invasion of polar regions and deep sea. [Lindberg, 1988 p.38]

Taxon Rank: Suborder [Lindberg, 1988]

Scurriopsis top view

Scurriopsis side view

Scurriopsis neumayri Gemmellard 1879
height 1.5 or 2 cm; diameter about 2 or 3 cm
Lower Lias (Early Jurassic (Hettangian/Sinemurian)) of European Laurasia (Sicily)

image © xxxx Knight, et al., 1960 p.*I*233

Nacelloidea:

Stratigraphic Range: Eocene to Recent [Knight, *et al.*, 1960 p. *I*235]

Phylogeny: Nacellina **:** Acmacoidea +

Characteristics: **$** Reduction of crossed-lamellar layers. Nacellidae : Loss of concentric crossed-lamellar layer. [Lindberg, 1988 p.38]

Taxon Rank: Superfamily and Family

Notes: Twelve species of *Nacella* are known; they are Antarctic or subantarctic in distribution and live attached to large seaweed. Thirty species of *Cellana* are found on intertidal rocks in the indo-Pacific. Some species brood their young, which upon hatching simply crawl away [Rosenberg 1992 p.30].

Cellana tramoserica (Holten, 1802)
length up to 5 or 6 cm
South-East Australia

image © Keith Davey Life on Australian Seashores

Acmacoidea:

Stratigraphic Range: Middle Triassic to Recent [Knight, *et al.*, 1960 p. *I*233]

Phylogeny: Nacellina **:** Nacelloidea + **:** Lepetidae + Acmaeidae + Lottiidae

Characteristics: **$** 10 pairs of chromosomes, **$** nuchal cavity gill, **$** loss of pallial gill **$** 1 pair marginal teeth. [Lindberg 1988 p.38]

Taxon Rank: Superfamily [Lindberg 1988]

Lepetidae:

Stratigraphic Range: Miocene to Recent [Knight, *et al.*, 1960 p. *I*235]

Phylogeny: Acmacoidea **:** Acmaeidae + Lottiidae +

Characteristics: **$** Fusion of lateral teeth, **$** loss of nuchal cavity gill, **$** loss of osphradial ganglia. [Lindberg 1988 p.38]

Taxon Rank: Family [Lindberg 1988]

Notes: These animals, which live in polar and deep water with some living as deep as 3400 meters. There are seven genera altogether. [Rosenberg 1992 p.29]. A typical form, *Lepeta*, lack gills, and gas exchange occurs across the general mantle surface. [Barnes 1980 p.331]

Acmaeidae:

Stratigraphic Range: ?Triassic to Recent [Knight, *et al.*, 1960 p. *I*233, but most of these actually belong under the Lottiidae]

Phylogeny: Acmacoidea **:** Lepetidae + Lottiidae +

Characteristics: **$** Simplified basal plates, **$** V-ed radular rows, **$** loss marginal teeth, temperate and deep water. [Lindberg 1988 p.38]

Taxon Rank: Family [Lindberg 1988]

Notes: Most species previously placed in this family have since been transferred to the Lottiidae. Only ten species remain placed here, most of which go under the genus *Pectinodonta*, a genus of small deep-sea blind forms. The only other species is *Acmaea mitra* [Rosenberg 1992 p.29]

Acmea mitra Rathke, 1833
length 3 cm
Aleutian Islands to Baja California
from Marine Ecology Online Habitat Series - Limpet Relatives
The pink color is from algae on which the animal feeds

image © xxxx by Gotshall, D.W. 1994. *Guide to Marine Invertebrates Alaska to Baja California*. Sea Challengers, Monterey, CA

Lottiidae:

Stratigraphic Range: Middle Triassic to Recent [Knight, *et al.*, 1960 p. *I*233]; *Lottia*: Late Pliocene to Recent [Lindberg 1988 p.45]

Phylogeny: Acmacoidea **:** Lepetidae + Acmaeidae +

Lottia pelta
average diameter 2 cm
from Marine Ecology Online Habitat Series - Shield Limpet

image © xxxx from Maclachlan, D., and Ayers, J. 1979. *Sea Creatures*. Naturegraph, CA.

Characteristics: $ Loss of foliated shell structure. [Lindberg 1988 p.38]

Taxon Rank: Family [Lindberg 1988]

Notes: There are about 100 extant species, which range from 12 mm to 10 cm in size, and in shape from flattened to deep. Most live intertidally, although some live on sea grasses. The family has worldwide distribution, although the greatest diversity is on the west coast of North America. Rosenberg 1992. These animals possess only the left gill, which extends to the right side of the body. The inhalant current enters the mantle on the left side, some of the current flows in the left lateral mantle groove; the rest over the gill and then down the right mantle groove, before the two exhalant streams converge and exit posteriorly. [Barnes 1980 p.331]

Systematics

```
Order Patellogastropoda Lindberg, 1986 (=Docoglossa)
 incert� sedis
        Incert� sedis
                 Family ?Metoptomatidae Wenz, 1938

 Suborder Lepetopsina
          Superfamily Lepetopsoidea
                Family Lepetopsidae McLean, 1990
                Family Neolepetopsidae McLean, 1990

 Suborder Patellina von Ihering, 1876
          Superfamily Patelloidea Rafinesque, 1815
                Family Patellidae Rafinesque, 1815
               "Scutellastriids" (informal grouping)

 Suborder Nacellina, Lindberg 1988
          Superfamily Nacelloidea Thiele, 1891
                Family Nacellidae Thiele, 1891

         Superfamily Acmacoidea Forbes, 1850
               Family Lepetidae Dall, 1869
               Family Acmaeidae Forbes, 1850 (= Acmaeidae Carpenter, 1857)
               Family Lottiidae Gray, 1840
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The Gastropod Radula

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA  (crown group)
            |==Eogastropoda  (paraphyletic or
polyphyletic)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
```

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Glossary
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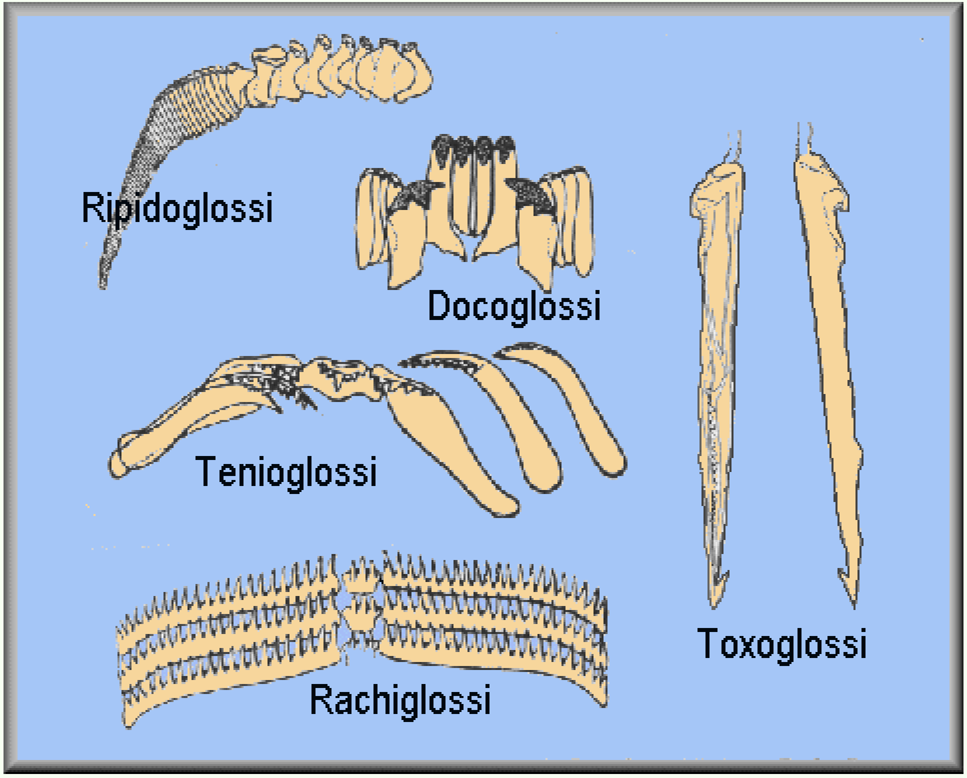
The following sketch of different types of radula is from Radula System



Description of Radula Types

The following description is taken from Lindner 1975 pp.21-22, (I have added some comments in brackets) and constitute a rough evolutionary sequence (apart from the Ptenoglossan condition which represents a specialized side-branch):

> "In the **docoglossan** radula **[4]** above, there is one usually small central tooth, flanked by 1-3 laterals and a few (3 at the most) hooked marginals. (This is the most primitive radula type, and we could assume it represents the plesiomorphic condition, such as would be possessed by the first molluscs (Eogastropoda, also Polyplacophora **[7]**))
>
> In the **rhipidoglossan** radula, **[5]** there is a large central tooth, flanked on each side by five laterals and numerous closely packed marginals (the rhipidoglossan radula marks an improvement over the primitive docoglossan type with a greater number of small side-teeth [Vetigastropoda, Neritomorpha]).
>
> In the **taenioglossan** radula (**[1]**, **[3]**, **[6]**, above), the central tooth is flanked on each side by one lateral and two marginal teeth (characteristic of the majority of Mesogastropoda);
>
> In the **ptenoglossan** radula has no central tooth but a series of several uniform, pointed teeth (Epitoniodea)
>
> In the **stenoglossan** or **rachiglossan** radula **[2]**, has one central tooth and one lateral tooth on each side (most Neogastropoda)
>
> in the **toxoglossan** radula **[8]** each row has only two teeth of which only one is in use at a time. These teeth are very long and pointed, with venom channels and barbs, and are not firmly fixed to the basal plate. The teeth can therefore be individually transferred to the proboscis and ejected into the prey as a sting (Conoidea)."

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Gastropoda: Systematics

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA  (crown group)
            |==Eogastropoda  (paraphyletic or
polyphyletic)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
```

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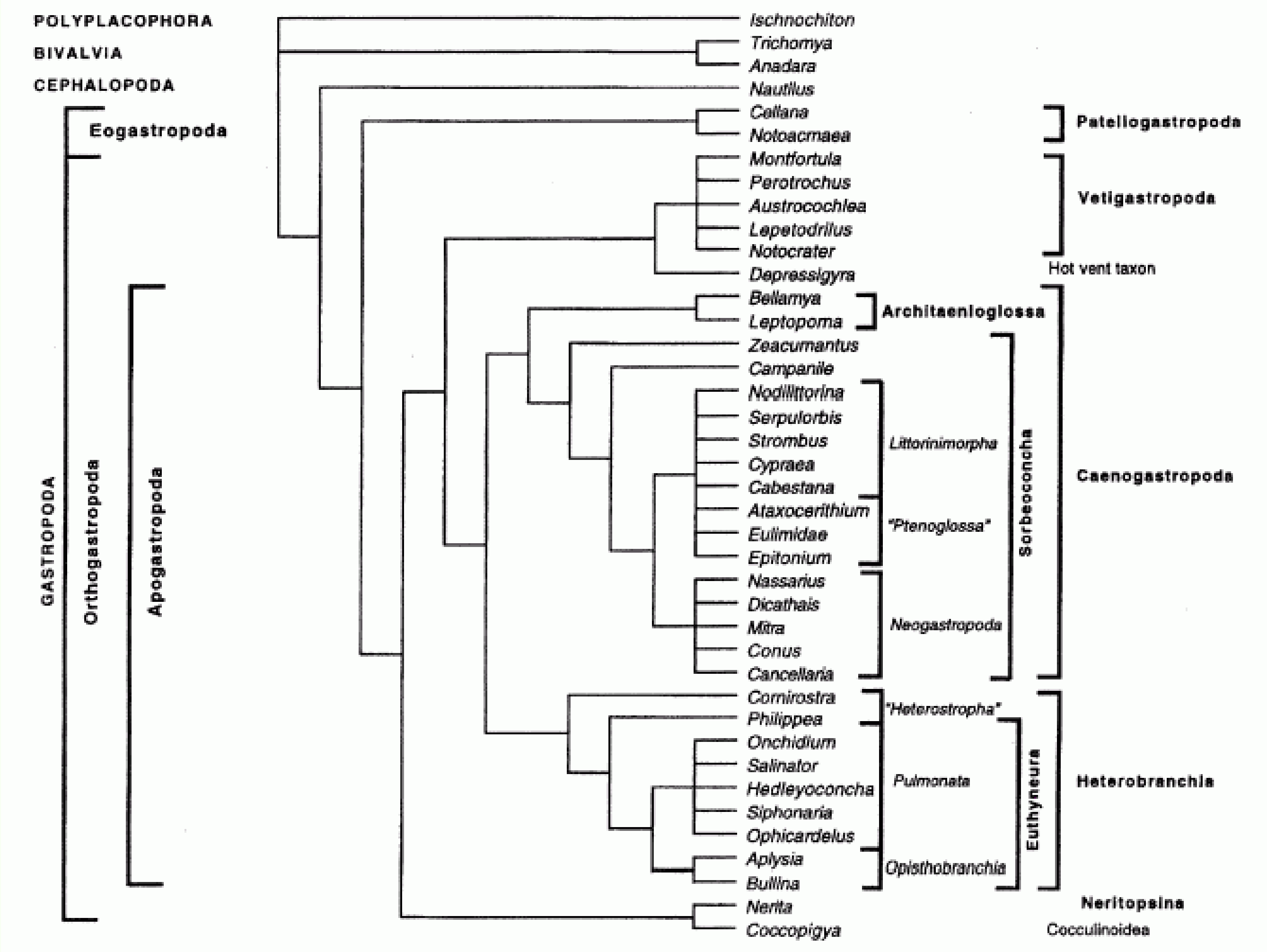
While there were a number of 19th century studies of gastropod relationships using fossil taxa, a consensus view about gastropod phylogeny - based on both fossil and extant forms (i.e. paleontology and neontology) - did not develop until the early 20th century, (e.g., Wenz, 1938; see also Knight, et al., 1960) and this continued basically until the 1980s. In this interpretation, Gastropods were classified into either two or three subclasses - the *Prosobranchia* or *Streptoneura* (mostly marine, torted (so the nervous system is twisted in a figure-8 shape and the gills are in front of the heart), the *Opisthobranchia* (marine, detorted with a single gill behind the heart, internal or absent shell), and *Pulmonata* (also detorted, lungs instead of gills, freshwater or terrestrial), the latter two also being grouped together as the subclass *Euthyneura*, having undergo detorsion and regained bilateral symmetry. The Prosobranchia in turn have been divided into *Archaeogastropoda* (most primitive, including many Palaeozoic types), *Mesogastropoda*, and *Neogastropoda* (most advanced types); the latter two groups being combined as the*Caenogastropoda*. It was assumed that Pleurotomarioid Archaeogastropods are the most primitive living group, these having arose from bilaterally symmetrical bellerophontid ancestors and were barely changed since the Paleozoic. As well as the Pleurotomarioidea, the archaeogastropods included Patelloidea, Neritoidea, and Trochoidea, as well as the extinct Bellerophontoidea and Euomphaloidea/Macluritoidea. With the exception of the latter superfamily/suborder, fossil taxa either were lumped into modern groups (e.g., the Platyceratoidea with the Trochoidea) or were considered their ancestors (e.g., the Loxonematoidea relative to Caenogastropods and the Subulitoidea relative to neogastropods [Knight, et al., 1960].

In the last couple of decades however, the discovery of completely new groups, such as deep water hot-vent (the "black smokers") taxa, along with adoption of a neontological (and later paleontological)cladistic analysis, led to radical revisions in the tidy three-fold schema [Wagner 2001]. Phylogenetic analyses of extant groups have showed that many of these taxa diverged early in gastropod history [Haszprunar 1988; Ponder and Lindberg, 1997; Sasaki, 1998; Colgan, et al., 2000], while study of fossil taxa shows that many Paleozoic species attributed to the Pleurotomarioidea and the Trochoidea are actually polyphyletic assemblages derived from euomphalid and murchisoniid gastropods, and other groups like the Bellerophontoidea, Euomphaloidea, and Subulitoidea are likewise polyphyletic [Wagner 1999, 2001]

While the old three-fold classification can still be found in many books, it is no longer consider valid by many workers in this field. The Prosobranchia and Archaeogastropoda have been shown to be simply grades united by shared primitive characteristics. In addition they include such a diverse range of gastropod groups as to be almost meaningless. The Mesogastropoda taxon also has been rejected; first divided into two distinct groups, the Architaenoglossa (being more primitive), and the Neotaenioglossa [Haszprunar 1988], and then the Neotaenioglossa shown to be paraphyletic (since some forms gave rise to the Neogastropoda) [Ponder and Lindberg, 1997], and it is speculated that the Opisthobranchia may be likewise, having given rise to the Pulmonata [Colgan, et al., 2000], although evidence is still somewhat controversial on this point.

The following cladogram by Ponder and Lindberg 1997 represents the most popular current hypothesis of gastropod relationships.



Independent analysis by Sasaki, 1998 of the Archaeogastropoda alone came up with a very similar picture.

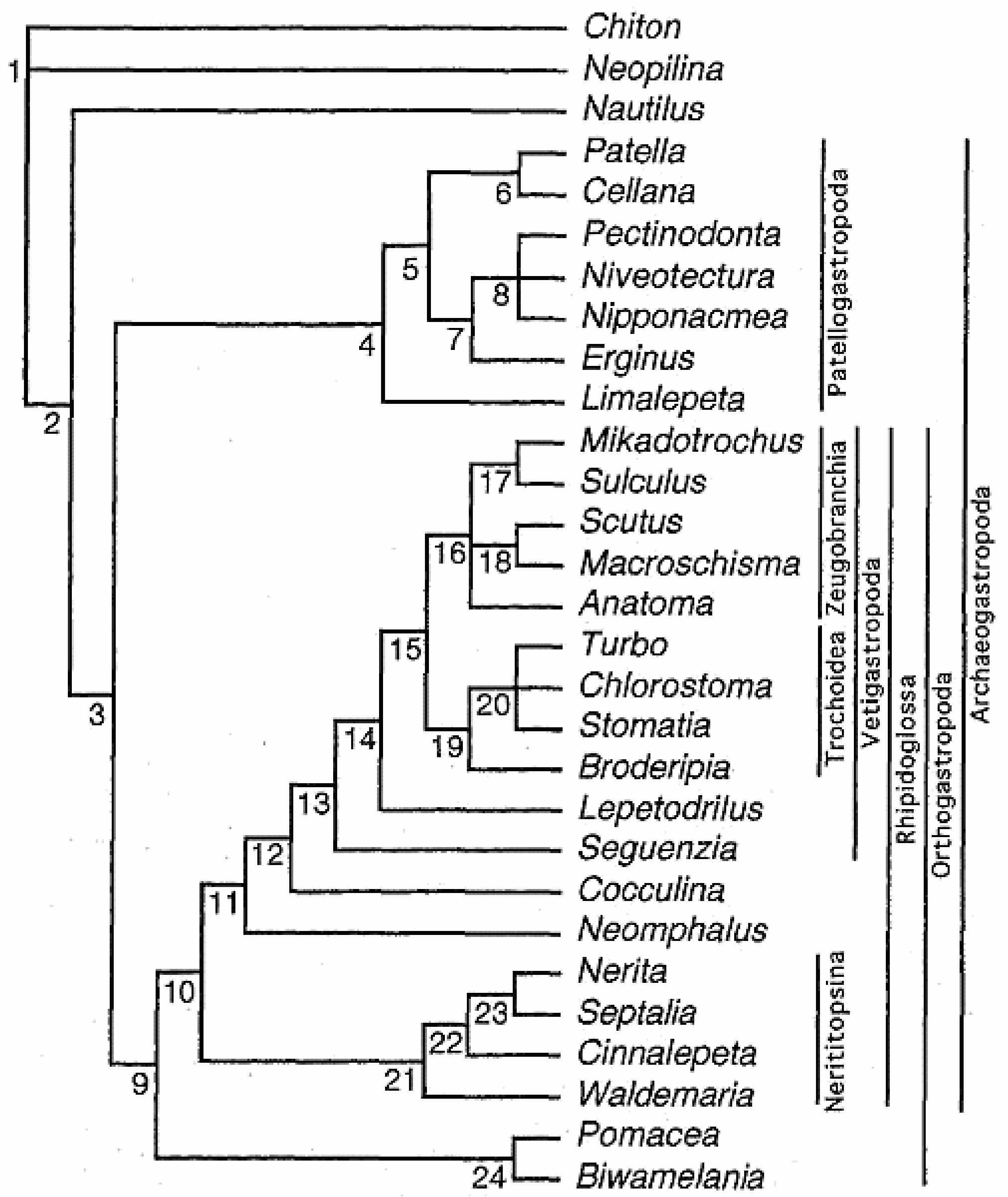


Fig. 104. Strict consensus tree of four most parsimonious trees. Higher taxonomic names are indicated on the right side of the tree.

It should be noted however that molecular evidence does not seem to support the monophyly of the Eogastropoda [Colgan, Ponder, & Eggler 2000], even if other cladistic analysis does. So even these diagrams may warrant revision and modification.

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Gastropoda: Dendrogram

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA  (crown group)
            |==Eogastropoda  (paraphyletic or
polyphyletic)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
```

