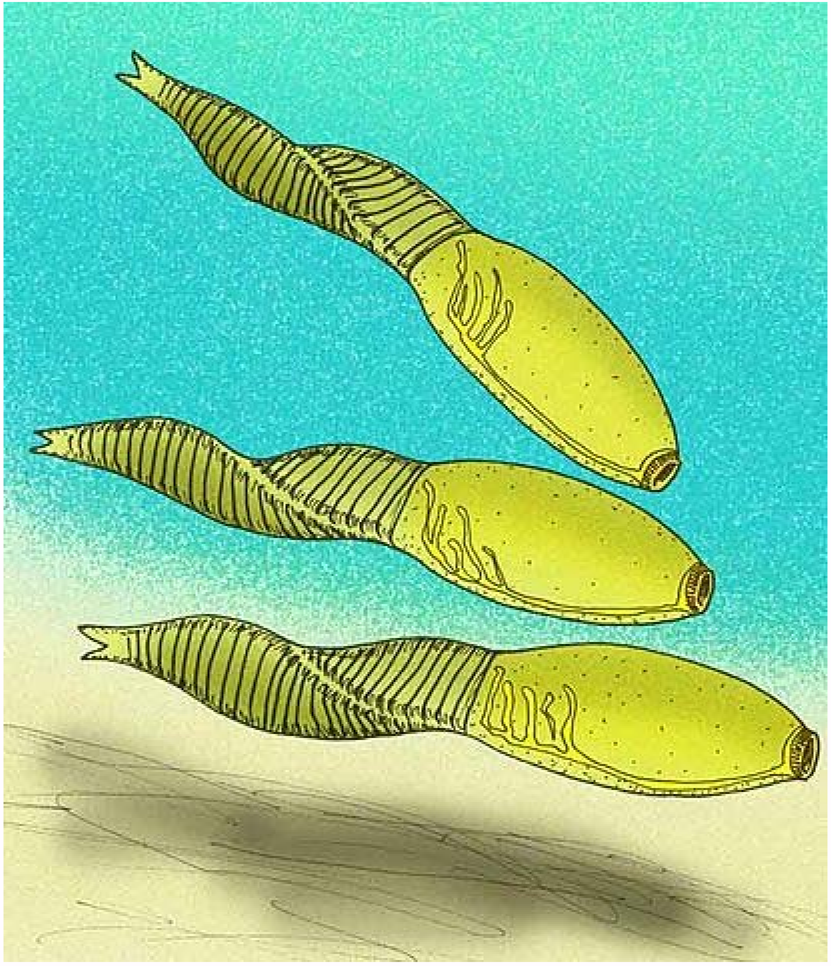
Deuterostomia

```
METAZOA
|==Porifera
`--+--Radiata
   `--Bilateria
      |--DEUTEROSTOMIA
      |  |--Vetulicolia
      |  `--+--CHORDATA
      |     `--Ambulacraria
      |        |--Hemichordata
      |        `--+--Vetulocystidae
      |           `==Homalozoa
      |              `--ECHINODERMATA
      `--Protostomia
         |--Ecdysozoa
         `--LOPHOTROCHOZOA
```

Deuterostomia
Vetulicolia
Ambulacraria
Homalozoa
Dendrogram
References



Reconstruction of a purported deuterostome, *Banffia constricta* (phylum Vetulicolia). Fossils of this enigmatic animal have been found in the Middle Cambrian Burgess Shale lagerstatten of British Columbia.