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Gastropod phylogeny is in near total dissaray. For organizational purposes only, we will follow this cladogram:

```
Helcionelloida (paraphyletic)
|==Rostroconchia
|   `--Scaphopoda
|--Bivalvia
`--+--Paragastropoda
   |  |--Pelagiellida (= Pelagielloidea)
   |  `--Mimospirida (= Onychochiloidea)
   `--+--Tergomya (paraphyletic)
      |-?Bellerophontoidea?
      `--Gastropoda (crown group)
         |--Eogastropoda
         |  `--Euomphalida (=-na?)
         |     |?--Macluritoidea
         |     `--+--Euomphaloidea
         |        `--Patellogastropoda (stem group)
         |           `--Metoptomatidae
         `--Orthogastropoda
            ?= Sinuopeidae)
            |-? Murchisoniida
            |--Neritopsina
            |  |--Neritoida
            |  `--+--Cocculinoidea
            |     `--Vetigastropoda
            `--APOGASTROPODA
               |--Caenogastropoda
               |  |--Architaenioglossa
               |  `--Sorbeoconcha
               |     |--Neogastropoda
```

```
|     `--everything else
`--HETEROBRANCHIA
   |--Opisthobranchia
   |  |--Sacoglossa
   |  `--+--Cephalaspidea (followed by various others)
   |     `--Nudibranchia
   `--PULMONATA
      |--Systellommatophora
      `--+--Basommatophora
         `--+--Acteophila
            `--Stylommatophora
```

This scheme reflects some elements found in the following references:

Grande, C, J Templado, JL Cervera & R Zardoya (2004), *Molecular phylogeny of Euthyneura (Mollusca: Gastropoda)*. **Mol. Biol. Evol.** 21: 303�313. **WWW**

Ponder, WF & DR Lindberg (1997), *Towards a phylogeny of gastropod molluscs: Analysis using morphological characters*. **Zool. J. Lin. Soc.** 119: 83-265.

Sasaki, T (1998), *Comparative anatomy and phylogenyof the Recent Archaeogastropoda (Mollusca: Gastropoda)*. **Univ. Tokyo Mus. Bull.** No. 38, ??pp. **WWW**

A fuller classification, which has not yet been converted to a proper cladogram format, shows the relationships of various recent and fossil groups according to a Linnaean format.

```
Class GASTROPODA
        INCERT� SEDIS
                INCERT� SEDIS
                        Pragoscutulidae Fr�da, 1998
                        Pragoserpulinidae Fr�da, 1998
                Order MIMOSPIRINA
                        Onychochiloidea

        Subclass EOGASTROPODA
                Order EUOMPHALINA
                        Ophiletoidea
                        Euomphaloidea
                        Platyceratoidea

                Order DOCOGLOSSA [=PATELLOGASTROPODA ]

        Subclass ORTHOGASTROPODA
                INCERT� SEDIS
                        Order MURCHISONIINA {fide Wagner, undated}
                                Murchisonioidea
                                Loxonematoidea
                                Lophospiroidea [=Trochonematacea & Eotomarioidea]
                                Grade Subulitoidea
                        Superorder NERITOPSINA [=NERITIMORPHA]
                                Order CYRTONERITIMORPHA
                                        Orthonychiidae Bandel & Fr�da, 1999 (euomphalid like???)
                                        Vltaviellidae Bandel & Fr�da, 1999  (euomphalid like???)
                                Order NERITOIDA [=CYCLONERITIMORPHA]
                                        Neritoidea
                                        Symmetrocapuloidea
                                        ?Peltospiroidea
                                        ?Palaeotrochoidea
                                Order Neomphalida
                                        Neomphaloidea
                        Superorder VETIGASTROPODA
                        Superorder COCCULINIFORMIA

                Infraclass APOGASTROPODA
                        Superorder CAENOGASTROPODA
                                INCERT� SEDIS
                                        Incert� sedis
                                                Ladinulidae Bandel, 1992
                                                Lanascalidae Bandel, 1992
                                                Popenellidae Bandel, 1992
                                                Prostyliferidae Bandel, 1992
                                                Settsassiidae Bandel, 1992
                                        Pseudomelanioidea
                                                Pseudomelaniidae Fischer, 1885 [=Trajanellidae Pchelintsev, 1953]
                                Order ARCHITAENIOGLOSSA
                                Order SORBEOCONCHA {Cerithioidea to Buccinoidea}
                                        ?Spanionematoidea Golikov & Starobogatov, 1987
                                        Cerithioidea
                                        Campaniloidea [=suborder Campanilimorpha]
                                                Campanilidae Douvill�, 1904
                                                Plesiotrochidae Houbrick 1990
                                        Suborder HYPSOGASTROPODA {Calyptraeoidea to Buccinoidea} [LATROGASTROPODA
Riedel, 2000]
                                                ?Superfamily
                                                        ?Weeksiidae Sohl, 1960
                                                infraorder LITTORINIMORPHA
                                                infraorder PTENOGLOSSA
```

infraordinal grade NEOGASTROPODA

Superorder HETEROBRANCHIA {TRIGANGLIONATA to EUTHYNEURA} [=HETEROSTROPHA sensu Bandel]
INCERT� SEDIS
Incert� sedis
Dolomitellidae Bandel, 1994 {Triassic}
Misurinellidae Bandel, 1994 {Triassic}
Zardinellidae Bandel, 1994 {Triassic}
Ordinal Grade TRIGANGLIONATA [=ALLOGASTROPODA, & HETEROSTROPHA]
Intraorder EUTHYNEURA {OPISTHOBRANCHIA + PULMONATA - monophyletic fide Yoon & Kim, 2000 and Wade & Mordan, 2000}
Ordinal Grade OPISTHOBRANCHIA[=OPISTHOBRANCHIATA]
Order PULMONATA

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Gastropoda: Glossary

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA  (crown group)
            |==Eogastropoda  (paraphyletic or
polyphyletic)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
```

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Acuminate: Gradually tapered to a point. Sharply pointed.

Acute: Sharply angled. Sharp; a spire with an angle of less than ninety degrees.

anistrophic - a shell which is spirally coiled and is asymmetrical.

Anal canal: An opening in the gastropod shell through which excrement is expelled.

Anterior: an-te'ri-or (L *ante*=before)   at or towards the front or head end of a shell.

Anterior canal: An open or closed tubular shell extension at the anterior end of a shell, through which the siphon is extended. Same as siphonal canal

Aperture::   ap'er-ture (L *apertures*=an opening)   The major opening of a univalve shell (gastropod, paragastropod, cephalopod, etc).

Apical whorls: Those whorls near the apex.

Apex:: a'pex (L *apex*=the tip, summit) the tip of the spire of a gastropod and generally consists of the embryonic shell.

Apical cavity: A space under the apex of patellate gastropods.

Axial: Pertaining to or more or less parallel to the axis of coiling. Parallel, or nearly so, with the shell axis. Longitudinal, following the direction of the axis of the shell. Longitudinal ribs or color bands. In the same direction as the axis; from apex to the base of a snail shell. Axial ribs are those parallel to the edge of the outer lip. Transverse is a preferred term. In gastropods, running parallel to the shell's axis, or from spire to base.

Axial sculpture: Sculpture running parallel to the axis of coiling.

Axis: An imaginary line through the apex of a gastropod shell, about which the whorls are coiled.

Bead: A small, more or less hemispherical protuberance resembling a bead. Beads are smaller than nodules.

Beaded: Sculptured so as to resemble beads, or strings of beads.

Body whorl: The most recently formed whorl of a spiral shell, terminating in the aperture.

Buccal: Pertaining to the organs of the mouth area in gastropods, especially to the bulging flexible mass that supports the radula.

Buccal bulb: The bulging mouth extension carrying the ribbon of teeth (radula).

Buccinid or Buccinoid: Like the whelk *Buccinum*.

Ceras cer'as (Gr *Keras* = horn) a horn or horn like appendage located on nudibranchs

Columella col-u-mel'la. The thickened axial pillar around which the whorls of univalves are built.

Conch (L *concha* = shell) a trumpet shell; a large marine mollusks with a univalve shell

Coronate: Encircled by a row of spines or prominent nodes, especially at the shoulder of the last whorl in gastropods.

Detorsion de-tor'sion. the act of twisting back or removing torsion; unwinding

Dextral dex'tral (L *dexter* = to the right) Having the aperture on the right side of the shell when the apex is upwards and the aperture is facing you. The whorls spiral in a clock-wise manner.

Digitation: Finger-like projection outwards from outer lip.

Dorsal dor'sal (L *dorsum* = the back) The back of a gastropod remote from the aperture; The conical top surface of a limpet

Estivate es'ti-vate (L *aestivare* = to spend the summer) to pass the summer in a state of torpor; the dormancy in the summer of some lank snails.

Foliated: Having branched or crimped outer ends; applied to the appearance of spines of certain gastropods such as some Muricidae.

Fusiform: Spindle-shaped with a long canal and an equally long spire, tapering from the middle toward each end; applied to univalves as in the genus Fusinus.

Height: In gastropods (except in cowries) the distance from the embryonic whorls or apex to the siphonal canal (the term "length" is also used).

Heterostrophic: Apical whorls coiled opposite to adult whorls.

Labial teeth: Tooth-like processes around the aperture of some gastropods, notably cowries.

Labrum or Labial lip: Outer lip or right margin of aperture of univalves.

Lip(s): In gastropods, the margin of the aperture: the inner lip (labium) extends from the base of the columella to the suture and is divided into a columellar lip and a prietal lip; the outer lip (labrum) is that part of the lip furthest from the axis of coiling.

Lira (plural lirae): Fine linear elevation of shelly material usually within outer lip of some gastropod shells.

Lirate: Sculptured with fine (or thread-like) lines or grooves.

Nodule: A rounded protuberance on the shell sculpture; larger than a bead.

Nodose, Nodulose or Nodular: Bearing rounded protuberances on the shell; sculptured with small tubercles, knobs, nodes or projections.

Nuclear tip: The apex of a gastropod shell.

Nuclear whorl(s): Small, and generally smooth and unsculptured whorls which have been formed within the egg and which constitute the apex of gastropod shells.

Nucleus: Earliest formed part of a shell or operculum. In gastropods, the initial whorls of the shell (protoconch) or the first-formed portion of an operculum; in bivalves, the prodissoconch.

Operculate; having an operculum

Operculum o-per'cu-lum. A horny or shelly (calcareous) plate attached dorsally to the foot serving to close the aperture, wholly or partially, when the animal withdraws into its shell. A chitinous or calcareous plate present in many mollusks.

Ornament: Surface sculpture standing out in relief on shell surface.

Osphradium: "a sense organ located in the mantle cavity close to the gill; in the Archaeogastropoda and Mesogastropoda it consists of sense cells arranged in groups, in the Neogastropoda it is a complex organ with comb-like lamellae and hair cells that react to chemical stimuli. It has also been held that the osphradium is used to indicate the amount of suspended matter in the water." [Lindner 1975 p.22]

Outer lip: The lip of the aperture of a gastropod shell furthest from the shell axis. The outer lip itself has inner and outer surfaces.

Phaneromphalus: having a very large or prominent umbilicus

Plait: Spiral fold or ridge on the columella. Plica.

Plica: (plural plicae) Fold or ridge on the columella, a less conspicuous feature than columella fold but the two terms are more or less interchangeable.

Plicate: Folded or twisted or bearing plaits. Folded or plaited. Bearing plicae; also occasionally used here as equivalent to crenulate.

Plication(s): A raised ridge, fold, or plait, especially on the columella of a gastropod shell.

Plicate: Folded or twisted; having plicae.

Posterior: The rear or tail end of an animal; in a gastropod shell, towards the apex.

Posterior canal: Anal canal; Notch, or trough-like or tubular extension of the posterior aperture margin supporting the excurrent siphon.

Propodium pro-po'di-um (Latinized Gr *Pro-* = before + *-podis* = foot) The foremost division of the foot of a gastropod used to push aside sediment as the animal crawls.

Protoconch pro'to-conch (Gr Proto = first; konche=shell) The embryonic shell. It is present in the adult as the apical or nuclear whorls and often demarcated from the teleoconch whorls by a change of sculpture, design, texture or colour..

Reticulate: Lines, riblets, threads or grooves crossing each other like a net.

Rib: An elongate sculptural element of a shell, raised above the surrounding surface. A fine rib is a riblet, and a very fine rib is a thread.

Riblet: A small rib, but coarser than a thread.

Selenizone: Spiral band of crescentic growth lines, associated with marginal slit or foramen in certain univalves (Pleurotomariine, Bellerophontid, etc).

Sinistral sin'is-tral (L sinister=left) Having the whorls of a spiral shell turning towards the left when a shell is held with its apex pointed up and its aperture facing the viewer. This is a counter-clockwise whorl.

Sinus si'nus (L sinus=a curve) A depression, bend, embayment; a recess or indentation.

Siphonal Canal, siphonal notch A tube-like extension or notch-like infolding of the lip of the aperture in a gastropod shell, often continuous with columella, also known as an anterior canal, through which the inhalant (anterior) siphon is extended.

Slit (AS slite=slit0 A shallow or relatively long incision in the outer margin of the aperture of a gastropod.

Spiral sculpture: Sculpture following the helical growth of a gastropod shell.

Spire: All whorls of a spiral shell exclusive of the body whorl.

Stria: (Pl. striae). Narrow and shallow incised groove.

Striate: Marked with striae.

Suture: The continuous spiral line of junction of the whorls.

Taenioglossa: A term for a group of mollusks equipped with a radular ribbon containing generally seven longitudinal rows of teeth (i.e. Cypraeidae, Cymatiidae). Radula with each row consisting of a central, a lateral, and a pair of marginal teeth.

Teleoconch: All the whorls of a gastropod shell after the protoconch.

Thread: A very fine sculptural element of a shell, raised above the surrounding surface. Finer than a rib.

Trochiform, Trochoid or Trochoidal: Conically shaped, like an inverted spinning top, or like the shell of a *Trochus* having a pointed spire, flat sides and flat base.

Tubercle(s): Elevated knob-like projections or protrusion; larger than pustule.

Turbinoform, Turbinate: Turban-shaped, with broadly conical spire and convex base, as in shell of *Turbo*.

Turreted: With the spire whorls like a succession of turrets, emerging one above the other, having a very high spire, the base usually flattened or slightly convex. In gastropods, tower-shaped, with a long spire and somewhat shouldered whorls.

Turriculate: Having the form of a turret; tower-shaped; spire whorls regularly stepped in outline forming a long spire with somewhat shouldered whorls; as in terebra.

Turriform: With a many whorled, slender spire.

Umbilicate: Navel-like; with depressed cavity. Having an umbilicus.

Umbilicus um-bil'I-cus (L umbilicus=naval Gr corde=string) Cavity or hollow around the axis of a gastropod shell, the hole around which the inner surface of a gastropod shell is coiled; a pit or chink in the shell next to or within the base of the Columella, formed when the inner walls of successive whorls do not meet. The opening at the base of a hollow columella, surrounded by the base of the body whorl.

Uncinus (plural uncini): In gastropods, a marginal or lateral tooth on the radula, more or less hook-like in shape.

Undulate: Having a wavy surface.

Varicose: Bearing a varix or varices.

Varical: Pertaining to a varix.

Varix: (Pl. varices). An thickened or elevated axial ridge in certain gastropods, more prominent than ribs and generally more widely spaced, formed by thickening of the outer lip at a resting stage in the growth of the shell

Velum: Ciliated mantle flap by which a molluscan larva swims.

Ventral ven'tral (L venter=the belly) Of, pertaining to, or situated on, the lower side of a dorsoventral organism; on the aperture surface of a gastropod shell; Opposite to dorsal.

Whorl: A single, complete turn of 360° in the spiral growth of a gastropod shell.

Abbreviations

(from Man and Mollusc Glossary)

AS = Anglo-Saxon
Fr = French
Gr = Greek
L = Latin

Links and References

Glossary/Mollusks - a very comprehensive glossary

Man and Mollusc Glossary - includes derivation of original word

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Gastropoda: References

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   `==Helcionelloida
      `--+--Bellerophontoidea
         `--GASTROPODA  (crown group)
            |==Eogastropoda  (paraphyletic or 
polyphyletic)
            |  |?--Macluritoidea
            |  |?--Euomphaloidea
            |  `--Patellogastropoda
            `--Orthogastropoda
               |--Vetigastropoda
               |--Neritimorpha
               `--+--Caenogastropoda
                  `--Heterobranchia
                     |--Opisthobranchia
                     `--Pulmonata
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Frýda, J. Racheboeuf, P.R., Frýdová, B., Ferrová, L., Mergl, M., Berkyová, S. 2009. Platyceratid gastropods – stem group of patellogastropods, neritimorphs or something else? Bulletin of Geosciences 84(1), 107–120 (5 figures). Czech Geological Survey, Prague. ISSN 1214-1119 **pdf**

Alexander Nützel 2002, An Evaluation of the Recently Proposed Palaeozoic Gastropod Subclass Euomphalomorpha, *Palaeontology* Volume 45, Issue 2, pages 259–266, March 2002 **pdf**

Peter J. Wagner, Phylogenetic Relationships of the Earliest Anisostrophically Coiled Gastropods **pdf**

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Paragastropoda

Abbreviated Dendrogram

```
CONCHIFERA
`==Helcionelloida
   `--+--PARAGASTROPODA
      |  |--Pelagiellida
      |  `--Mimospirida
      |     |--Onychochilidae
      |     `--+--Cliospiridae
      |        `-?Omphallocirridae
      `--+--Bellerophontoidea (torted)
         `--GASTROPODA (crown group)
```

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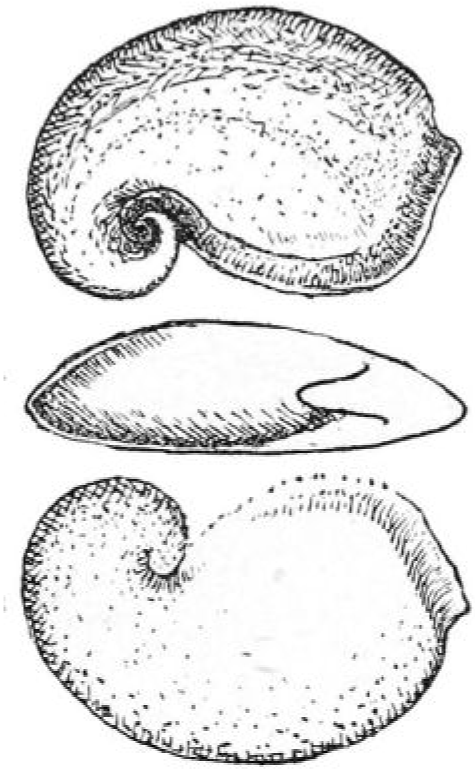

Drawing of the apical, apertural and basal view of *Pelagiella atlantoides* (Paragastropoda: Orthostrophina: Pelagielloidea: Pelagiellidae)

From Matthew G.F. 1895. The Protolenus fauna. Transactions of the New York Academy of Sciences 14: 101-153. Pelagiella on the page 131. Plate VI., figure 6 a-c. Cropped, rotated and retouched by User:Snek01. via Wikipedia, Public domain.

The Paragastropods are an enigmatic assemblage of early paleozoic molluscs, known from their gastropod-like coiled shells. There is no guarantee they are a monophyletic assemblage. Some or all of them may be Helcionelloids, Gastropods, or even some other group entirely. With little to go one either than hard shells and muscle scars, ear;y molluscan phylogeny is a highly problematic affair at best. For now we have followed Linsley and Kier in placing these animals ina distinct, and possibly paraphyletic, class of untorted, stem-group gastropods, the Paragastropods MAK120617

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Paragastropoda

Abbreviated Dendrogram

```
CONCHIFERA
`==Helcionelloida
   `--+--PARAGASTROPODA
      |  |--Pelagiellida
      |  `--Mimospirida
      |     |--Onychochilidae
      |     `--+--Cliospiridae
      |        `-?Omphallocirridae
      `--+--Bellerophontoidea (torted)
         `--GASTROPODA (crown group)
```

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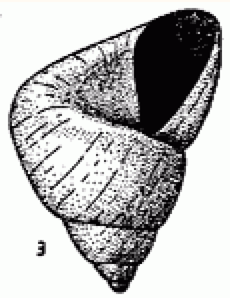
1. Paragastropoda



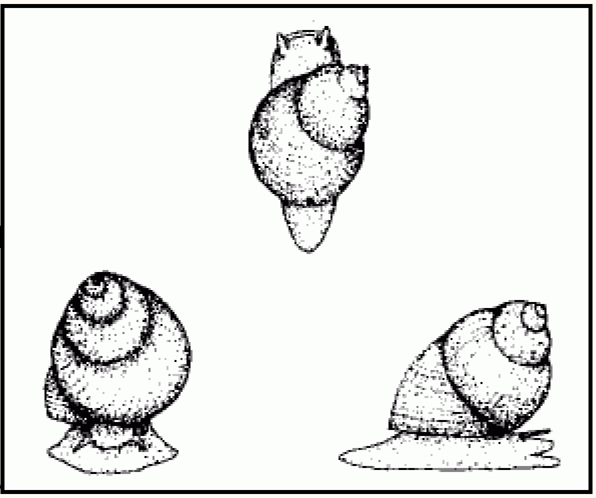
Matherella saratogensis (Miller 1889),
Latest Cambrian (Late Dolgellian) of (Laurentia), height about 1 cm Paragastropoda - Mimospirida - Onychochilidae

illustration © xxxx from Knight et al 1960 Systematic descriptions [Archaeogastropoda]. In Moore, R. C. (ed.) *Treatise on Invertebrate Paleontology* p. I 187

Introduction

The Paragastropoda are one of what must be a number of extinct molluscan clades that have been overlooked because of a superficial resemblance of their shells to gastropods, or (in other instances) lumped in the wastebasket taxon of "Monoplacophora". They were a group of mostly small non-torted proto-gastropod-like mollusks with asymmetrically (helically) coiled shells, that are restricted to the early and middle Palaeozoic. While never very numerous or diverse, they held their own with the gastropods for some hundred million years

History of the Concept



The class Paragastropoda was coined by Linsley & Kier (1984) on the basis of functional analysis of the shells of hyperstrophic (inverted - i.e. the apex points "downwards") and other Paleozoic forms considered to be gastropods because of the spiral (helical) shell. To make sense of the unusual shell shape (and hence deduced soft-part physiology and water flow patterns) of these early gastropod groups Linsley and Kier 1984 concluded that they were untorted and hence cannot be considered gastropods. Because they do not seem to be "Monoplacophora" either (and in any case the term Monoplacophora is polyphyletic grade, rather than a true taxon) they suggested a new class, the Paragastropoda.

In their paper Linsley and Kier include a number of groups traditionally considered gastropods - the Onychochilidae, Macluritidae, Clisospiridae, Pelagiellidae, and possibly the Euomphaloidea and the Aldanellidae. Of those, only the Aldanellidae and Pelagiellidae had a traditionally dubious status as Gastropods

Subsequent work, as Wagner (2001: 1130) summarizes, has partially supported Linsley and Kier's work. Dzik (1982, 1994) has shown that the protoconchs of onychochilids are similar to those of pelagiellids, but unlike gastropod protoconchs. Outgroup analyses of various Cambrian mollusks by Wagner (1999) also linked onychochilids to pelagiellids, and suggested that both were only distantly related to true gastropods.

Thus the evidence for a pelagiellid-onychochilid clade is looking good. As for the other taxa cited by Linsley & Kier, the protoconchs of macluritids still are unknown, but euomphalids exhibit a variety of protoconch types, all of which are found in gastropods [Wagner 2001]. Flow-tank studies (Morris, 1991) indicate that the shell morphology of *Maclurites* would encourage Bernoulli effects and thus facilitate suspension feeding, but only if it was a torted mollusk [*ibid*]. Also, cladistic analysis (Wagner 1999) indicates a close relationship between the Macluritiodea and the Euomphaloidea. So if the Euomphalids are conventional (albeit very primitive and early) gastropods, the Macluritids are as well.

Following Yochelson 1978, the Aldanellidae are here considered non-molluscs and hence also removed from the Paragastropoda

It should be pointed out that even today there is not unanimity regarding the status of the Paragastropoda, and a number of workers in this field still consider them to be an artificial group, or perhaps included in the Gastropoda. Linsley and Kier 1984 themselves admit that the Paragastropoda as they define it represents a grade, rather than a clade, and is unlikely to be monophyletic.

Image: *Onychochilius* from Linsley & Kier (1984).

Ecology and Possible Physiology

According to Linsley and Kier 1984, the less specialized Paragastropods like the Pelagiellidae and Onychochilidae were "mobile browsers", but later forms such as Cliospiridae and the Macluritidae (which, following Wagner 1999, it is suggested are actually gastropods), became sedentary, presumably filter feeders.

If the paragastropods are more basal than the gastropods, but more derived (belonging to the Gastropod-and-related-forms clade) than the Polyplacophora and Tryblidiida, it might not be unreasonable to assume that physiologically they would have characteristics shared by Polyplacophora, Tryblidiida, and the most primitive extant gastropods (the Docoglossa or Patelliforms), but lost in more specialized gastropods. Of course, they would probably have various specializations as well, although none were obviously sufficient to allow them to survive the Paleozoic. It can be suggested then that - as with chitons, Tryblidiida, and docoglossa gastropods, they had "docoglossa" radula, their sense organs were very rudimentary, they lacked antennae, only moved slowly, and were most probably (as with "archaeogastropods") confined to hard substrates, although sedentary types presumably would rest on sand or mud. However, the presence of a sinus in the Pelagiellidae indicates that these forms at least had a siphon, although it is not clear if mimospirid paragastropods had. Also, sedentary forms had some sort of way of catching suspended particles in the water currents, so we can tentatively assume a mucus net of some sort.

Technical Diagnosis

Class Paragastropoda Linsley & Kier, 1984

> "Anisostropically coiled, untorted mollusks. Shells either hyperstrophic or orthostrophic. Members with elongate apertures with these elongated at approximately right angles to aperture at elongation of torted gastropods. The inhalant water current enters under the spire with the result that the "base" of the shell is frequently concave to accommodate the inhalant stream. Position of anus frequently marked by angulation or re-entrant at the outer part of upper whorl surface of aperture. Pretorsional left gill presumably lost."
>
> Linsley and Kier 1984 p.249

Systematics

The upper table shows the original classification of Linsley and Kier, the one beneath it the classification adopted here. Faint text means the taxa is only tentatively placed here

Paragastropoda after Linsley & Kier:

```
Class PARAGASTROPODA Linsley & Kier
        Order Orthostrophina Linsley & Kier
                  Superfamily Pelagiellacea (= Pelagielloidea)
                          Family Pelagiellidae
                          Family ? Aldanellidae Linsley & Kier
         Order Hyperstrophina Linsley & Kier
                  Superfamily Onychochilacea (= Onychochiloidea)
```

- Family Onychochilidae
- Family Cliospiridae
    - Subfamily Cliospirinae
    - Subfamily Trochoclisinae
    - Subfamily Atracurinae

Superfamily Macluritacea (= Macluritoidea)

- Family Macluritidae

Superfamily ? Euomphalacea (= Euomphaloidea)

- Family Euomphalidae
- Family Omphalotrochidae
- Family Omphalocirridae
- Family Oriostomatidae

Paragastropoda as represented here:

Class PARAGASTROPODA

- Order **Pelagiellida**
    - Family Pelagiellidae
- Order **Mimospirida**
    - Family Onychochilidae
    - Family Cliospiridae
        - Subfamily Cliospirinae
        - Subfamily Trochoclisinae
        - Subfamily Atracurinae
    - Family Yangtzespiriidae
- Order Unspecified
    - ? Family Omphalocirridae

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Mimospirida

Abbreviated Dendrogram

```
CONCHIFERA
`==Helcionelloida
   `--+--PARAGASTROPODA
      |  |--Pelagiellida
      |  `--Mimospirida
      |     |--Onychochilidae
      |     `--+--Cliospiridae
      |        `-?Omphallocirridae
      `--+--Bellerophontoidea (torted)
         `--GASTROPODA (crown group)
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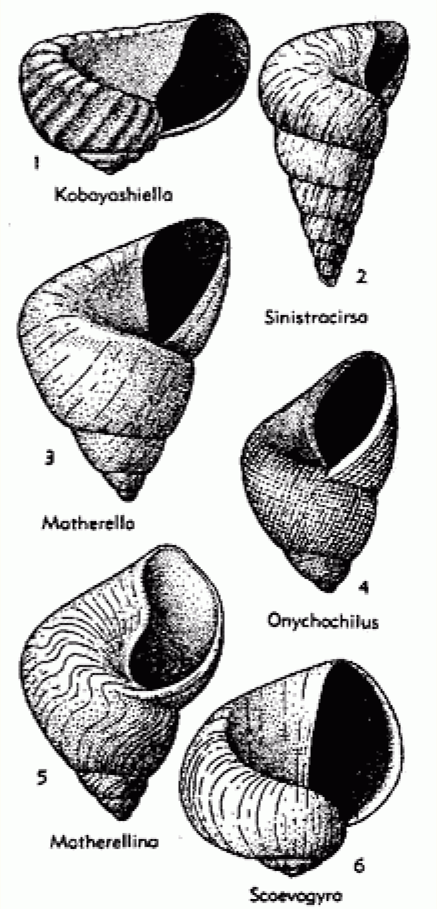
3. Onychochilidae
4. Yangtzespiriidae



Representative members of the family Onychochilidae

1. *Kobayashiella circe* (Walcott 1905) Furongian (= Dolgellian?) China, height about 2 mm;
2. *Sinistracirsa altera* (Perna 1903), Early Devonian, Czech Republic (Armorica) height about 3.5 cm;
3. *Matherella saratogensis* (Miller 1889), N.Y. (Laurentia), Furongian (Late Dolgellian) height about 1 cm;
4 *Onychochilus physa* (Cossman 1915) Middle Silurian (Wenlock) Gotland (Baltica), height about 4 mm;
5 *Matherellina walcotti* (Kobayashi 1933), Early Ordovician, China, height about 1 cm;
6 *Scaevogyra swezeyi* (Miller 1889), Furongian (Late Dolgellian) Wisconsin (Laurentia), height about 2.5 cm

drawings © xxxx from Knight et al 1960 Systematic descriptions [Archaeogastropoda]. In Moore, R. C. (ed.) *Treatise on Invertebrate Paleontology* p. I 187

Introduction

The Mimospirida (previously Mimospirina) are a group of extinct, superficially snail-like, Paleozoic mollusks with a moderately high-spired hyperstrophic / sinistrally coiled shell. Although conventionally included under the Gastropoda (Knight *et al*., 1960) it was suggested by Linsley & Kier (1984) that they and a number of related forms are not gastropods, but can be considered as part of a new class, the Paragastropoda. However, the status of the Paragastropoda remains controversial, and at least one recent classification considers the Mimospirida to be Gastropoda *incert� sedis*. I have assumed for the present that they are untorted mollusks and represent an early side branch of the post-Helcionelloida and proto-gastropod stem.

Ecology, Relationships, and Evolutionary History

The Mimospirids seem to have evolved from the Pelagiellids. The relationship is indicated not only by the hyperstrophic and other shell features but more specifically by the fact that both onychochilids and pelagiellids are known to share a unique protoconch that is unlike that of any gastropod protoconch. Wagner (2001: 1130). Evolution seems to have occurred away from areas of regular fossilization, as there seems to be a stratigraphic gap of some ten million years or so between the last Pelagiellid (middle Cambrian) and the earliest unambiguous Mimospirid (Trempealeauian = late Dolgellian = Latest Cambrian) . Whereas the pelagiellids were limited to the early and middle Cambrian, the mimospirids continued through to the middle Palaeozoic.

The earliest and least specialized of the Mimospirida were the Onychochilidae, which first appear in the Furongian, and according to Linsley Kier (1984: 248) are inferred from their shell to be mobile browsers.

It seems that these forms began with low spired forms like "Maclurites" *thomsoni*, *Scaevogyra swezeyi*, and *Kobayashiella circe*, which then gave rise to higher spired genera like *Matherella* and *Matherellina* (possibly these two genera are synonyms) (Wagner, 1999) and their descendents.

The Onychochilids persisted into the Devonian, a late representative being the high spired *Sinistracirsa altera*. But earlier, during the early Ordovician perhaps, they gave rise to the specialized Cliospiridae, which range from the Ordovician to the Devonian and became sedentary forms, probably filter feeders. In these high spired forms the high center of gravity means that the spire rests of the substrate, holding the animal in place.

According to Linsley & Kier (1984) the Onychochilids also evolved into another sedentary hyperstrophic group, the Macluritidae (both Onychochilidae and Macluritidae are included in the same superfamily - the Macluritoidae - by Knight *et al*. (1960), but cladistic analysis by Wagner (1999) interprets the Macluritids as true gastropods that developed from Euomphalids. Clearly there was a lot of parallelism of shell morphology among early gastropod and paragastropod groups, which makes determining relationships difficult.

As with a number of Tergomyan groups, the Mimospirida died out without leaving any descendents during the later Palaeozoic. The reason for this is not clear, as both the Onychochilidae and Cliospiridae had survived quite happily for well over a hundred million years.

Development

The Mimospirida had a distinct larval metamorphosis as these mollusks developed a large, smooth, sinistrally coiled (probably non-planktotrophic) larval shell consisting of several whorls and distinct from the teleoconch. Fr�da (2001).

Systematics

Under the Order Mimospirida is included the single superfamily Onychochiloidea with the following three families:

- Onychochilidae Koken, 1925
- Cliospiridae Miller, 1887
- Yangtzespiriidae Yu, 1984

The order Mimospirida listed by Jeffery 2001(as "Mimospirina") would seem to be the same as the Superfamily Onychochilacea (= Onychochiloidea) Koken, 1925 of Linsley and Kier 1984, except that it includes the more recently discovered family Yangtzespiriidae.

There is actually some controversy here over whether these actually are paragastropods, and if they are, whether they all belong together. I have followed Linsley and Kier 1984 in assuming they are Paragastropods, Wagner (iNet) in placing them to the Pelagiellida, and Jeffery 2001 in including all three families in the same order, fully aware that future discoveries may overturn this arrangement.

Mimospirida: Untorted hyperstrophic snail-like mollusks

Stratigraphic Range: Furongian (Late Dolgellian) to Early Carboniferous

Phylogeny: Paragastropoda/Pelagiellida **:::** Mimospirida **:** Onychochilidae + Cliospiridae + Yangtzespiriidae

Characteristics: Paragastropoda with hyperstrophic shells with highly prosocline tangential apertures. Shell form varying from high-spired to moderately low spired.

Taxon: Order Mimospirida

Onychochilidae:

Stratigraphic Range: ?Middle, or Latest Cambrian (Trempealeauian = Late Dolgellian) to Early Carboniferous [Wagner 2001]. According to Curry and Morris 1967, p.426, *Matherella* and *Scaevogyra* are known from the Eminence Dolomite, Trempealeauian, of Missouri, and *Kobayashiella* from the "Upper Cambrian" South Korea

Phylogeny: Mimospirida **:** Onychochilidae + Cliospiridae + Yangtzespiriidae

Characteristics: Mimospirida in which the area of the depressed spire is gently rounded into umbilical area with only a gentle angulation to mark exhalant area [Linsley and Kier 1984 p.150]

Taxon: Family Onychochilidae Koken, 1925 (Linsley & Kier, 1984).

Genera included: - ?*Protoscaevogyra* Kobayashi 1939; *Matherella* Walcott. 1912; *Scaevogyra* Whitfield 1878; *Kobayashiella* Endo 1937; *Matherellina* Kobayashi, 1933; *Pervertina* Horny, 1964; *Invertospira* Horny 1964; *Helicotis* Koken 1925; *Laeogyra* Perner 1903; *Onychochilus* Lindström 1884; ?*Sinistracirsa* Cosamaenn 1908; *Hyperstrophema* Horny 1864; *Versispira* Perner 1903; *Antispira* Pemer 1903

Notes: genus list from Linsley & Kier (1984), who include *Scaevogyra* in the Macluritidae. Knight *et al*. (1960) and Wagner (1999 & iNet) both include *Scaevogyra* under the Onychochilidae, where I have placed this genus here. "Maclurites" *thomsoni* is also included in this clade by Wagner.

Cliospiridae:

Stratigraphic Range: Ordovician to Devonian

Phylogeny: Mimospirida **:** Onychochilidae + Yangtzespiriidae + Cliospiridae **:** Cliospirinae + Trochoclisinae + Atracurinae

Characteristics: Mimospirida in which the area of the depressed spire with a sharp ridge is on the upper whorl face. [Linsley and Kier 1984 p.150].

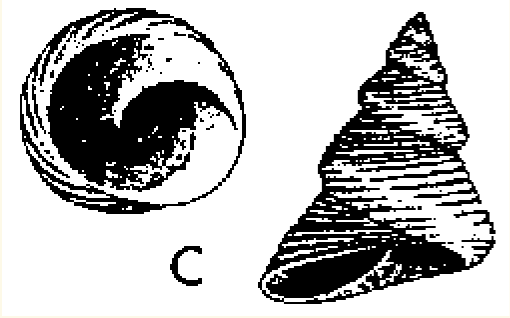
Taxon: Family Cliospiridae Miller 1889 (Linsley & Kier, 1984; Jeffery, 2001)

Subfamilies included: - Linsley & Kier 1984 divide this family into three subfamilies and I have followed this arrangement here, although it may turn out that these are not natural groups: Cliospirinae, Trochoclisinae, Atracurinae

Cliospirinae:

Stratigraphic Range: Ordovician to Silurian

Phylogeny: Cliospiridae **:** Cliospirinae + Trochoclisinae + Atracurinae



Mimospira cochleata (Lindstrom, 1884)
height about 7mm
Late Silurian of Baltica (Sweden)

image © xxxx from McLean 1981 from Wängberg-Eriksson, 1979

Characteristics: Low spired clisospirids with sharp ridge surrounding depressed spire at periphery and extended upwards and outwards as a frill (Linsley & Kier, 1984: 151)

Taxon: Subfamily Cliospirinae Miller, 1889 (Linsley & Kier, 1984)

Genera included - *Cliospira* Billings 1865; *Ferrogyra* Horny 1964.