Artwork by Stanton F. Fink, via Wikipedia, GNU Free Documentation/Creative Commons Attribution / Share Alike

Along with the Lophotrochozoa and Ecdysozoa (both belonging to the protostome clade), the Deuterostomes are one of the three main categories of "higher" animals (Bilateria). They include two very distinctive groups, the Echinoderms and the Chordates, along with a few minor phyla. Like the other two major bilaterian clades, they are exceedingly diverse, although rather less speciose or numerically abunadant than the other two groups. However they make up for the fewer numbers of species and individuals by the great success especially of one of their crown clades, the vertebrates, a group that began with tiny fish-like ancestors, but soon giving rise to creatures as diverse as dimetrodons and dinosaurs, teleosts and tainodonts, and holocephali and humans. Our story begins however with ancestral forms from the early Cambrian MAK120113

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Deuterostomia

Starfishes > Silverfishes

```
METAZOA
|--PORIFERA (paraphyletic?)
`--+--Radiata
   `--Bilateria
      |--DEUTEROSTOMIA
      |  |--Vetulicolia
      |  `--+--CHORDATA
      |     `--Ambulacraria
      |        |--Hemichordata
      |        `--+--Vetulocystidae
      |           `--HOMALOZOA
      |              `--ECHINODERMATA
      `--Protostomia
         |--Ecdysozoa
         `--LOPHOTROCHOZOA
```

Deuterostomia
Vetulicolia
Ambulacraria

Dendrogram
References

Introduction

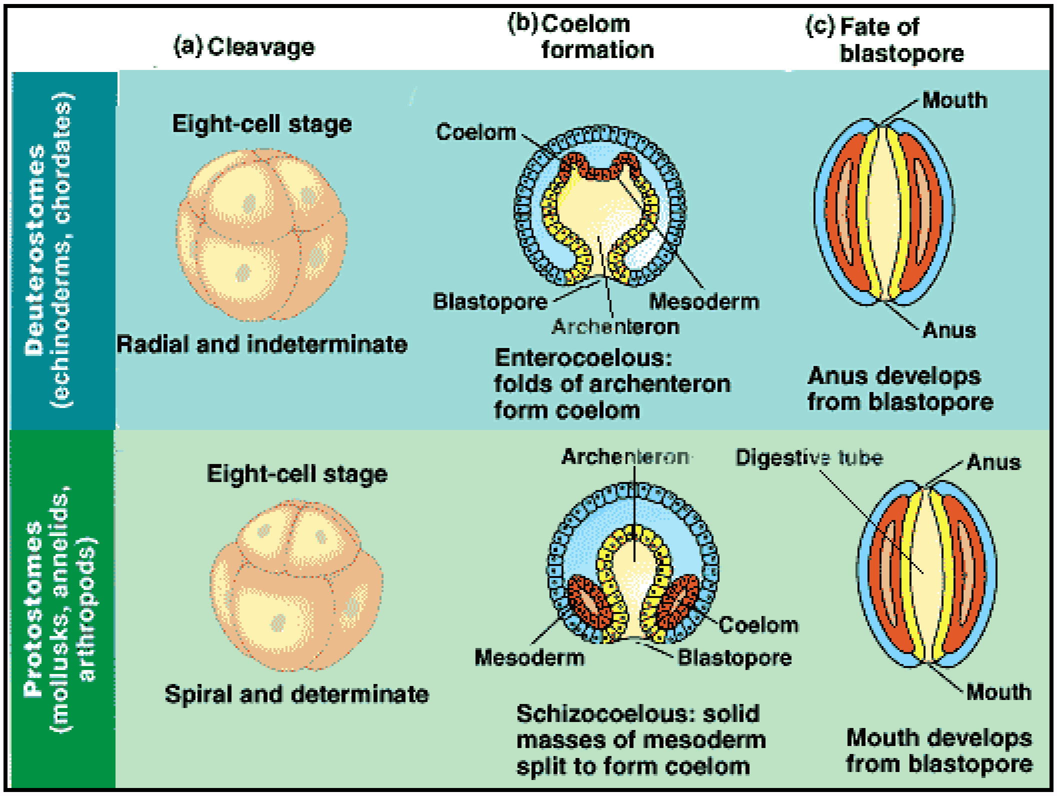
Compared to the protostomes, the deuterostomes are far less diverse, including among the invertebrates only the Echinoderms and a few minor taxa, but having as their main claim to fame the fact that Chordata belong to this sub-division. The deuterostome condition is often associated with an initial embyonic cleavage pattern which is "radial" and in which cleavage planes are either parallel or perpendicular to the vertical axis of the embryo. Deuterostomes also commonly exhibit an indeterminate cleavage in the early stages of embryo development. That is, each early embryonic cell retains the capacity to develop into a complete embryo if isolated from other cells. (this enables the production of twins in vertebrates.). Deuterostomes also possess enterocoelous coelom development, in which the mesoderm arises as lateral outpocketings of the archenteron (embryonic gut) with hollows that become the coelomic cavities, and the development of the embryonic blastopore (the original opening) into the anus (rather than into the mouth as in most protostomes). MAK020407, rev'd ATW050814.