Trochoclisinae:

Stratigraphic Range: Silurian to Devonian

Phylogeny: Cliospiridae **:** Cliospirinae + Trochoclisinae + Atracurinae

Characteristics: Medium-spired conical clisospirids. Sharp angulation located at whorl periphery. Angulation may be extended upwards and outwards as a frill. [Linsley and Kier 1984 p.151]

Taxon: Subfamily Trochoclisinae Horny, 1964 (*emend*. Linsley & Kier, 1984)

Genera included - *Conoctisa* Horny 1964; *Trochoclisa* Horny, 1964.

Atracurinae:

Stratigraphic Range: Ordovician to Devonian

Phylogeny: Cliospiridae **:** Cliospirinae + Trochoclisinae + Atracurinae

Characteristics: Medium-spired conical clisospirids. Sharp angulation located in from the periphery. (Linsley & Kier, 1984: 151).

Taxon: Subfamily Atracurinae Horny, 1964 (*emend*. Linsley & Kier, 1984)

Genera included - *Mimospira* Koken, 1925; *Antigyra* Horny 1964; *Antizyga* Horny, 1964; *Atracura* Horny, 1964; *Bodospira* Wängberg-Eriksson, 1979; *Angulospira* Wängberg-Eriksson, 1979; *Tapinogyra* Wängberg-Eriksson, 1979; *Undospira* Wängberg-Eriksson, 1979.

Yangtzespiriidae:

Phylogeny: Mimospirida **:** Onychochilidae + Cliospiridae + Yangtzespiriidae

Taxon: Family Yangtzespiriidae Yu, 1984 (Jeffery, 2001)

Notes:

Apart from the listing in Jeffery (2001) I have no information on the Yangtzespiriidae. One might presume from the name that they include one or several Chinese forms. If anyone has any further information on this group could they please contact me.

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note: In keeping with the convention of the *Treatise* authors of the volumes on Gastropoda and Cephalopoda, the suffix -*ina* is used for suborders, and -*ida* for orders. Since the Mimospirina are here considered of ordinal rank, the suffix -ina has been changed accordingly

> "although ICZN does not address ordinal level taxa, the Zoological Sciences Section of the American Association for the Advancement of Science has recommended that zoological orders be given the ending -ida (as has long been done by the Treatise on Invertebrate Paleontology)."

Ken Kinman - Phylocode Discussion

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Paragastropoda

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```
CONCHIFERA
`==Helcionelloida
   `--+--PARAGASTROPODA
      |  |--Pelagiellida
      |  `--Mimospirida
      |     |--Onychochilidae
      |     `--+--Cliospiridae
      |        `-?Omphallocirridae
      `--+--Bellerophontoidea (torted)
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Omphalocirrus goldfussi
Diameter about 10 cm Middle Devonian (Armorica (Germany)

These strange Devonian snail-like molluscs do not seem to have any clear relations. The distinctive frills would presumably be for the inhalent siphon, and the animal was most likely sedentary, probably a filter feeder. Knight, *et al.*, 1960 placed them in the Macluritidae (gastropods), although they lived in the Devonian, long after the last Macluritids died out. Linsley and Kier 1984 considered them members of the Euomphaloid paragastropods. Flow-tank studies by Morris (1991) indicate they would seem to be untorted, but muscle scars are ambigious [Wagner 2001]. I have tentatively left them in the Gastropoda, but I acknowledge they may equally belong among the Paragastropoda.

Paragastropoda

Abbreviated Dendrogram

```
CONCHIFERA
`==Helcionelloida
   `--+--PARAGASTROPODA
      |  |--Pelagiellida
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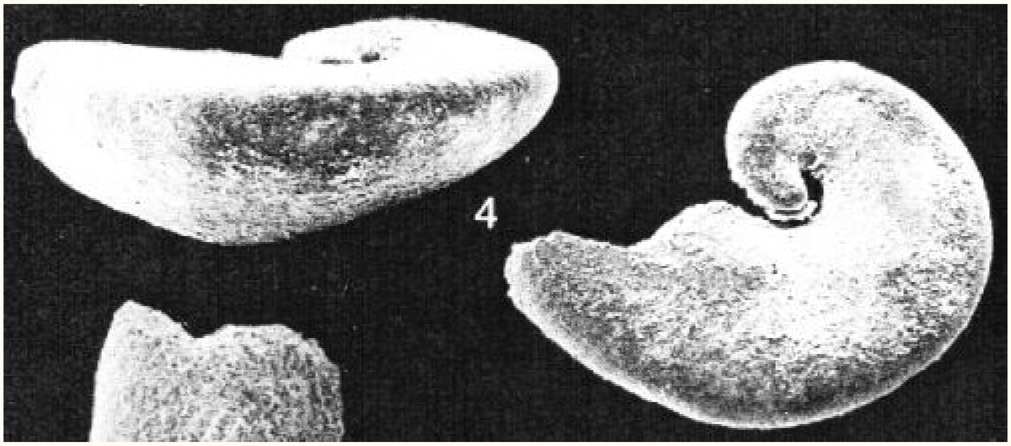

Pelagiella emeishanensis (Phosphatic steinkern)
Bed 68, Maidiping, Sichuan, China (Late Atdabanian)
length: 1 mm

from Brasier, 1989 plate 7.4.

Introduction

The pelagiellids include a single family of small Cambrian snail-like forms of uncertain affinity. They appear in the Atdabanian and have no clear antecedents, and continue through to the Middle Cambrian.

Relationships

Pelagiellids have been included in the Gastropoda, the "Monoplacophora", as possibly a distinct class of untorted asymmetrical mollusks by Yochelson 1978, and by Linsley & Kier 1984 in the new class Paragastropda. Protoconch studies by Dzik and cladistic analyses by Wagner both link the pelagiellids with the onychochilids [Wagner 2001 p.1130],, and I have therefore considered these small mollusks to be the earliest members of that class, and, following Wagner, an early side-branch in what could be called the "gastropodomorph" clade. Presumably they evolved from Helcionelloid ancestors some time in the early Atdabanian or perhaps Tommotian, and gave rise to Onychochilids shortly before dying out in the middle (or late?) Cambrian.

Ecology

According to Linsley & Kier 1984, Pelagiellids were "mobile browsers", which indicates they were comparable to true gastropods in this regard. However, Brasier, 1989 p.138 reports that *Pelagiella* seems to occur widely with a pandemic assemblage close to the appearance of *Serrodiscus bellimarginatus* or other eodiscid trilobites, possibly indicating a pelagic or epiplanktonic habit.

Whatever the ecology, it is likely that - as with chitons and docoglossa gastropods, their sense organs were very rudimentary, they lacked antennae, only moved slowly, and were most probably confined to hard substratum. Cambrian ecosystems seem to have been fragile and susceptible to mass-extinction, and the Pelagiellids did not survive even to the end of the period. They did however give rise to their more diverse descendents, the Mimospirida

Pelagiella has a cosmopolitan distribution, which indicates either a long planktonic larval stage, or a planktonic or epiplanktonic adult stage. The genus appears suddenly with no clear antecedents (assuming *Aldanella* is non-molluscan). Various species are widely reported from the late Atdabanian through to Early Botomian of Siberia and equivalent of Shropshire, Nova Scotia, Greenland, Morocco, northern Iran, the Himalayas, and Sichuan in China. [Brasier, 1989 p.138]

Systematics

Pelagiellida:

Stratigraphic distribution - Atdabanian to Middle Cambrian

Characteristics: Orthostrophic Paragastropoda with elongated apertures

Taxon: Order Pelagiellida
The Order Pelagiellida is here considered the same as the Order Orthostrophina Linsley & Kier 1984 and, one may assume, the Superfamily Pelagiellacea Knight, 1956. Following Yochelson 1978 the Aldanellidae, which Linsley and Kier tentatively include here, are considered non-mollusks (although like the Hyolithida they may be "Molluscomorphs").

Contains: Pelagiellidae

Reference: Linsley & Kier 1984 p.250

Pelagiellidae:

Stratigraphic distribution - Atdabanian to Middle Cambrian

Characteristics: Orthostrophic, right-handed paragastropods with an elongated tangential apertures. Inhalant current entering near umbilical area, frequently marked by a sinus. Exhalant current exiting near periphery of shell and marked by angulation or even a selenizone generating sinus. Shell rather flattened on top and arched below.

Taxon: Family Pelagiellidae Knight, 1956

Genera included *Pelagiella* Matthew, 1895; *Cambretina* Horny, 1964; *Costipelagiella* Horny, 1964; *Proeccyliopterus* Kobayaahi, 1939.

Reference: Linsley & Kier 1984 p.250

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Paragastropoda

Abbreviated Dendrogram

```
CONCHIFERA
`==Helcionelloida
   `--+--PARAGASTROPODA
      |  |--Pelagiellida
      |  `--Mimospirida
      |     |--Onychochilidae
      |     `--+--Cliospiridae
      |        `-?Omphallocirridae
      `--+--Bellerophontoidea (torted)
         `--GASTROPODA (crown group)
```

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Pelagiellida
Mimospirida
Omphallocirridae
Dendrogram

The following dendrogram represnts one possible phylogeny, by no means the only one, maybe nort even the most likely. It's posted here until a proper revision can be made. MAK120617

```
<== o HELCIONELLOIDA
   |-- Helcionella subrugosa
   |-- Oelandia rugosa
   `--+-- Latouchella merino
      `--+-- Coreospirida
         `--+--+-- Euomphalopsis involuta
            |  `-- Macluritella? walcotti
            `--+--o PARAGASTROPODA
               |  |--o Pelagiellida (= Pelagielloidea)
               |  |  `--o Pelagiellidae
               |  |     |-- Costipelagiella zazvorkai
               |  |     `-- Pelagiella subangulata
               |  `--o Mimospirida (= Onychochiloidea)
               |     |--o Onychochilidae
               |     |   |-- "Maclurites" thomsoni
               |     |   `--+-- Scaevogyra swezeyi
               |     |      `--+-- Kobayashiella circe
               |     |         `--o Matherella/Matherellina
               |     |            |-- Matherellina walcotti
               |     |            `-- Matherella saratogensis
               |     |--o Cliospiridae
               |     |   |-- Cliospirinae
               |     |   |-- Trochoclisinae
               |     |   `-- Atracurinae
               |     |  ?-- Omphalocirridae  (gastropod or paragastropod)
               |     |  ??--Macluritidae  (probably stem or possibly crown-group gastropods,
possibly paragastropod)
               |     `--o Yangtzespiriidae
               `--+--BELLEROPHONTOIDEA (torted)
                  `--+?--Euomphaloidea (if stem gastropod, may be crown-group, very possibly
paragastropod)
                     `--GASTROPODA (crown group)
```

References

Peter Wagner [no date] Outgroups (website at http://pjw3.fmnh.org no longer current)

Paul Jeffery [no date] Suprageneric classification of Class GASTROPODA (website at http://www.nhm.ac.uk/palaeontology/i&p/gastroclass/gastroclass.htm no longer current)

Linsley and Kier 1984 pp.250-1

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checked ATW050720

Polyplacophora

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
|  |--Phthipodochiton
|  `--+--+--Solenogastres
|     |  `--Caudofoveata
|     `--POLYPLACOPHORA
`--CONCHIFERA
```

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The chiton *Tonicella marmorea* (O Fabricius, 1780), Loch Melfort, W. Scotland
Photo © National Museums Northern Ireland and its licensors, Creative Commons Non-Commercial Attribution Share Alike via Encylopedia of Life.

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Polyplacophora

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
|  |--Phthipodochiton
|  `--+--+--Solenogastres
|     |  `--Caudofoveata
|     `--POLYPLACOPHORA
`--CONCHIFERA
```

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1. Polyplacophora

Introduction

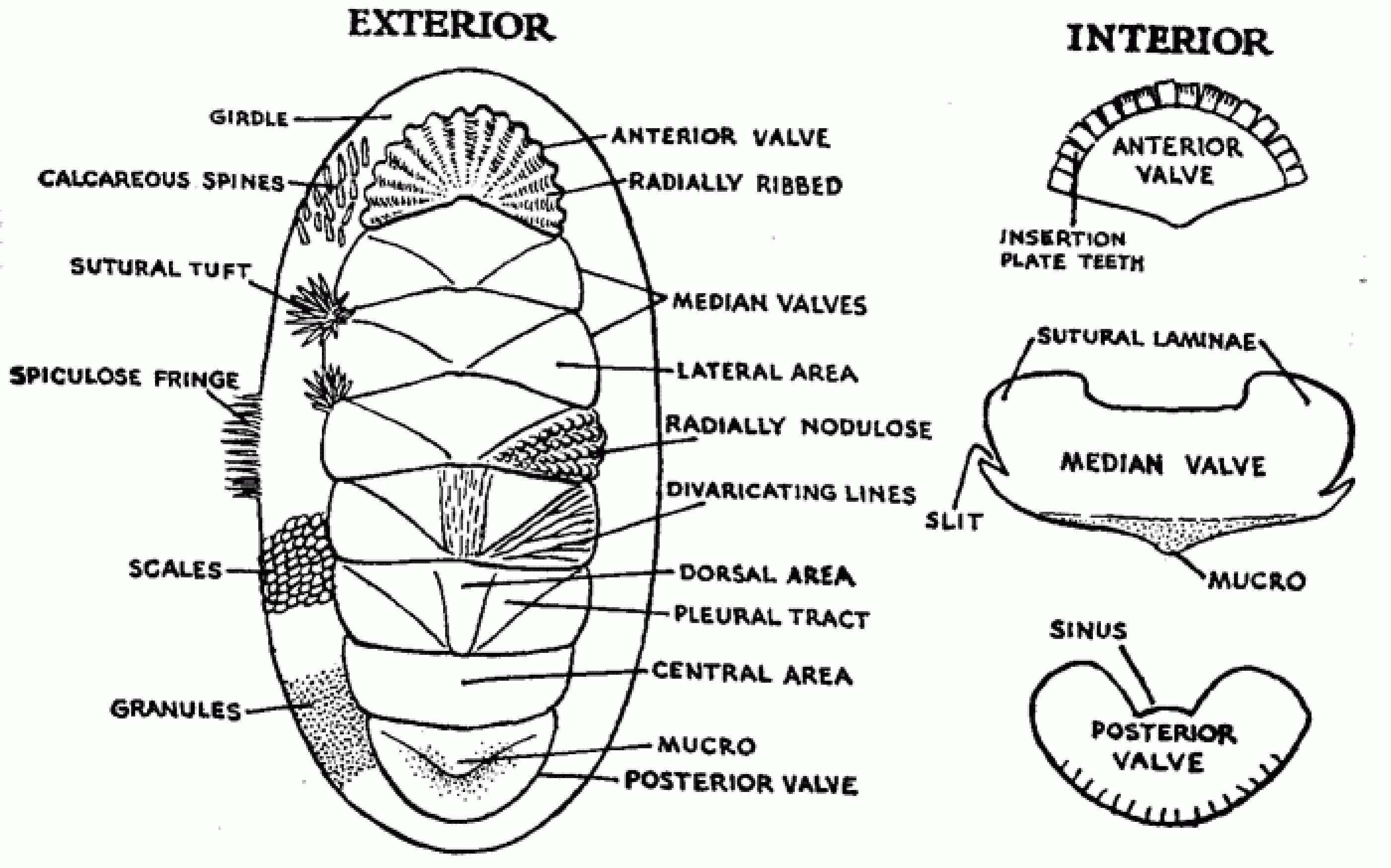
Tonicella lineata
(Chitonida - Ischnochitonina - Lepidochitonidae - Lepidochitoninae
length 5 cm
this specimen from Snowfall, BC, Canada

image copyright © Keith Clements and Jon Gross Marine Life of the Northeast Pacific

Polyplacophorans, or chitons, are a class of persistently primitive marine mollusks commonly occurring on rocks and seaweed in the intertidal zone. A few species They have also been found at depths down to 5,000 meters. There are about 600 recent species

Chitons do not vary much in form. All have eight shell plates (although a Palaeozoic lineage, the Sempteochitonida, had seven), are generally oval in outline and have a flattened body, usually with the greatest thickness of about one-fourth their greatest width.

The chiton shell normally consists of eight, articulating calcareous valves with the joints between them running perpendicular to the axis of the body. These valves are constructed in such a way that the animal can often roll up when disturbed or removed from the rock. The parts of the shell are shown here

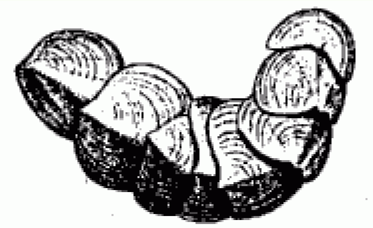


drawing © xxxx by G. J. Browning from *Marine Molluscs of Victoria*

There is a creeping foot, a primitive feature in molluscs, and the radula is of the "docoglossan" type, like limpets (Patellogastropoda) and Tryblidiida. The radula are mineralized with magnetite (a compound of iron). The head is poorly developed, and visible only from the ventral side (again like the Tryblidiida). A band of muscular tissue, the girdle, runs along the dorsal periphery of the animal (*see illustration above*). The girdle commonly has embedded in it small calcareous spines, scales or spicules, not unlike the spicules of the very primitive and wormlike Caudofoveata and Solenogastre Aplacophora. Indeed, at one time the Aplacophora and Chitons were grouped in the same class, the Amphineura. However it is now known that there are many differences between these types of primitive molluscs, despite the shared primitive features (symplesiomorphies) that unite them.

Chitons lack normal molluscan sense organs like statocysts, cephalic eyes, and tentacles. The chief senses is a subradular organ and the "aesthetes". These latter, which among living molluscs are unique to chitons, are special mantle shells found within tiny vertical canals in the upper tegmentum (upper shell layer) [Barnes 1980 p.386]. Interestingly, very similar canals are found in the shell of *Tryblidium reticulatum* (Silurian period, family Tryblidiidae, Tryblidiida) [Knight and Yochelson 1960 p.77], although they are absent in the recent *Neopilina* (presumably lost when the animal migrated to deep water). The aesthetes are supplemented by tactile and photoreceptor cells in the mantle and girdle. The animal is thus able to detect light, which it responds negatively to. These shy creatures only become active at night, when they creep over rocks scraping algae and other microscopuc organisms off the surface with their radula. Like limpets, the animal will often return to its resting place for the day.

Again as with the Tryblidiida, with which the chitons would seem to be related, the animal is metameric or pseudometameric, with repeated gills and shell muscles. This led to the view that these animals (and thus the Mollusca as a whole) evolved from a segmented annelid-like ancestor. However, analysis of chiton embryo, larval, and postlarval development and metamorphosis shows that the "segmented" or serial nature of the polyplacophoran shell musculature is a secondary condition, and an unsegmented ancestor at the base of molluscan evolution is more likely [Wanninger and Haszprunar 2001].



Helminthochiton priseus, a rare example of a complete fossil chiton
length if straightened - 8 cm
(Lepidopleurida - Lepidopleuridae)
Tournaisian, Belgium

image © xxxx from *Treatise on Invertebrate Paleontology*. Part I. Mollusca 1., p.53

Fossil chiton specimens are almost always loose, disarticulated valves. They have been found in rocks of the Furongian onwards, but are rare, probably because chitons tend to occupy environments where the possibility of preservation is not high. There are about three extinct orders, mostly Palaeozoic.

Descriptions

Polyplacophora

Range: Silurian or Carboniferous to Recent

Phylogeny: Aculifera **:::** polyphyletic Aplacophora + *

Characters: inhabit rocks and feed on algae in the intertidal zone. Elongate or oval and dorsoventrally flattened, shell of eight overlapping plates embedded in, and sometimes covered by tissue. They have a large, muscular, ventral foot and a poorly-differentiated head without eyes or tentacles. The mantle cavity is a groove around the foot, with 6-88 pairs of ctenidia, which together with the overlapping plates, gives it a segmented appearance. The animals feed with a radula, and the anus is subterminal. The sexes are separate and most taxa have larval stages. - Jack R. Holt

Comments: here used as synonymous with Neoloricates, which date from either the Silurian or Carboniferous. The status of Paleoloricates is sometimes ambiguous, as many taxa are stem or basal aculiferan. MAK120612

Links Polyplacophora introduction to the group - gives a comprehensive list of orders, families and genera, but no other information as yet other than a reference for each, the reference gives the author and year and page number, but no link to a bibliography (the menu without frames here); Class Polyplacophora - short intro with some images - Animal Diversity Web; Polyplacophora - the Chitons! - intro; Mollusca - Class Polyplacophora - short intro; Class Polyplacophora (The Chitons or Coat-of Mail Shells) - more on chitons

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Pulmonata

Abbreviated Dendrogram

```
GASTROPODA
|--Caenogastropoda
`--Heterobranchia
   |--Opisthobranchia
   |
   `--PULMONATA
      |==Basommatophora
      `--+--Stylommatophora
         `--+--Systellommatophora
            `==Acteophila
```

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Mesodon altivagus (Pilsbry, 1900), (Heterobranchia: Pulmonata: Eupulmonata: Stylommatophora: Sigmurethra: Helicoidea: Polygyridae) Clingmans Dome, Tennessee.
Photo by John Slapcinsky Creative Commons Non-Commercial Attribution via Encylopedia of Life.

The Pulmonata or land snails, slugs, pond snails, and air-breathing mangrove snails are a huge group a gastropods characterised most distinctively by advanced Heterobranchia morphology and the opossesison of a lung rather than gills, which gives them the ability to breathe air. They are also united by a number of other advanced gastropod features such as a single auricle and kidney, a uncrossed or loop-like nervous system and hermophroditism. Previously considered a subclass, it now seems that the pulmonates, are a polyphyletic assemblage, with several lineages of Euthyneuran gastropods independently aquiring air-breathing capacity. Molecular phylogeny and other advances have also improved our understanding of this important assemblage of molluscs. Although the pages in this unit are therefore somewhat dated, they have been retained as is, pending a more comprehensive study and revision. MAK120621

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Pulmonata

Abbreviated Dendrogram

```
GASTROPODA
|--Caenogastropoda
`--Heterobranchia
   |--Opisthobranchia
   |
   `--PULMONATA
      |==Basommatophora
      `--+--Stylommatophora
         `--+--Systellommatophora
            `==Acteophila
```

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Montenegrina subcristata wohlberedti (Möllendorff 1899)
(Stylommatophora - Sigmurethra - Clausilioidea - Clausiliidae - Alopiinae]
Recent, Albania
Photo © V. Wiese, Haus der Natur Cismar, from Albanian non-marine molluscs

Pulmonates are the third of the traditional sub-classes of gastropods. They include the only terrestrial molluscs. are also the only subclass of the three that can confidently be considered a monophyletic clade, although their ancestry (whether from Heterostropha or Opisthobranchia, or even "Prosobranchia" (which latter would apply a degree of parallelism with the Opisthobranchia)) is still debated.

The Pulmonates differ from the "Prosobranchs" by detorsion and symmetrical concentrated nervous system, primitively loss of gills and a mantle cavity converted into a lung for gas exchange with air (or secondarily breathing water) and (with only exception) lack of an operculum. They also are hermaphroditic, each individual having two sets of sex organs. [Barnes 1980 p.338, 377]

The shell may be external, internal, vestigial (as in the land slug*Testacella*), and in a number of lineages has disappeared absent altogether (e.g. terrestrial slugs). If external, the shell is often thin, and the morphology is typically conispiral and rather bulbous, although a few aquatic forms [*Planorbis*, etc] have a planispiral shell; which is unusual in modern gastropods.

Pulmonates have adapted to a wide range of environments. Many are terrestrial or live in freshwater (pond, swamp or river) environments. While most common in temperate and tropical areas, some species are found in deserts and mountains. Some forms readapted to water and again populated freshwater and marine habitats, others are confined to land.

The pulmonate body type and life habits is defined by the problem of how to conserve water and prevent desiccation (drying up). A major part of the solution was to seal off the mantle (pallial) cavity. This one innovation greatly reduced evaporative water loss. The mantle cavity is vascularized and lined with blood vessels for gas exchange, becoming a lung, and a single narrow passage, the *pneumostome*, provides access to the exterior [Barnes 1980 p. 338, Chase 2002 p.13].

Behaviors include the ability to retreat into the shell and drastically reduce metabolic activity during dry periods (aestivation), although shell-less forms (slugs) frequent moist environments.

It is not known whether Pulmonates evolved from terrestrial or freshwater ancestors, but the fact that both Heterostropha and Opisthobranchia include almost only marine forms, and the Siphonaroid limpets retain a veliger larva, would indicate the latter. It is speculated that they evolved from ancestral forms inhabiting estuarine marshes and mud flats, the pulmonate condition having evolved a s a means of gas exchange when the animals were confined to small stagnant puddles during the dry season [Barnes 1980 p.338]. Pulmonates first appear during the Jurassic period. [Clarkson, 1979 p.163] earlier forms now known to be terrestrial prosobrancha

Taxonomists typically divide the Pulmonata into at least three orders (sometimes superorders [Barnes 1980 p.377], the Basommatophora, Stylommatophora, and a small apparently primitive group of uncertain relationships, Systellommatophora.

Cladistic analysis has modified this picture somewhat. Jeffery 2001 divides the clade Eupulmonata into three branches, the Acteophila, Trimusculiformes, and Stylommatophora. Each are given the Linnaean rank of infraorder, in order to fit the whole hierarchy into a cladistic perspective. However it is my contention that the Linnaean ranks shouldn't be made to fit the cladistic tree (or vice-versa). So as the Stylommatophora are traditionally of ordinal rank, the same should go for the Acteophila (which would seem to be equivalent to Salvini-Plawen 1980's order Archaeopulmonata) and Trimusculiformes.

Vaught 1989 includes the Trimusculidae (a group of marine limpets) with the Siphonariidae in the Siphonarioidea (Order Basommatophora), but if placed there this would make the taxon paraphyletic. The Trimusculiformes includes only the superfamily Trimusculoidea and the family Trimusculidae Zilch, 1959

Links

Links

The trail of the Snail - non-technical introduction to Pulmonates (snails and slugs). Includes list of superfamilies and description of selected families and species (with illustrations) A-K and L-Z - **best on the web**

Pulmonates - short intro

Pulmonates (Air Breathing Land Snails) some information on Pulmonata and terrestrial

Prosobranchia. Includes a classification by Abbott & Dance, 2000 which is different from the one used here

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Pulmonata

Abbreviated Dendrogram

```
GASTROPODA
|--Caenogastropoda
`--Heterobranchia
   |--Opisthobranchia
   |
   `--PULMONATA
      |==Basommatophora
      `--+--Stylommatophora
         `--+--Systellommatophora
            `==Acteophila
```

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Acteophila

```
Heterobranchia
|--Opisthobranchia
`--PULMONATA
   |--ACTOPHILA
   |--SYSTELLOMMATOPHORA
   `--+--BASOMMATOPHORA
      `--STYLOMMATOPHORA
```

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shell of *Ophicardelus ornata* (Ferrusac, 1821)
Melampoidea - Melampidae
found in mangrove mud, Eastern Australia. Length of shell, 12 mm
Ophicardelus ornata image © Capricornica Publications Natural History Books

Included here are a small group of pulmonates that might be closely related to the Stylommatophora, or even possibly ancestral to them. Their taxonomic position has varied over the past decades. The Ellobioidea are included under the Order Basommatophora in Macpherson & Gabriel (1962), and the superfamily Ellobioidea in Salvini-Plawen's (1980) order Archaeopulmonata by Vaught (1989). But Jeffery 2001 includes the Ellobioidea in the clade Acteophila, in turn a subclade of the Eupulmonata (which also includes the Trimusculiformes and the Stylommatophora.

These animals inhabit salt marshes and mangroves near the sea. Most members of the family are tropical. The shell is rather solid, the aperture contracted by columnella teeth, although the inner walls of the shell are usually absorbed, leaving a single cavity. Macpherson & Gabriel (1962).

The following classification is from Jeffery (2001).

Melampoidea [=Ellobioidea & Auriculoidea]
    Melampidae Stimpson, 1851 [=Ellobiidae Adams & Adams, 1854/5]
    Carychiidae Jeffreys, 1830
    Leucophytiidae ?author
    Mesocochliopidae Yu, 1987
    Zaptychiidae Zilch, 1959

Links: Belongkeng Family Ellobiidae - Ellobiidae in Singapore

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Basommatophora

Abbreviated Dendrogram

```
GASTROPODA
|--Caenogastropoda
`--Heterobranchia
   |--Opisthobranchia
   |
   `--PULMONATA
      |==Basommatophora
      `--+--Stylommatophora
         `--+--Systellommatophora
            `==Acteophila
```

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Lymnaea stagnalis, the common European pond snail
(Lymnaeoidea - Lymnaeidae]

image © Chris Elliott

The Basommatophora are pulmonates with a single pair of tentacles; the eyes are located at the base of the tentacle.

This category includes more primitive members of the subclass than the land snails or Stylommatophora. The majority of Basommatophora species are found in freshwater, but there are also terrestrial and a few marine species. Some breathe air, others take oxygen from the water, and some do both. The freshwater genus *Lymnaea* includes species exhibiting all three respiratory habits. Chase (2002).

The shell varies widely from high-spired to flat and limpet-like, and the Planorbidae actually have planispiral shells. There are no shell-less species. Chase (2002).

The following classification is from Jeffery 2001. Superfamilies are in **bold**, families in normal font. The Lymnaeoidea, Planorbioidea, and Physoidea are listed as distinct superfamilies in Vaught (1989), but I have followed Jeffery (that being the more recent reference) in uniting them.

Amphiboloidea
- Amphibolidae Adams & Adams, 1855

Acroloxoidea
- Acroloxidae Thiele, 1931

Chilinoidea
- Chilinidae Adams & Adams, 1855
- Latiidae

Siphonarioidea

```
        Siphonariidae Gray, 1840

Lymnaeoidea [=Physoidea & Planorbioidea]
        Lymnaeidae Rafinesque, 1815
        Ancylidae Rafinesque, 1815 [=Rhodacmeidae ?author]
        Bulinidae Oken, 1815 [Bullinidae Vaught, 1989 err. pro Bulinidae]
        Lancidae Hannibal, 1914
        Neoplanorbidae Hannibal, 1912
        Physidae Fitzinger, 1833
        Patelloplanorbidae ?Hubendick, 1957
        Planorbidae Rafinesque, 1815
        Protancylidae Walker, 1923

Glacidorboidea
        Glacidorbidae Ponder, 1986
```

The **Amphibolids** are the only operculate pulmonates. They inhabit salt marshes near the sea, and are able to seal the shell with the operculum and so survive dry periods buried in mud. Macpherson & Gabriel (1962).

The **Siphonariids**, which inhabit marine intertidal environments, and are considered the most primitive forms. *Siphonaria* is one of the few pulmonates that possesses a veliger larva, indicating its marine habitat is not a secondary return to the sea, it also has a secondary gill. Barnes (1980).

Planorbis sp., a pond snail with a Planispiral shell
[Lymnaeoidea - Planorbidae - Planorbinae - Planorbeae]

images from Photogallery of snails and csiga

The **Lymnaeoidea** include a large number of freshwater forms. Species like *Lymnaea* , *Bulinus*, and *Physea* come to the surface to obtain air. But some deep lake lymnaeids have abandoned air breathing and fill the mantle cavity with water. Secondary gills are found in Ancylids, which are freshwater limpets adapted to life in fast-flowing streams. They are also found in some Planorbids, which may also have secondary gill folds inside the mantle cavity. Barnes (1980).

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Stylommatophora

Abbreviated Dendrogram

```
GASTROPODA
|--Caenogastropoda
`--Heterobranchia
   |--Opisthobranchia
   |
   `--PULMONATA
      |==Basommatophora
      `--+--Stylommatophora
         `--+--Systellommatophora
            `==Acteophila
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Helix aspersa, (M�ller, 1774) the common European garden snail. Width and height of shell about 2.5 to 3 cm. This successful and adaptable species is found throughout Europe, the Middle-East, North and South America and Australia, where it has been introduced and established itself in suburban areas. See Snail Species - the Family Helicidae for more.
(Sigmurethra - Helicoidea - Helicidae - Helicinae]

image © Chris Elliott

The higher pulmonates, or Stylommatophora, are a successful clade that far outnumber the Basommatophora in species. This order, the most advanced and specialized of all the pulmonates, includes most land snails and slugs represent one of the major metazoan invasions of the land, comprising some 30,000 to 35,000 species (with many more probably awaiting discovery) - almost equivalent to vertebrates as a whole. They include the familiar garden snail and slug, but also thousands of less known species. They Stylommatophora are major components of many terrestrial ecosystems, and have also become important models for studies on the mechanisms of evolution and biogeographic studies (Wade, iNet). They frequently occur beneath leaf litter, stones and bark, and are especially abundant on oceanic islands, such as the Pacific [Barnes 1980 p.340]. The name "Stylommatophora" means "slender eye-bearing stalk", and refers to the fact that these animals have two pairs of tentacles, with eyes located at the tips of the upper (posterior / dorsal), pair, rather than at the base, as is the case with the Basommatophora. All species are terrestrial, and many are locally abundant. Although most stylommatophores feed on plants and detritus, a few are carnivores that feed on other snails. Chase 2002 p.15

Agathylla biloba (A. J. Wagner 1914)
(Sigmurethra - Clausilioidea - Clausiliidae - Alopiinae]

Photo © V. Wiese, Haus der Natur Cismar, from Albanian non-marine molluscs

Most species have thin to moderately thick calcareous conispiral shells, which range from very low-spired to steep-sided, high-spired forms. A majority have many whorls, generally but not always more than among basommatophorans. [Moore, et al 1952, p.332]. There are also includes shell-less slugs and semi-slugs with residual shells that are too small to accommodate the body. In fact, as with the Opisthobranchia, shell reduction has occurred independently a number of times in different lineages. Slugs seem to have evolved in environments of low calcium and high humidity [Barnes 1980 p.340].

The aperture usually has a rather evenly rounded outer lip, often with a thickened rim. Tooth-like projections of the inner lip, and in some shells of the outer lip also, serve to keep out predators such as insects but allow the soft snail to squeeze through [Barnes 1980 p.340]. . Such features especially characterize genera of the Pupidae, and largely because of the close resemblance of some Pennsylvanian non-marine gastropods to the modern *Pupa*, these Paleozoic fossils were at one time thought to belong among the stylommatophorans [Moore, et al 1952, p.332]. This is now no longer believed to be the case, and it is generally agreed that the Pulmonates, including the Stylommatophora, evolved much later, during the Jurassic period. [Clarkson, 1979 p.163]

Most Stylommatophora are fairly small, averaging less than a centimeter in shell length or width, although the giant African snail *Achatina achatina*, have shells that reach 27 cm [Barnes 1980 p.340]

In terms of diversity, they are the largest clade of gastropods, with some 35,000 species, and from 71 to 92 families, depending on the classification scheme used (Bieler, 1992; Wade et al., 2001). Part of this diversity may be due to the fact that local populations easily become isolated, as the animals move slowly, and have little need to migrate. This leads to both greater speciation and greater intraspecific genetic variation [Chase 2002 pp.13-14]. According to Thomaz et al., 1996, *Cepaea nemoralis* has the most extreme intraspecific variation of mitochondrial DNA of any animal.

the European land snail *Cepaea nemoralis*
(Sigmurethra - Helicoidea - Helicidae - Helicinae]
Earliest Pleistocene to Recent
Width and height of shell about 2 cm.
This very variable European species is found throughout the world. See Snail Species - the Family Helicidae for more.

image Michigan State University

The monophyletic composition of the Stylommatophora has been confirmed by molecular analysis of ribosomal RNA (Wade & Mordan, 2000, Wade et al., 2001).

The origins and the deep-level evolutionary relationships of their major groupings within the Stylommatophora are controversial, with anatomical studies giving confusing and conflicting results. The following arrangement from Jeffery 2001 (contrast with older classification by Abbott & Dance, 2000) has been modified in the light of molecular research by Chris Wade involving ribosomal RNA gene sequencing. Dr Wade's research reveals a single assemblage including the families Achatinidae, Subulinidae and Streptaxidae near the base of the group, forming a sister group to all remaining stylommatophorans and dividing the order into 'achatinoid' and 'non-achatinoid' taxa. The Orthurethra appear to be relatively advanced within the 'non-achatinoid clade', and broadly equivalent to other super-familial clusters, indicating that supposedly primitive features such as the orthurethran kidney are in fact derived. (Wade, iNet)

I have also modified the Linnaean ranking in keeping with the standard ordinal grade normally given to the Stylommatophora

Although the molecular tree also suggests that the origin of the Stylommatophora is much earlier than the main period of their diversification (Wade, iNet), this may simply (as with the Cambrian explosion and other important events) be a result of evolutionary heterochrony.