A Working Phylogeny of Deuterostomia

Our working phylogeny of the Deuterostomia is discussed below. In outline, it looks like this:

```
Deuterostomia
|--Vetulicolia
|--Yunnanozoa
```

```
|--Chordata
  |--Urochordata
  `--+--Cephalochordata
    `--Craniata
`--+--Xenoturbella
  `--Ambulacraria
    |--Hemichordata
    `--+--Vetulocystidae
      `--+--Stylophora
        `--+--Soluta
          `--+--Cincta
                   `--+-
-Ctenocystoidea
                  `--+--
Helicoplacoidea
                `--+--Edrioasteroidea
                  `--Echinodermata
```

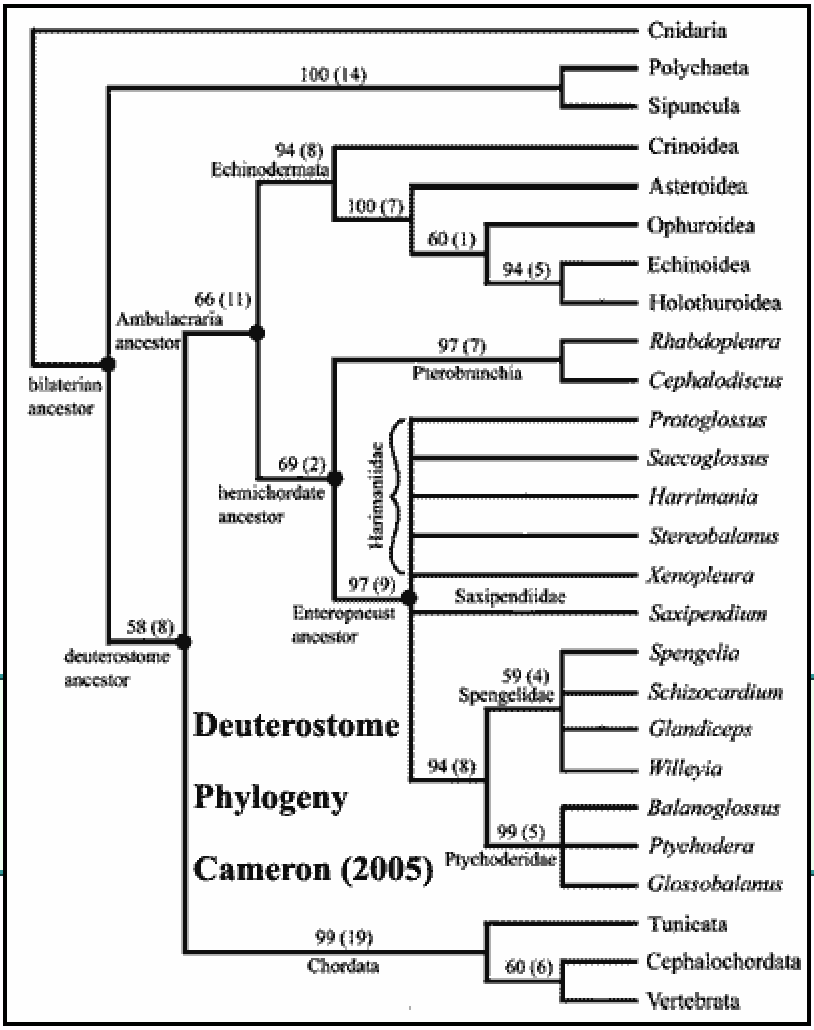


The deuterostomes make up on of the earliest divisions with the Bilateria. Included in this clade are three very different-looking phyla - the echinoderms, hemichordates and chordates.