Order STYLOMMATOPHORA

- **'achatinoid' taxa** (unnamed clade).
- **Achatinoidea** (formerly included under Sigmurethra)
    - Achatinidae Swainson, 1840
    - Coeliaxidae Pilsbry, 1907
    - Ferrussaciidae Bourguignat, 1883
    - Glessulidae Schileyko, 1996
    - Subulinidae Thiele, 1931
    - Thyrophorellidae Thiele, 1926
- **'non-achatinoid' taxa** (unnamed clade)

Suborder SIGMURETHRA

- **Buliminoidea**
    - Buliminidae Clessin, 1879 [?Pfeiffer, 1879] [=Enidae Woodward, 1903, in part]
    - Cerastuidae Wenz, 1923 [=Enidae Woodward, 1903, in part]

- **Clausilioidea**
    - Clausiliidae M�rch, 1864
    - Triptychiidae ?author

- **Orthalicoidea** [=Bulimulacea]
    - Orthalicidae Albers-Martens, 1860
    - Amphibulimidae Crosse & Fischer, 1873
    - Anadromidae Zilch, 1959
    - Cerionidae Pilsbry, 1901 [=Ceriidae]
    - Coelociidae Nordsieck, 1986
    - Grangerellidae Russel, 1931
    - Megaspiridae Pilsbry, 1904 [=Coelociontidae Iredale, 1937]
    - Microceramidae Pilsbry, 1903
    - Odontostomidae Pilsbry & Vanatta, 1898
    - Urocoptidae Pilsbry & Vanatta, 1898 [?1896]

- **Aillyoidea**
    - Aillyidae Baker, 1930
    - Oleacinoidea
    - Oleacinidiae Adams & Adams, 1855
    - Spiraxidae Baker, 1939
    - Testacellidae Gray in Turton, 1840

- **Streptaxoidea**
    - Streptaxidae Gray, 1806

- **Strophocheiloidea**
    - Strophocheilidae Thiele, 1926
    - Dorcasiidae Thiele, 1926
    - Megalobulimidae Leme, 1973

- **Acavoidea**
    - Acavidae Pilsbry, 1895
    - Caryodidae Thiele, 1926
    - Macrocyclidae Thiele, 1926
    - Megomphicidae Baker, 1930 [=Ammonitellidae ?author]

- **Rhytidoidea**

Rhytididae Pilsbry, 1893 [?1895; =Paryphantidae ?author]
Aperidae ?author [=Chlamydephoridae Cockerell, 1935]
Haplotrematidae Baker, 1925
Systrophiidae Thiele, 1926 [=Scolodontidae Baker, 1925]

Plectopylidoidea
Plectopylididae Moellendorf, 1900 [=Corillidae ?author]
Sculptariidae ?Vaught, 1989

Arionoidea
Arionidae Gray in Turton, 1840
Philomycidae Gray, 1847

Punctoidea [=Endodontoidea]
Punctidae Morse, 1864
Charopidae Hutton, 1884
Discidae Thiele, 1931
Endodontidae Pilsbry, 1895
Helicodiscidae Baker, 1927
Oopeltidae Cockerell, 1891
Oreohelicidae Pilsbry, 1939
Otoconchidae Cockerell, 1893
?Philiomycidae ?author

Sagdidoidea
Sagdidae Pilsbry, 1895 [=Sagdididae Tracey, Todd & Erwin, 1993]

Gastrodontoidea
Gastrodontidae Tryon, 1866

Helixarionoidea [=Helicarionoidea]
Helixarionidae Bourguignat, 1883 [=Helicarionidae Bourguignat, 1883 & Godwin & Austen, 1883/8]
Ariophantidae Godwin-Austen, 1888 [?Germain, 1921]
Cystopeltidae ?Vaught, 1989
Dyakiidae ?author
Euconulidae Baker, 1928 [?Strebel & Pfeffer]
?Sesaridae ?author
Trochomorphidae Moellendorf, 1890
Urocyclidae Simroth, 1889

Vitrinoidea [=Zonitoidea]
Vitrinidae Fitzinger, 1833
Daudebardiidae Kobelt, 1906
Milacidae Ellis, 1926 [?Germain, 1930]
Parmacellidae Gray, 1860
Plutoniidae Wiktor & Backeljau, 1995
Plutoniinae Cockerell, 1893
Zonitidae M�rch, 1864

Limacoidea
Limacidae Rafinesque, 1815
Agriolimacidae Wagner, 1935
Boetgerillidae ?author
Thyphorellidae ?author

Trigonochlamydoidea
Trigonchlamydidae Hesse, 1882
?Papillodermidae Wiktor, Martin & Castillejo, 1990

Polygyroidea [=Mesodontoidea]
Polygyridae Pilsbry, 1894/5 [?1940] [=Mesodontidae Tryon, 1866]
Thysanophoridae Pilsbry, 1926

Camaenoidea
Camaenidae Pilsbry, 1895
Solaropsidae Nordsieck, 1986

Helicoidea [=Xanthonychoidea]
Helicidae Rafinesque, 1815
Cochlicellidae Schileyko, 1972 {from Cochlicellinae (Hygromiidae)}
Eulotidae Moellendorf, 1898 [=Bradybaenidae Pilsbry, 1934]
Hygromiidae Tryon, 1866 [=Helicellidae ?author]
Monadeniidae Schileyko, 1996
Monadeniinae Nordsieck, 1987
Sphincterochilidae Zilch, 1960
Xanthonychidae Strebel & Pfeffer, 1880 [?=Helminthoglyptidae Pilsbry, 1939]

Suborder ORTHURETHRA

Achatinelloidea
Achatinellidae Gulick, 1873 [?=Pacificellidae Steenberg, 1925]
Cochlicopoidea [=Cionelloidea]
Cochlicopidae Pilsbry, 1900 [=Cionellidae ?author]
Amastridae Pilsbry, 1911
Pupilloidea

```
          Pupillidae Turton, 1831
          Chondrinidae Steenburg, 1925
          Orculidae Pilsbry, 1918
          Pleurodiscidae Wenz, 1923
          Pyramidulidae Kennard & Woodward, 1914
          Strobilopsidae Pilsbry, 1918
          Valloniidae Morse, 1864 [?Pilsbry, 1900]
          Vertiginidae Fitzinger, 1833 [?Stimpson, 1851]
          Partuloidea
          Partulidae Pilsbry, 1900
```

?**Succineoidea** [=Heterurethra]
Succineidae Beck, 1837

?**Athoracophoroidea** [=Tracheopulmonata]
Athoracophoridae Fischer, 1883

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Systellommatophora

Abbreviated Dendrogram

```
GASTROPODA
|--Caenogastropoda
`--Heterobranchia
   |--Opisthobranchia
   |
   `--PULMONATA
      |==Basommatophora
      `--+--Stylommatophora
         `--+--Systellommatophora
            `==Acteophila
```

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The Systellommatophora include several families of slug-like animals that have been continuously shuffled from one taxon to another (Chase, 2002), but don't seem to fit in either the Basommatophora and Stylommatophora. All have the anus located at the posterior end of the body, but the intertidal Onchidiidae have a posterior pulmonary sac, while the tropical Veronicellidae have lost the pulmonate lung. Barnes (1980).

The Systellommatophora are considered a polyphyletic taxon by Wade & Mordan (2000).

The following classification is from Jeffery 2001

Suborder SYSTELLOMMATOPHORA **Otinoidea** Otinidae Adams & Adams, 1855 Smeagolidae Climo, 1980 **Onchidoidea** Onchidiidae Gray, 1824 **Rathouisioidea** [= Order Soleolifera [Solem 1978]] Rathouisiidae Sarasin, 1899 Veronicellidae Gray, 1840

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Rostroconchia

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   |==TRYBLIDIIDA (Monoplacophora)
   |   `--CEPHALOPODA
   `==HELCIONELLOIDA
       |--ROSTROCONCHIA
       |  |--+--Conocardiida
       |  |   `--+==Ribeirioida
       |  |      `--SCAPHOPODA
       |  `--BIVALVIA
       `--GASTROPODA
```

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Apotocardium sp, (Rostroconchia - Conocardiida - Bransoniidae) Graham Formation (Late Carboniferous), Jack co., Tx. .
Photo © Lance L. Hall, North Texas Fossils, Rostroconchia.

The Rostroconchia are a group of exclusively Paleozoic molluscs which combine the features of scaphopods and bivalves and may or may not (depending on your preferred phylogeny) be related to both. Alrthough typical rostroconches only come after the first bivalves, earlier stem forms such as *Heraultipegma* and *Watsonella* may well be ancestral to both groups. Alternatively, rostroconches may simply be stem group scaphopods, and bivalves may have evolved from separate conchiferan ancestors. MAK120614

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Rostroconchia

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   |==TRYBLIDIIDA (Monoplacophora)
   |   `--CEPHALOPODA
   `==HELCIONELLOIDA
       |--ROSTROCONCHIA
       |  |--+--Conocardiida
       |  |   `--+==Ribeirioida
       |  |      `--SCAPHOPODA
       |  `--BIVALVIA
       `--GASTROPODA
```

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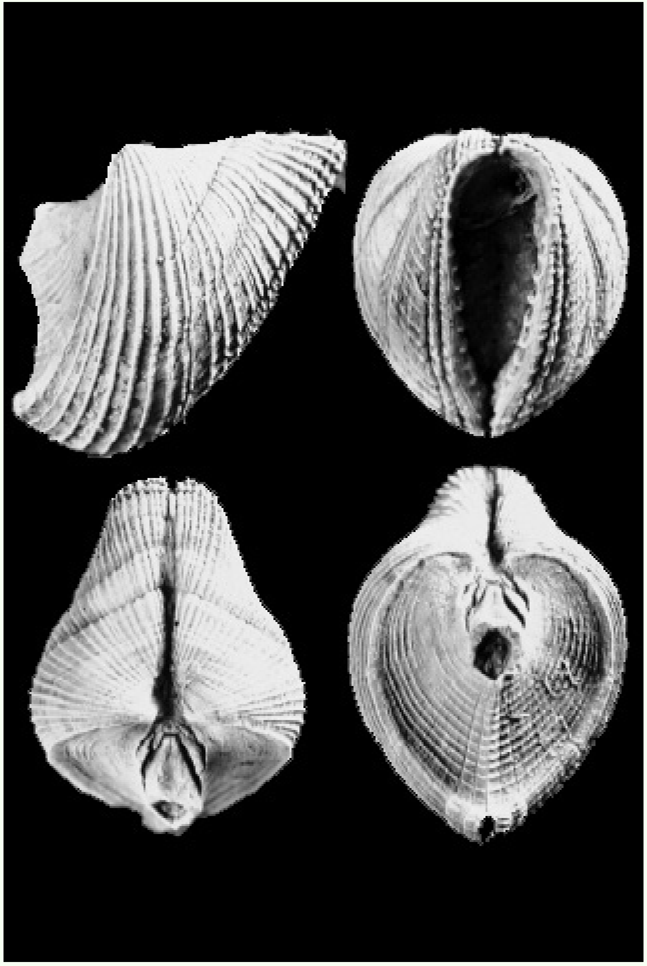
1. Rostroconchia

Introduction



Conocardiiid rostroconch

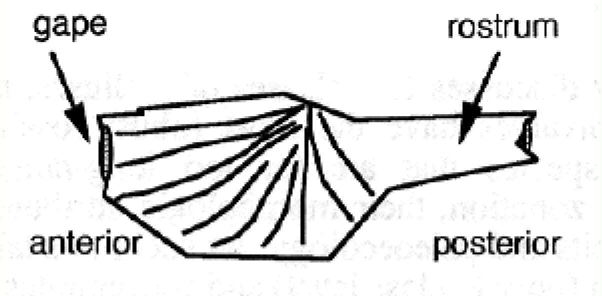
image © xxxx from Lecture 8 Origin and Evolution of the Mollusca (former page) / Lecture 11 Evolution of the Mollusca: bivalves (former page)

The Rostroconchia are a group of Palaeozoic bivalved molluscs that were originally considered Bivalves, but were then realised to belong to a distinct class of their own. Pojeta *et al*. (1972); Pojeta & Runnegar (1976). According to the latter workers, rostroconches are Conchifera with "an uncoiled and untorted univalved shell which straddles the dorsal midline, and a bivalved adult shell… [with] dorsal commissure lacking." They are characterized by a single, pseudobivalved shell which enclosed the mantle and muscular foot. The anterior, probably downwards-orientated, part of shell has a gape from which the foot may have emerged. They probably lived a sedentary semi-infaunal lifestyle

To date, about three dozen genera and a greater number of species have been described. Most rostroconches are small, often less than two centimeters in length, but large forms, about 15 cm long, can be found inDevonian limestones of the midcontinental United States.

Physiology and Lifestyle

The following sketch © xxxx from McRoberts 1998 shows the main parts of the rostrochonch shell.



Rostroconchs look superficially like bivalves and like them probably had an extensible foot, as indicated by a prominant anterior gape in the shell. However, the shape of the foot, and perhaps the internal anatomy, were probably much closer to the scaphopods, which, according to one theory, they gave rise to.

Rostroconchs began life as a small limpet-like, bilaterally symmetrical protoconch larva, probably (like the scaphopod larva) planktonic. From this the adult, likewise bilaterally symmetrical shell (dissoconch) grew down as a pair of valves.

The adult rostroconch superficially resembles a bivalve, but differs in that there is no functionalhinge. Instead of a flexible ligament or articulating system that charcterises the bivalve hinge, some or all of the shell layers -- layers of stiff calcite -- are continuous across the region of the dorsal margin. The effect is that the rostroconch shell functions more like a taco shell than a clam shell. The two shell valves would have been rigidly fixed in place. Rather than having a hinge, the dorsal margin would, at most, have formed a poorly elastic structure. The shell apparently broke periodically at the margin to permit shell growth.

The posterior of the shell is usually elongated into a flattened tube called the *rostrum* through which inhalent and exhalent siphons may have emerged. It can be assumed that the animal positioned itself so that the rostrum was above the layers of sediment in which the creature had burrowed; perhaps also the rostrum which may have aided in water filtration.

Evolutionary History

The earliest known rostroconch genus, *Heraultipegma*, dates from the Late Terreneuvian (Tommotian), but is much more primitive than the typical or true rostroconchs. These appeared and flourished during the Early Ordovician, almost rivalling true bivalves, with which they may or may not have shared a similar lifestyle, in numbers and variety. But with the end-early Ordovician (Floian) turn-over they declined, and only one order, the Conocardioida, continued until the Guadalupian (Middle Permian). Clarkson (1993); Paleobiology Database (acc. 080222).

The earlier and more primitive rostroconchs such as *Ribeiroia* (order Ribeirioida) had a hinge in which all the shell layers traversed the dorsal margin, resulting in a rigid shell. In more advanced forms, like *Conocardium*, the outer layer does not cross the margin, suggestiung an independent step towards the condition already achieved by bivalves. *Conocardium*, has a gape at one end and very pronounced rostrum at the other.

According to Engeser & Riedel (1997), during the Devonian, the conocardoid rostroconchs gave rise to the Scaphopoda, which would therefore be Rostroconchia (in the same way that birds are dinosaurs). MAK021208, revised ATW080222.

Evolutionary Relationships

Rostroconchs almost certainly evolved from helcionelloid molluscs (Pojeta & Runnegar, 1976; Peel, 1991; Wagner, no date) during the early Cambrian. It was originally suggested (Runnegar & Pojeta, 1974; Pojeta & Runnegar, 1976) that they gave rise to the bivalves on the one hand (by separation of the valves and development of a proper hinge), and the Scaphopoda on the other (with the valves forming into a long tube). However, some cladistic and molecular evidence (Waller, 1998; Steiner & Dreyer, 2002) indicates that bivalves are only distantly related to scaphopods, but that cephalopods are closely related to scaphopods.

Embryological evidence (Scaphopod protoconchs) might support the thesis that Scaphopods evolved from rostroconchs. Engeser & Riedel (1997). Moreover, cephalopods (Pojeta, 1980) or both scaphopods and cephalopods (Runnegar, 2002; Steiner & Dreyer, 2002), are closely related to, or descended from, laterally compressed helcionelloids. Now, these early primitive helcionelloids are precisely the same forms that can be seen as the ancestors of the Rostroconchia [Wagner no date]. So, the implication might be that helcionelloids gave rise to both rostroconchs and cephalopods, but not to Bivalves, and that rostroconchs in turn were the ancestors of scaphopods.

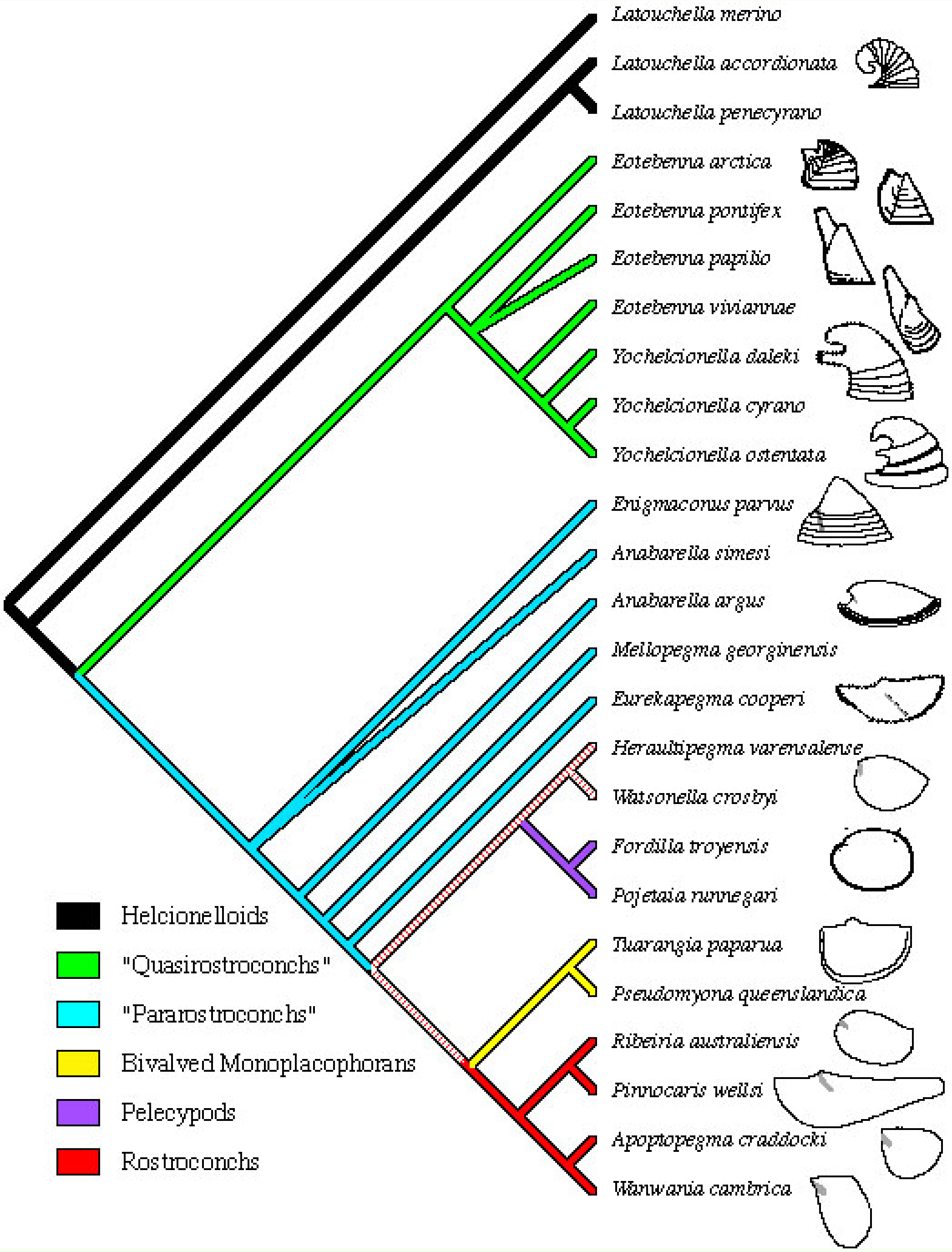
Truthfully, we find these ancestor-descendant hypotheses unnecessary and confusing. Like Steiner & Dreyer (2003), we reject them. Those authors argue that both molecules and morphology unite scaphopods and cephalopods. If so, then rostroconches are either some sort of (probably) paraphyletic group at the base of the Conchifera, or they share a branch with the bivalves. The similarity of rostroconchs to the helcionelloids (Peel, 2004) is interesting, but doesn't help much, because the Helcionelloida are (definitely) some sort of paraphyletic group at the base of the Conchifera. Therefore, the helcionelloid chracters shared by rostroconchs are likely to be uninformative characteristics of the ancestral conchiferans. Our choice is thus somewhat arbitrary, but it is natural to believe that the pseudo-bivalved rostroconchs might have a more than casual relationship with real bivalves; and that is where we have placed them. MAK021208, last revised ATW080222.

Systematics and Classification

The Class Rostroconchia (Pojeta, Runnegar, Morris & Newell,1972) is usually divided into two orders, as follows:

Order **Ribeirioida** (Early Cambrian to Early Silurian)
Order **Conocardiida** (also spelt Conocardioida) (Furongian to Late Permian)

The Ribeirioida are actually a paraphyletic grade, as they give rise to the Conocardiida. The following cladogram by Wagner shows the relationships between the earliest Rostroconchia and their Helcionellid ancestors:



graphic © Peter Wagner

Note that this cladogram has the Bivalvia (Pelycopods - in purple) emerging from proto-rostroconchs. This disagrees with morphological cladistic evidence, according to which the Scaphopods are most closely related to Cephalopods, and only distantly to bivalves. Thus either Scaphopods or Bivalves, but not both, evolved from Rostroconch ancestors, in which case they independetly developed similar morphotlogies as a result of exploiting similar infaunal lifestyles, rather than actual ancestor-descent relationships. Some current molecular phylogenies however have scaphopods, bivalves, and gastropods forming a single clade (with gastropods either closer to bivalves or scaphopods). In this case simialrities between scaphopods and cephalopods are due to convergence. This hypothesis is hard to explain ecologically, as the two evolutionary lineages would have occupied very different ecological niches (infaunal and weakly nektonic repsectively). So either the current (circa 2011) molecular consensus is completely wrong, or proto-cephalopods also went through an infaunal stage. revised MAK120614

Descriptions

Rostroconchia

Range: Cambrian Epoch 2 to Late Permian

Phylogeny: Paraphyletic Helcionelloida **:** Gastropoda + Bivalvia + * **:** (Conocardiida + (Ribeirioida + Scaphopoda)

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Rostroconchia: Conocardiida

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   |==TRYBLIDIIDA (Monoplacophora)
   |   `--CEPHALOPODA
   `==HELCIONELLOIDA
       |--ROSTROCONCHIA
       |  |--+--Conocardioida
       |  |   `--+==Ribeirioida
       |  |      `--SCAPHOPODA
       |  `--BIVALVIA
       `--GASTROPODA
```

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1. Conocardiida

Genera

The following list of genera is from the Systema Naturae 2000 Rostroconchia page on Conocardioida

All photos are from LAB 3 Chapter 8: Phylum Molusca, Boardman et al, 1987

Genus *Arceodomus*
Stratigraphic range: Late Mississippian to Early Permian

Genus *Bigalea*
Stratigraphic range: Middle Devonian

Genus *Bransonia*
Stratigraphic range: Early Ordovician to Permian

Genus *Conocardium*
Stratigraphic range: Middle Devonian to Pennsylvanian

Genus *Eopteria*
Stratigraphic range: Early Ordovician

Genus *Euchasma*
Stratigraphic range: Early Ordovician

Genus *Hippocardia*
Stratigraphic range: Middle Ordovician to Pennsylvanian

Genus *Mulceodens*
Stratigraphic range: Middle Silurian to Late Silurian

Genus *Pseudoconocardium*
Stratigraphic range: Late Pennsylvanian

Genus *Pseudotechnophorus*
Stratigraphic range: Furongian

Descriptions

Conocardiida Neumayr 1891

Synonyms: Conocardioida, Conocardioidea

Range: Furongian (Late Cambrian) to Lopingian (Late Permian)

Phylogeny: Rostroconchia **:** (Ribeirioida + Scaphopoda) + *

Comments: more commonly spelt Conocardioida, we have used the original spelling (preferred by the Paleobiology database). The ancestry of the Scaphopoda is still uncertain, as either rostroconch group may have given rise to them (see comments at the Beak-Shells' Legacy). MAK120614

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Rostroconchia: Ribeirioida

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   |==TRYBLIDIIDA (Monoplacophora)
   |   `--CEPHALOPODA
   `==HELCIONELLOIDA
       |--ROSTROCONCHIA
       |  |--+--Conocardiida
       |  |   `--+==Ribeirioida
       |  |      `--SCAPHOPODA
       |  `--BIVALVIA
       `--GASTROPODA
```

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1. Ribeirioida

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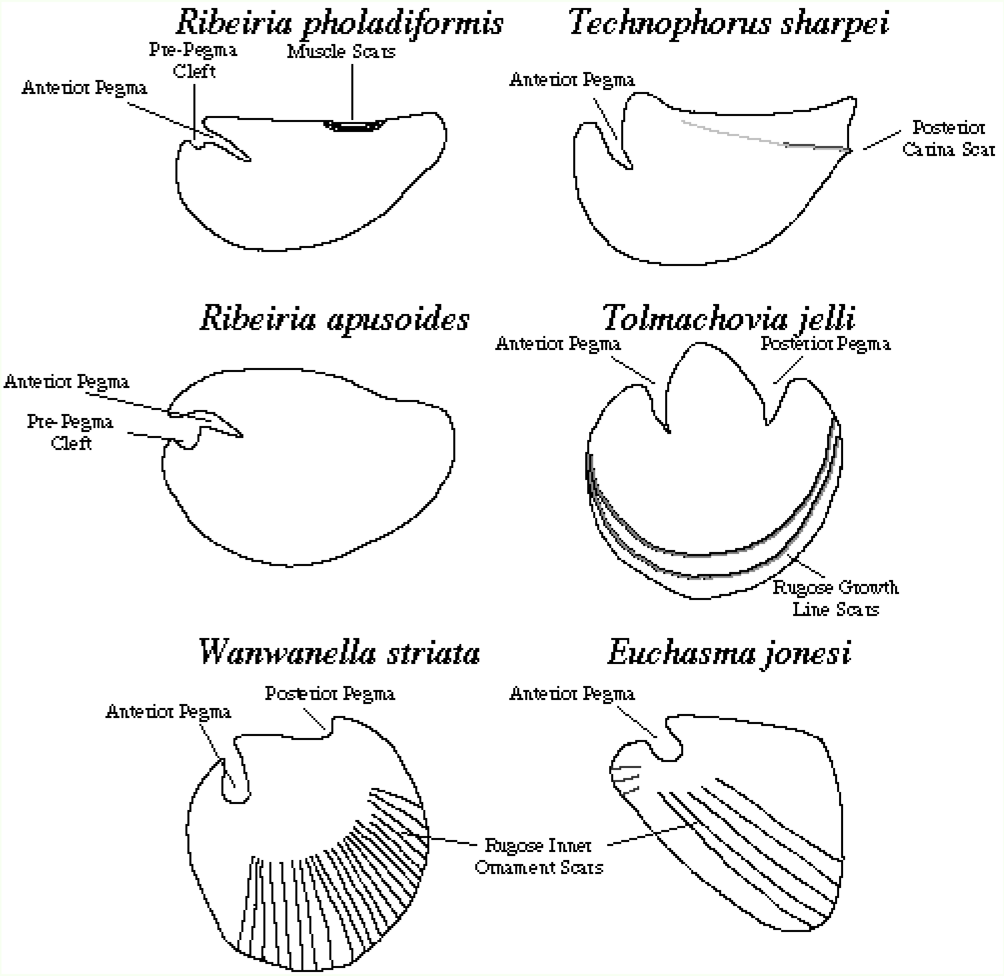

drawings © Peter Wagner

Genera

The following list of genera is from the Systema Naturae 2000 Rostroconchia page on Ribeirioida

Genus *Anisotechnophorus*

Genus *Apoptopegma*
Stratigraphic range: Early Ordovician

Genus *Cymatopegma*
Stratigraphic range: Furongian

Genus *Heraultipegma*
Stratigraphic range: Early Cambrian

Genus *Ischyrinia*
Stratigraphic range: Middle Ordovician to Late Ordovician

Genus *Kimopegma*
Stratigraphic range: Furongian

Genus *Myocaris*
Stratigraphic range: Middle Ordovician

Genus *Oepikila*
Stratigraphic range: Furongian

Genus *Pauropegma*
Stratigraphic range: Early Ordovician

Genus *Pinnocaris*
Stratigraphic range: Furongian to Late Ordovician

Genus *Pleuropegma*

Genus *Ptychopegma*
Stratigraphic range: Early Ordovician

Genus *Ribeiria*
Stratigraphic range: Furongian to Middle Ordovician

Genus *Technophorus*
Stratigraphic range: Early Ordovician to Late Ordovician

Genus *Tolmachovia*
Stratigraphic range: Early Ordovician to Middle Ordovician

Genus *Wanwania*

Descriptions

Ribeirioida

Range: Early Cambrian to Llandovery

Phylogeny: Rostroconchia **:** Conocardiida + (Scaphopoda + *)

Comments: may or may not be paraphyletic group ancestral to extant Scaphopods (see comments at the Beak-Shells' Legacy). MAK120614

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The Beak-Shells' Legacy

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   |==TRYBLIDIIDA (Monoplacophora)
   |   `--CEPHALOPODA
   `==HELCIONELLOIDA
       |--ROSTROCONCHIA
       |  |--+--Conocardiida
       |  |   `--+==Ribeirioida
       |  |      `--SCAPHOPODA
       |  `--BIVALVIA
       `--GASTROPODA
```

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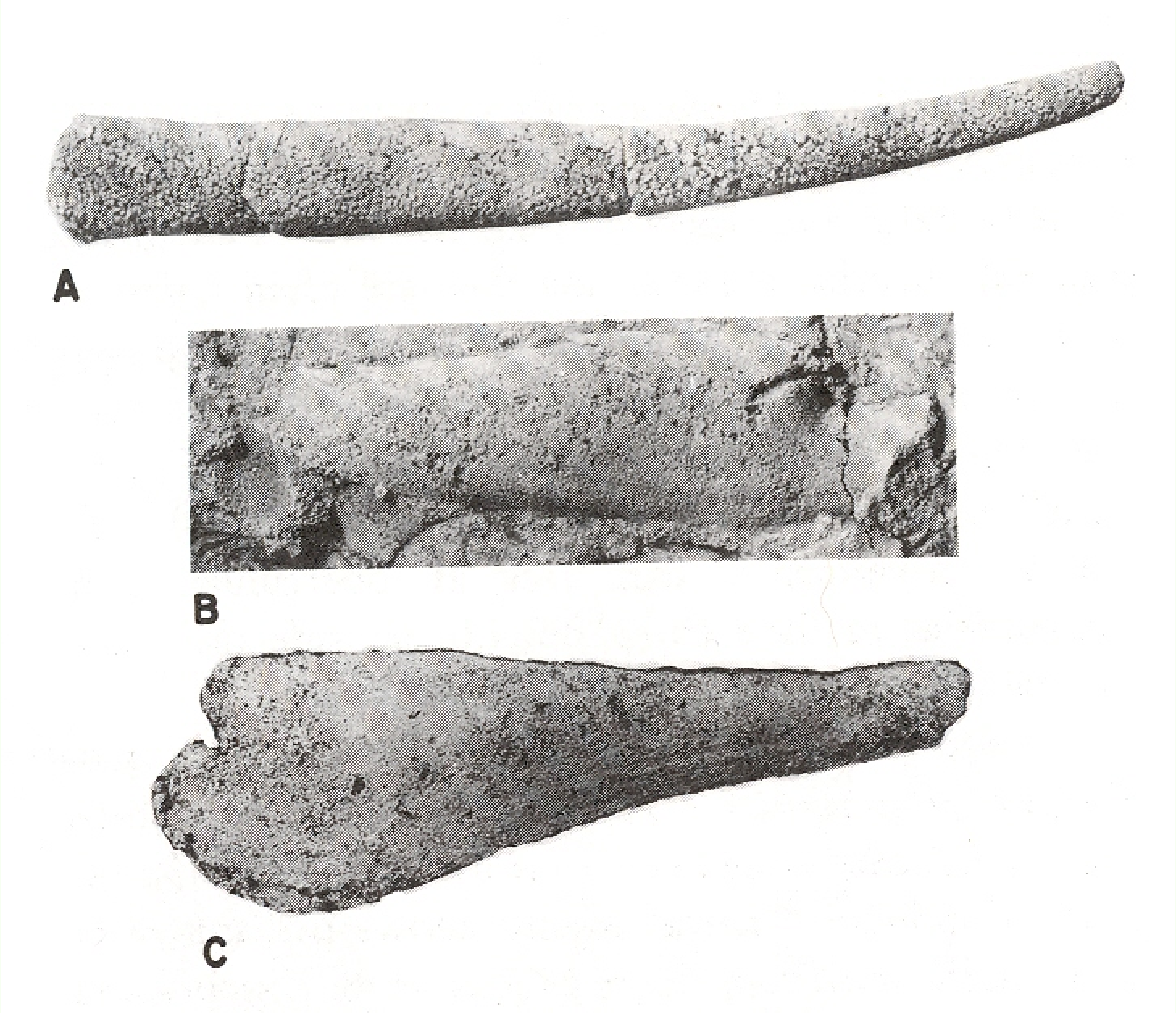
The Beak-Shells' Legacy

By Christopher Taylor - Catalogue of Organisms

Specimen of *Conocardium japonicum*, from here.

The Rostroconchia were a group of molluscs that lived during the Palaeozoic, being definitely found from the Late Cambrian to the latest Permian. The name means, roughly, 'beak-shell', and refers to the shape of the shell. Similar to bivalves (with which rostroconchs were classified prior to the 1970s), rostroconchs had a shell divided into left- and right-hand valves, which in many species were elongate in one or both directions forewards and backwards. The shells of different species gaped to varying degrees at the posterior and anterior ends. Rostroconchs differed from bivalves, however, in that the original larval shell was not divided. Instead, the shell of a rostroconch was initially cap-shaped and entire. As the animal developed past the larval stage, the shell developed lateral lobes that would eventually become the two valves. As a result, rostroconchs did not have a toothed hinge connecting the valves like that of bivalves. Nevertheless, in many species, the pressure of the valves growing outwards eventually caused the larval shell to break through (Pojeta & Runnegar 1976). Like many bivalves, rostroconchs would have been infaunal, living buried in the sediment; however, the absence of a toothed hinge or the adductor muscles that connect the valves in bivalves means that the shell of rostroconchs would have been less flexible.



The Ordovician scaphopod *Rhytiodentalium* (topmost image) and the scaphopod-like rostroconch *Pinnocaris* (lower two images), from here.

The largest work to date on rostroconchs was that of Pojeta & Runnegar (1976), who suggested that rostroconchs included the ancestors of two living classes of molluscs, the bivalves and the scaphopods. Scaphopods, tusk-shells, are a group of tubular molluscs with an opening at each end of the tube that also live buried in sediment. According to Pojeta & Runnegar's suggestion, the bivalves evolved through the evolution of two calcification centres in the larval stage. The scaphopods would have evolved through the fusion of the valves along the ventral margin (as embryological studies have shown the scaphopod shell does develop), together with the restriction of growth to the anterior direction only.

However, more recent studies of molluscan phylogeny (Wilson et al. 2010) have mostly indicated that bivalves and scaphopods are not closely related relative to other molluscs. Bivalves are probably a relatively basally derived group, while scaphopods are closer to cephalopods. The upshot of this for rostroconchs is that they may be related to bivalves or scaphopods, but not to both. Of the two, it seems more likely that rostroconchs are related to scaphopods (or, as some authors have put it more bluntly, scaphopods are living rostroconchs). As well as the anatomical arguments that have been made in favour of such a relationships, a scaphopod connection has the advantage over a bivalve one of stratigraphy. The oldest definite rostroconchs, as previously noted, are known from the Late Cambrian. However, the oldest definite bivalves come from the Early Cambrian—that is, some 40 or 50 million years earlier than the first known rostroconchs. Scaphopods, on the other hand, do not appear until the Ordovician or Devonian (depending on whether the earlier forms are accepted as scaphopods), well after the known appearance of their supposed ancestors. Pojeta & Runnegar (1976) did not recognise a stratigraphic conflict in deriving bivalves from rostroconchs as they had identified the Early Cambrian *Heraultipegma* as a rostroconch. This identification, however, was disputed by MacKinnon (1985), who held that the characters cited by Pojeta & Runnegar in support of their assignation had been misinterpreted and were not truly present in *Heraultipegma*.

The conocardioid rostroconch *Arceodomus longirostris*, from here.

Pojeta & Runnegar (1976) recognised three orders of rostroconch: the Ribeirioida, Ischyrinioida and Conocardioida. This division has been followed by all subsequent authors, though it should be noted that Pojeta & Runnegar recognised the Ribeirioida as explicitly paraphyletic with regard to the other orders. Pojeta & Runnegar (1976) regarded the scaphopods as derived from ribeirioids (specifically related to the somewhat scaphopod-like Pinnocaris), but Peel (2004) stated that protoconch characters indicated a derivation from conocardioids. The ribeirioids and ischyrinioids both became extinct at the end of the Ordovician, leaving only the conocardioids and their descendent scaphopods until the former also became extinct at the end of the Palaeozoic.

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Rostroconchia: Dendrogram

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   |==TRYBLIDIIDA (Monoplacophora)
   |   `--CEPHALOPODA
   `==HELCIONELLOIDA
       |--ROSTROCONCHIA
       |  |--+--Conocardiida
       |  |   `--+==Ribeirioida
       |  |      `--SCAPHOPODA
       |  `--BIVALVIA
       `--GASTROPODA
```

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Rostroconchia Dendrogram

Rostroconch phylogeny remains contentious. One possible arrangement is the following. Note however that it is both inconsistent with our backbone phylogeny and does not account for the Ribeirioida.

```
   <==o "ROSTROCONCHOMORPHA"
     `--+--Stenothecidae [Helcionellida; = "Pararostroconchs"]
        |--+-- Heraultipegma varensalense
        |   `-- Watsonella crosbyi
        `--+--+-- Taurangia paparua
           |  `-- Pseudomyona queenslandica
           `--o ROSTROCONCHIA
              |--Eopteroidea
              `--o Conocardioidea
                 |-- Hippocardiidae
                 |-- Bransoniidae
                 `--+-- Conocardiidae
                    `-- SCAPHOPODA
```

The following more complex dendrogram is by Christpher Taylor CKT071117 and mainly dfscuses on the Conocardioida (= Conocardiida)

```
     Rostroconchia
      |   i. s.: Hippocardia Brown 1843
      |            |--H. alborza
      |            |--H. bohemica (Barrande 1881)
      |            |--H. cunea (Conrad 1840)
```

```
|           `--H. kermani Hoare & Aghababalu 2001
|         Riberia apusoides Schubert & Waagen 1903
|         Heraultipegma
`--Conocardioida [Conocardioidea]
     |--Pseudobigaleaidae
     |    |--Pseudobigalea Hoare et al. 1982
     |    |    `--*P. crista Hoare, Mapes & Brown 1982 (see below for synonymy)
     |    |--Exalloschema Hoare, Mapes & Yancey 2002
     |    |    `--*E. batilia (Hoare, Mapes & Brown 1982) [=Hippocardia batilia]
     |    |--Minycardita Hoare & Plas 2003
     |    |    `--*M. sectilis Hoare & Plas 2003
     |    |--Baiosoma Hoare, Mapes & Yancey 2002
     |    |    |--*B. pala (Hoare, Steinker & Mapes 1988) [=Hippocardia pala]
     |    |    `--B. cucullata (Hoare et al. 1988) [=Hippocardia cucullata]
     |    `--Hadropipetta Hoare, Mapes & Yancey 2002
     |         |--*H. ancora (Hoare, Steinker & Mapes 1988) [=Hippocardia ancora]
     |         `--H. nevadaensis Hoare & Plas 2003
     |--Bransoniidae
     |    |--Pseudoconocardium Zavodowsky 1960
     |    |    `--*P. licharewi
     |    |--Bransonia Pojeta & Runnegar 1976
     |    |    |--*B. wilsoni Pojeta & Runnegar 1976
     |    |    `--B. robustum (Fletcher 1943) [=Conocardium robustum]
     |    `--Apotocardium Hoare, Mapes & Yancey 2002
     |         |--*A. lanterna (Branson 1965) (see below for synonymy)
     |         |--A. cordatum (Hoare et al. 1982) [=Pseudoconocardium cordatum]
     |         |--A. obliquum (Meek & Worthen 1875) [=Conocardium obliquum]
     |         |--A. plautum Hoare, Mapes & Yancey 2002
     |         |--A. polymitarium (Hoare et al. 1982) [=Pseudoconocardium polymitarium]
     |         `--A. snideri (Morgan 1924) [=Conocardium snideri, Pseudoconocardium snideri]
     `--Conocardiidae
          |--Conocardium Bronn 1835
          |    |--C. acadianum Dawson 1891
          |    `--C. nicholasensis Price 1921 (n. d.)
          |--Oxyprora Hoare, Mapes & Yancey 2002
          |    |--*O. parrishi (Worthen 1890) [=Conocardium parrishi]
          |    |--O. missouriensis (Girty 1915) (see below for synonymy)
          |    `--O. oklahomaense (Beede 1902) [=Conocardium oklahomaense]
          `--Arceodomus Pojeta & Runnegar 1976
               |--*A. glabrata (Easton 1962) [=Conocardium glabratum]
               |--A. angusta Hoare, Mapes & Yancey 2002
               |--A. langenheimi (Wilson 1970)
               |--A. prolata Hoare & Mapes 1990
               `--A. sphairikos Hanger et al. 2002
```