The characters uniting these taxa are mostly developmental (Miller & Harley, 1996). The name Deuterostomia ("second mouth") refers to the development of the embryo blastopore into the anus, with the mouth developing as a secondary opening, in contrast to protostomes ("first mouth") with the process reversed. The initial embryonic cleavage in deuterostomes is radial and indeterminate, and coelom development is from outpockets of the gut (enterocoelous). Molecular data have supported monophyly of the Deuterostomia.

This section will cover the deuterostomes that lie outside the echinoderm and craniate crown groups. Deuterostomia is here defined as all animals more closely related to *Homo* (Chordata) and *Echinus* (Echinodermata) than to *Scarabaeus* (Arthropoda) or *Helix* (Mollusca). It should be noted that "deuterostomy" (the anus developmentally proceeding the mouth) is not unique to Deuterostomia, but is also found in Bryozoa, Brachiozoa and Chaetognatha. On this page, "Deuterostomia" and "deuterostome" always refer to the clade, while "deuterostomy" and "deuterostomous" refer to the developmental pathway.

The evolutionary relationships of deuterostomes have gone through a fair amount of contention in recent years. Traditionally. mainly after the work of Hyman, deuterostomes have been placed quite high up in the animal tree, forming a clade with the other deuterostomous taxa nestled within the coelomate clade (see Bilateralia 2). Within the Deuterostomia, chordates and hemichordates were united by possession of ciliated pharyngeal gill pores/slits and a stiffened notochord-like structure (the notochord in chordates, the stomochord in hemichordates). The similarities in larval form between hemichordates and echinoderms were regarded as ancestral for deuterostomes, and subsequently lost in chordates.



Humans being the chauvanistic animals we are, there's a lot of appeal in this tree, which appears to sit us at the top of ever-increasing complexity. Unfortunately, recent phylogenies, mostly molecular, rather put the kybosh on this view (Maddison, 2002). Deuterostomia is much lower down, probably the second branch of Bilateria to split off after the Acoelomorpha. Compared to its sister group, the omnipresent and spectacularly diverse Protostomia (containing the arthropods, molluscs and nematodes as its particular success stories), the deuterostomes are merely minor players. Interestingly, while protostomy has been generally regarded as ancestral to deuterostomy, modern phylogenies suggest the opposite, as shown by this phylogeny based on Giribet *et al.* (2000) where D = deuterostomous and P = protostomous:

```
0--Deuterostomia (D)
`--+--Chaetognatha (D)
   `--+--Bryozoa (D)
      `--+--Ecdysozoa (P)
         `--+--Platyzoa (P)
            `--+--Brachiozoa (D)
               `--other Trochozoa (P)
```

While deuterostomy probably represents a secondary reversal in Brachiozoa (other phylogenies place Brachiozoa nested within other Trochozoa, reinforcing this probability), protosotomous taxa as a whole are unmistakably nested within deuterostomous taxa.

Within the Deuterostomia, molecular data have argued convincingly for a rearrangement of the main relationships (Cameron *et al.* 2000). The primary division of living members appears to be between the chordates on one hand and the echinoderms + hemichordates (forming a clade called Ambulacraria) on the other. This suggests that the characters shared between chordates and hemichordates may be ancestral for deuterostomes as a whole, and subsequently lost in echinoderms - a not-too-surprising state of affairs considering the greatly altered morphology of echinoderms. Heinzeller & Welsch (1999) regarded the hydrocoel of echinoderms as homologous with the notochord of chordates, as suggested by similarities in development and gene expression. The tornaria-type larva of Ambulacraria can no longer be assumed to be ancestral for Deuterostomia - it may represent an autapomorphy of Ambulacraria.

Recently, a molecular study has suggested that the obscure worm *Xenoturbella* might also fall within the Deuterostomia, specifically as the sister taxon to Ambulacraria. We therefore give it a look here. Also covered are the Vetulicolia, a group of Cambrian fossils that may represent the stem-group of crown deuterostomes, as well as a number of fossil groups regarded as stem echinoderms.

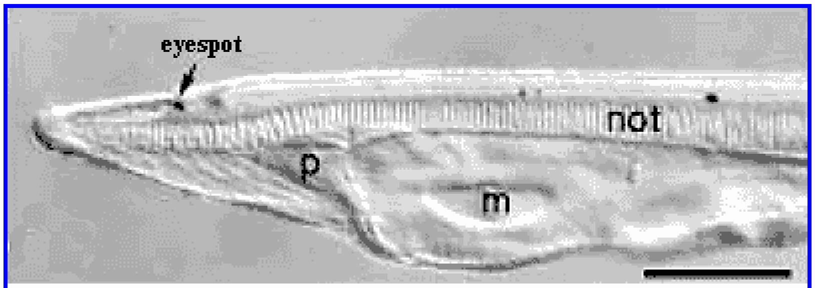
Not covered for now are a few other fossil groups that have been less certainly referred to Deuterostomia at one time or another, such as Odontogriphidae, Cambroclavida and *Dinomischus*. Also absent are the Chaetognatha (arrow-worms), which have been considered the basalmost branch of the Deuterostomia in the past, but are currently regarded by many as basal protostomes (Helfenbein *et al*., 2004).

� Christopher Taylor, CT050815

Image credits: Deuterostomes picture not even remotely to scale. Komodo Lizard from **Manfreds Travel Pictures**. *Dolichoglossus* from the Bio **3650L Review Page** (Clayton State University). *Asterias amurensis* from **Kenya Yamamoto** (Gifu University). Cameron (2005) cladogram from Cameron (2005).

The Fall and Rise of Orders of Symmetry

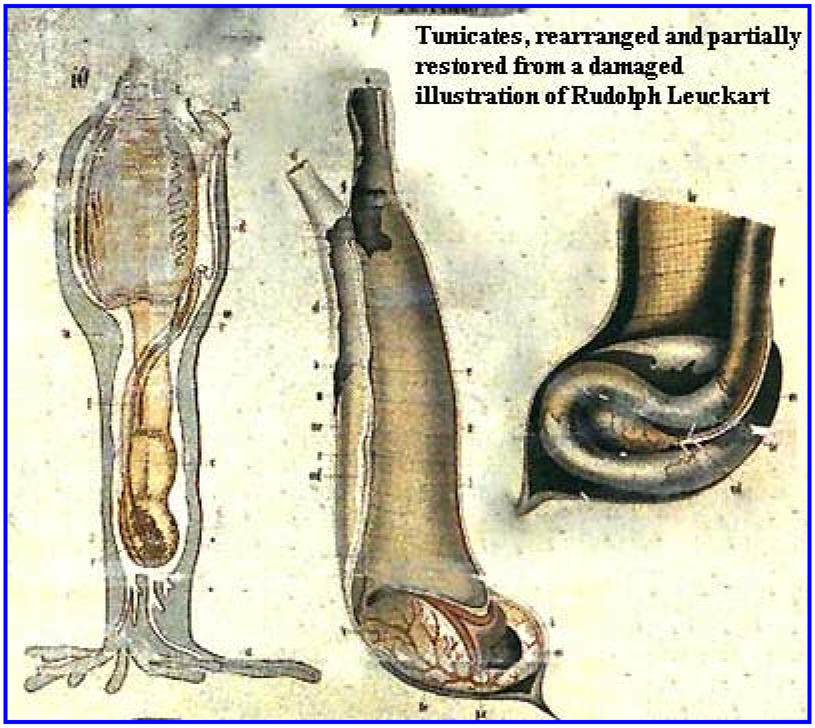
One feature of the deuterostomes deserves a closer look - the widespread occurrence across the clade of deviations from the bilateral symmetry found in most Bilateria. Almost all the deuterostomes are asymmetrical to some degree, and in echinoderms bilateral symmetry has been lost entirely in the adult and replaced by pentaradial symmetry.