*Apotocardium lanterna (Branson 1965) [=Conocardium lanterna, Pseudoconocardium lanterna]
Oxyprora missouriensis (Girty 1915) [=Conocardium missouriensis, Pseudoconocardium missouriensis]
Pseudobigalea crista Hoare, Mapes & Brown 1982 [=Pseudoconocardium parrishi (Worthen) in Hoare, Sturgeon & Kindt 1978 non Conocardium parrishi Worthen 1890]
* Type species of genus indicated

References:

Wagner [no date]
Engeser and Riedel 1997
Hoare, R. D., R. H. Mapes & T. E. Yancey. 2002. Structure, taxonomy, and epifauna of Pennsylvanian rostroconchs (Mollusca). Journal of Paleontology 76 (Suppl.): 1-30.
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Scaphopoda

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   |==Tryblidiida (Monoplacophora)
   |   `--Cephalopoda
   `==Helcionelloida
       |==Rostroconchia
       |   `--Scaphopoda
       |--Bivalvia
       `--Gastropoda
```

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Antalis entalis (Scaphopoda: Dentaliida: Dentaliidae); empty shells washed up after storms; Swanage Beach, England.
Photo © BioImages Creative Commons Non-Commercial Attribution Share Alike via Encylopedia of Life.

The Scaphopods are called tooth or tusk shells because some types resemble miniature elephant tusks. These little-known molluscs are actually relict survivors of a more diverse Paleozoic group known as Rostroconchs. Where they belong on the molluscan evolutionary tree is uncertain; they have been variously grouped with bivalves and cephalopods (it is hard to imagine two more diverse clades of molluscs), such is the lack of consensus in molluscan phylogeny. MAK120614

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Scaphopoda

Abbreviated Dendrogram

```
MOLLUSCA
|--ACULIFERA
`--CONCHIFERA
   |==Tryblidiida (Monoplacophora)
   |   `--Cephalopoda
   `==Helcionelloida
       |==Rostroconchia
       |   `--SCAPHOPODA
       |--Bivalvia
       `--Gastropoda
```

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1. Scaphopoda

Introduction

Scaphopods are a small group of mostly small, infaunal or semi-infaunal, marine mollusks. There are an estimated 500 extant species known. They are fairly common in deeper water environments (being found at depths from 6 to 1,830 meters), and only a few species live nearshore. Because of this they are little known to the average person; and, unlike gastropods and bivalves, their shells are rarely washed up on beaches.

The scaphopod shell is quite unlike the usual molluscan form. It is a slender tapering and usually gently curved tube, not unlike a miniature elephant tusk, hence the common name "tusk shells". It is open at both ends, the large end of the shell being the anterior. The exterior has finely spaced growth lines and usually some type of longitudinal ornamentation or ribs. In color it is usually white or yellowish, although one species is a brilliant jade green. Barnes (1980: 434).

Scaphopod or "Tusk Shells." photo © Ralph Body, from Preface to Class of Scaphopoda.

Most scaphopods are small; the largest living forms being usually no longer than 8cm, with the maximum diameter of about 6 mm; and most species being much smaller than this (often only about 4 or 5 mm.). The largest living species, *Dentalium vernedei*, found off the coast of Japan, has a maximum length of 15cm. A fossil species of the genus is known to have attained twice that length, with a maximum diameter of well over 3 cm

A protrusible burrowing conical foot extends from the anterior end; the mantle cavity is large and extends along the ventral side of the animal to the smaller, posterior opening, through which respiratory currents pass. There are no gills, so respiration is accomplished by direct exchange with mantle tissue. The head is poorly-developed. The animal feeds on microscopic organisms, mostly foraminifers and organic detritus. This food is passed to the mouth via tentacles (called *captacula*) and tentacular cilia, and is processed by the radula.

Scaphopoda first appear in the Ordovician (*see also* Reynolds for references for the Ordovician date) or the Devonian (Engeser & Riedel) or even the Mississippian, depending on one's interpretation of the earliest forms. Yochelson (1978). They are fairly rare in the fossil record, except for occasional concentrations in Cenozoic deposits.

At one time Scaphopods were believed to be closely related to bivalves, as their early development very closely parallels that of marine bivalves (in the course of development the shell is originally bivalve). It was suggested that both groups descended from extinct bivalved mollusks called rostroconches. Runnegar & Pojeta (1974). There is now strong evidence (Steiner & Dreyer, 2002) that the Bivalves diverged from the main evolutionary sequence of the mollusks much earlier than the Scaphopods, which are actually much more closely related to Cephalopods. According to one hypothesis, both Cephalopods and Scaphopods evolved from a tiny, semi-infaunal helcionellid ancestor, probably some time in the Furongian. However, Engeser and Riedel 1997 argue for an origin from Devonian conocardioid rostroconches, as the early scaphopod shell resembles the adult conocardid shell. If this hypothesis is correct, then the Scaphopods are by far the last Molluscan class to emerge.

The Class Scaphopoda is divided into two orders, the Dentaliida and the Gadilida or Siphonodentalioida). The latter is distinguished by the constriction of the anterior aperture and the shape of the central tooth of the radula (Reynolds. The Dentaliida may or may not be paraphyletic, as the appear much earlier, so it is possible the Gadilida (which first appeared in the fossil record in the Permian) evolved from them. However, the systematics of the group are still poorly worked out.

Scaphopod Dendrogram

```
<==o SCAPHOPODA
   |--o DENTALIIDA
   |  |?- Eboreidentidae
   |  |?- Omniglyptidae
   |  |-- Gadilinidae [Episiphonidae]
   |  `--+--+-- Dentaliidae
   |     |  `-- Fustiariidae
   |     `--+-- Calliodentaliidae
   |        `-- Rhabdidae [Laevidentaliidae]
   `--o GADILIDA
      |?- Siphonodentaliidae
      |-- Entalinidae
      `--+-- Pulsellidae
         `--+-- Wemersoniellidae
            `-- Gadilidae [Cadulidae, Loxoporidae]
```

Reference(s): Parker 1982

Descriptions

Scaphopoda

Range: Ordovician or Carboniferous to Recent

Phylogeny: Paraphyletic Helcionelloida **:** Gastropoda + (Bivalvia + (Rostroconchia paraphyletic Rostroconchia **:** Conocardiida + (Ribeirioida + *))

Comments: about 500 extant species, elongate body in a tubular tapered shell open at each end. The mantle cavity is large and extends along the whole ventral surface. No gills. The head of the Tusk Shell has no eyes, but it has paired clusters of clubbed contractile tentacles, called *capitula*. The head and cylindrical foot can emerge from the larger end of the tapered shell. The sexes are separate, and fertilization is external. All species are are benthic and marine Jack R. Holt. Evolved from rostroconchian ancestors. Previously grouped, on morphological and neontological evidence, with either the Bivalvia (as subphylum Diasoma) or the Cephalopda;current molecular phylogeny tends to favour a scaphopod-gastropod-bivalve clade, which supports the scenario of all three groups evoving from early Cambrian infaunal helcionelloid ancestors , MAK120614.

Links: The Scaphopod Page by Patrick D. Reynolds - a very informative introduction to recent and fossil members of the group. Introduction to the Scaphopoda - a good introduction to the group (UCMP website); Fossil Scaphopoda - information on fossil Scaphopoda, and the origin of the group; Mollusca - Class Scaphopoda - short intro; Scaphopoda - intro

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MOLLUSCA		TRYBLIDIIDA

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Tryblidiida

Abbreviated Dendrogram

```
MOLLUSCA
|==ACULIFERA
`--CONCHIFERA
   |--+--TRYBLIDIIDA
   |  `--CEPHALOPODA
   `--+--SCAPHOPODA
      |--BIVALVIA
      `--GASTROPODA
```

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Veleropilina reticulata (Seguenza, 1876) ("Monoplacophora" : Tryblidiida: Tryblidioidea: Neopilinidae), Tuscan Arcipelago, depth of 500 meters
Photo by Andrea Nappo, for World Register of Marine Species, Creative Commons Non-Commercial Attribution via Encylopedia of Life.

The Tryblidiida are a group of very primitive and ancient mollusks with mostly simple cap-shaped shells. They have previously been (and are often still) called the *Monoplacophora*. However, it is now known that "Monoplacophora" refers to a very diverse assemblage of basal mollusks, and is not a natural group. John Peel suggest that the Monoplacophora should be divided into two classes, the Tergomya and the Helcionelloida, but even the Tergomya may be a polyphyletic group.

Palaeos

MOLLUSCA

TRYBLIDIIDA

TRYBLIDIIDA (MONOPLACOPHORA)

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Unit Back: Conchifera	Clade Down: None for crown group Tryblidiida	References	Unit Next

Tryblidiida (Monoplacophora)

Abbreviated Dendrogram

```
MOLLUSCA
|==ACULIFERA
`--CONCHIFERA
   |--+--TRYBLIDIIDA
   |  `--CEPHALOPODA
   `--+--SCAPHOPODA
      |--BIVALVIA
      `--GASTROPODA
```

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1. Tryblidiida

Problems with defining the "Monoplacophora"

Trying to establish a systemmatic classification of the "Monoplacophora" is not easy, especially since it seems that "Monoplacophora" is a polyphyletic grade rather than a natural group.

As with all molluscs, and understanding of the soft parts are important, and, apart from the living *Neopilina*, representing only a single order and family of this once diverse group, and muscle scars on fossil shells, these are lacking. In the now dated volume of the *Treatise*, Knight & Yochelson (1960) review all known forms, and have two or three orders and 5 or 6 families (some taxa have a question mark next to them). Runnegar Jell (1976) present a simpler arrangement, synonymising several higher taxa. This results in 3 orders (including Bellerophontids) and eight or nine familes, but this includes many taxa that Peel (1991) transfers to the Helcionelloida, and Wagner to the Helcionelloida and "Quasirostroconchs". In any case, if the early evolution of other groups is anything to go on, it is likely that the "Monoplacophora" were quite diverse as far as high-level taxa go, even if there were not many different types on the level of species

It is quite likely that the "Monoplacophora" is a polyphyletic grouping, as cladistic analysis gives confusing results. Waller 1998 shows that the Tryblidiida are the sister group of all other Conchifera. While Wagner, in a more complex cladogram based on an analysis of a large number of early Paleozoic gastropods and other molluscs (see illustration above), has the "Tergomya" (*Kiringella*, Hypseloconida, and *Cyrtolites*) as the sister-group to Tropidodiscid Bellerophonts, and from those in turn the sister group of Gastropods proper. Which implies (Helcionelloida (Cyrtosoma (*Kiringella* + Hypseloconida (*Cyrtolites* (Tropidodiscidae (Gastropoda)))))).

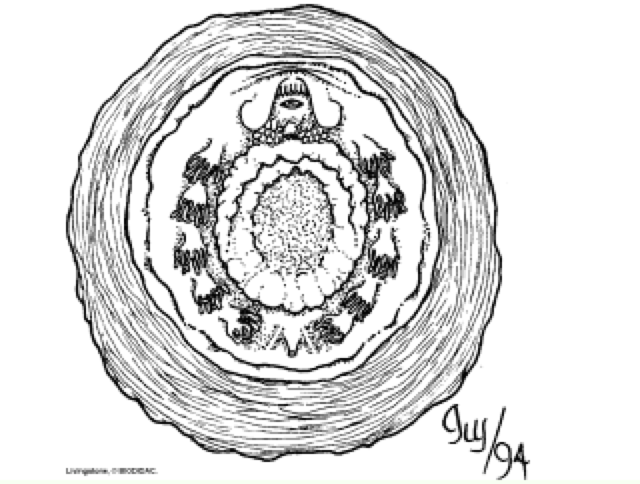
For this reason I would limit use of the term "Monoplacophora" *sensu strictu* to the Tryblidiida, which are a monophyletic off-shoot of the basal Conchifera, the Helcionelloida, which are a more derived but paraphyletic group of basal Conchifera, and the Tergomya minus the Tryblidiida, which are an early sister group to the proto-gastropods, also probably paraphyletic.

Eventually, as more studies and cladistic analysis is done on basal molluscs, a more complete picture should emerge.

The Tryblidiida

(= "Monoplacophora")

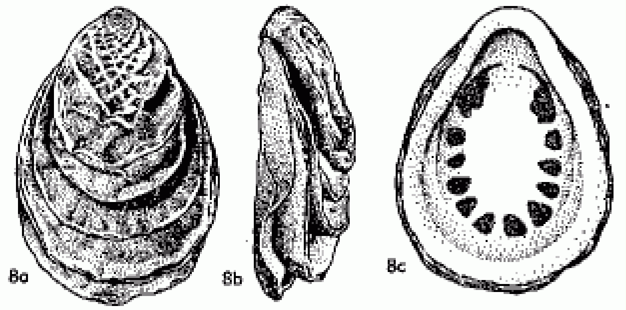
(Middle Cambrian-Recent)



Neopilina, ventral view, showing mouth (at top), multiple gills and mantle, foot (center) and shell (outer ring)
image © BIODIDAC, University of Ottowa

The Tryblidiida include the typical "Monoplacophora" - a number of early Paleozoic forms, and are represented among today's biota by the "living fossil" *Neopilina*. It is possible that they represent an ancestral molluscan type. Runnegar & Pojeta (1974). Cladistic analysis (Waller, 1998) shows that they are the sister group of all other Conchifera.

Evolutionary History



Tryblidium reticulatum, a typical Early Palaeozoic shallow-water Tryblidiid; length about 3.5 cm
Silurian (Wenlock Age) of Baltica (Gotland)
"Monoplacophora" - Tryblidiida - Tryblidiidae
image © xxxx from *Treatise on Invertebrate Paleontology*. Part I. Mollusca 1.

The Tryblidiida first appear in the fossil record during the earliest Middle (Runnegar & Jell, 1976) or Late (Yochelson 1978) Cambrian (earlier forms are now considered to be Helcionelloidans), a time when mollusks were undergoing a great evolutionary radiation with a number of new classes appearing. It is possible that they evolved from earlier soft-bodied ancestors. Alternatively they are a late group and their primitive features misleading.

Although never a diverse or abundant group, they are well-represented in the fossil record from the Furongian to the Devonian. After that time they disappear; so it can be assumed that is when they migrated to the deep water environments they still occupy today.

Until the discovery of the deep-sea mollusk *Neopilina* in 1952, the Tryblidiida and other "Monoplacophora" were considered to be an extinct branch of early primitive untorted gastropods, called "Amphigastropods" [Moore *et al*, 1952]. Modern forms appear to be little changed from their early Paleozoic ancestors. It is likely that these Paleozoic forms were benthic algal/bacterial grazers in shallow marine environment of varying energy [ref http://www.ualr.edu/~ersc/Paleontology/Mollusca.html], and that the migration to deep sea benthos probably occurred later.

Physiology

Seven or eight living species of *Neopilina* are known (with quite likely more awaiting discovery), and have usually been dredged from depths of between 2000 and 6500 meters in the South Atlantic, Gulf of Aden, and East Pacific. (Barnes, 1980). While a widespread part of the deep water benthos, their ecology is unknown. Modern forms appear to be little changed since the early Paleozoic.

Tryblidiids are modestly sized molluscs (*Neopilina* does not exceed 3 cm, and Paleozoic forms were mostly of similar size), with a simple exogastrically-curved limpet-like shell. They are distinguished by the fact that virtually all organ systems are found in multiples. *Neopilina* has 6 pairs of gills and of nephridia, 8 pairs of retractor muscles, 2 pairs of gonads and auricles, and so on. Barnes (1980); http://www.reefkeeping.com/issues/2002-08/rs/. While the soft parts of extinct forms are not known, the fact that fossil species show multiple muscle scars indicate a similar *bauplan*.

This pseudo-metameric or quasi-segmented body plan led to the idea that "Monoplacophora" had a common ancestry with other metameric coelomates like annelids and arthropods. However, neither extant aplacophoran primitive molluscs or Cambrian pre-annelid and pre-molluscan halwaxiids like *Wiwaxia* and *Halkeria* are obviously segmented (although the regular series of scales in the latter two forms may be the beginning of segmentation). It is possible then that the multiple organ systems and body segments developed independently among a number of different organisms.

Runnegar & Pojeta (1974) suggest that Polyplacophora with their segmented shells evolved from "Monoplacophora" ancestors, but it is also possible again that this adaptation developed independently, although Knight & Yochelson suggest a relationship between the Polyplacophora and Tryblidiida. However, Waller 1998 and other cladistic analysis does not indicate that the Polyplacophora and Tryblidiida are a natural group or clade within the Mollusca.

Descriptions

Tryblidiida Lemche, 1957

Synonyms: Monoplacophora Odhner, 1940 (para/polyphyletic as originally defined)

Range: Fr ECambrian

Phylogeny: Conchifera **:** (Scaphopoda + Bivalvia + Gastropoda) + (Cephalopoda + *)

Characters: relict, deep sea, limpet-like forms, bilaterally symmetrical, metameric (quasi-segmented). The body has a distinct head, but there are no eyes or sensory tentacles (except around the mouth). The foot is weakly muscular; anus median, posterior; mantle cavity large, extending laterally and posteriorly around the foot with 5-6 pairs of ctenidia; 8 pairs of pedal-retractor muscles; 6 metanephridia; sexes separate; fertilization external. - mostly from Jack R. Holt

Comments: Originally considered the ancestral molluscan type, then the sister taxon to all other conchiferan groups (gastropods, cephalopods, scaphopods, and bivalves), one recent molecular phylogeny makes them the sister taxon to cephalopoda alone. In any case, they would be close to the conchiferan ancestor. Well represented in the fossil record from the Cambrian to the Devonian and thought to be extinct, until living animals were found off the Pacific coast of Costa Rica in 1952 (cited in Ruppert et al. 2004). About 20 extant species are known, although many more are presumed to occur in the deep oceans. Jack R. Holt, MAK120612

Monoplacophora sensu lato. as defined in Runnegar & Jell (1976) would include three orders including the Tryblidiida. Problems arise from the ambiguous position of some paleozoic fossil taxa which could be monoplacophorans or gastropods, or (worse) stem-group gastropods derived from monoplacophorans, thus making Monoplacophora paraphyletic. Preference for the name Tryblidiida follows Waller's (1998) conclusion that these are the sister-group to all other Conchifera, thus escaping being paraphyletic. Giribet et al. (2006): claimed that the monoplacophoran Laevipilina is recovered within a branch containing polyplacophoran taxa in an analysis including several nuclear and mitochondrial sequences. As mentioned above, this result based on a very small specimen is ignored in the classification draft until further confirmed. - Gofas, S. (2012). Monoplacophora. (Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=415 on 2012-06-07 Creative Commons Attribution)

Reference: Lemche H. (1957). A new living deep-sea mollusc of the Cambro-Devonian class Monoplacophora. *Nature* 179: 413-416 fig. 1-4

Links Monoplacophora - intro; Mollusca - Class Monoplacophora - short intro

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K. A. von Zittel, & Eastman C. R. *Text Book of Paleontology* edited by C. R. Eastman adapted from German of K. A. von Zittel, 2nd edition revised and enlarged by the editor in collaboration with the following named specialists: R.S. Bassler, W. H. Dall, C. D. Walcott. Volume 1. MacMillan & Co., London. xii + 839 pp. Internet Archive