Developing amphioxus from Lacalli et al. (1999). P is Hatschek's pit. M is the lateral mouth, and 'not' is the notochord.

In vertebrates, left-right asymmetry is mostly found in the viscera- we're probably all aware that our heart and digestive organs are not positioned directly down the midline, but are coiled and directed to one side or another depending on the organ. Other features, such as the skeleton, are more or less symmetrical.

The immediate outgroup of craniates, the Cephalochordata (*e.g.*, amphioxus), show strong asymmetry during development. From the appearance of the fifth somite, the anterior borders of the somites move visibly out of register. Minguillon & Garcia-Fernandez (2002); Boorman & Shimeld (2002). After neurulation, paired cavities called Hatschek's diverticula (possible pituitary homologue) form in the head endoderm. The left cavity moves posteriorly to form the pre-oral pit, while the right expands to fill the vacated space in the head. The larval head becomes significantly asymmetrical, with the mouth appearing on the left side and the gill slits (originating on the ventral midline) spreading up to right side only. At metamorphosis, the mouth moves to the front, the pre-existing gill slits move from the right side to the left, and new gill slits open on the right. The adult therefore regains pharyngeal symmetry. Other asymmetries remain, such as the displaced muscle blocks, the position of Hatschek's pit (an organ derived from the pre-oral pit, and probably homologous to the pituitary gland) on the left side, and a blind gut diverticulum on the right (Boorman & Shimeld, 2002).

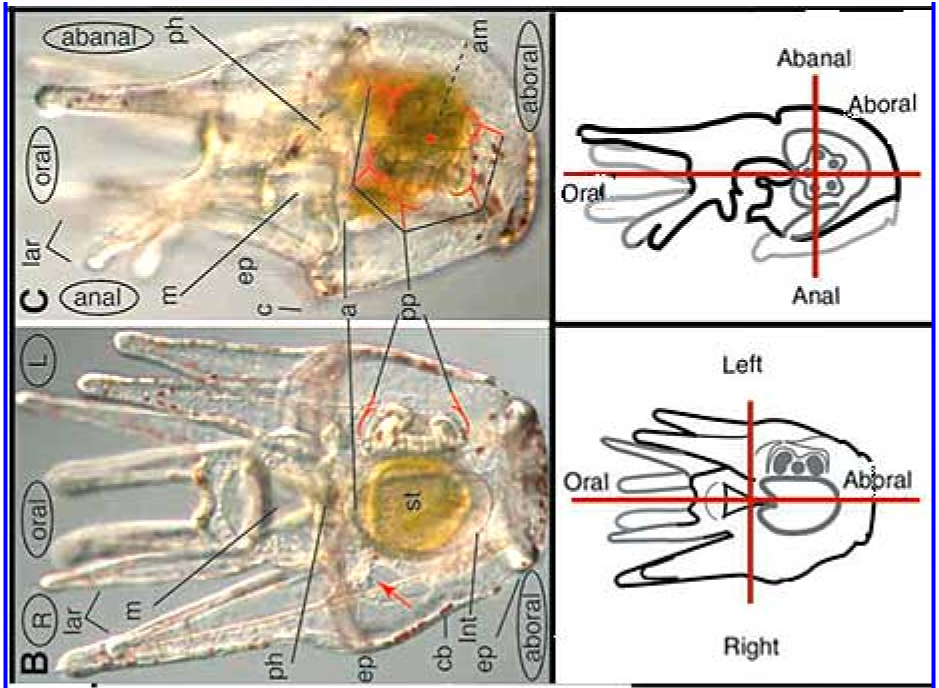


Tunicates, rearranged and partially restored from a damaged illustration of Rudolph Leuckart

Urochordata, the next group out, show little asymmetry in the larva, except in the positions of the two sensory pigment spots and adjoining regions of the brain. In the adult, the gut becomes asymmetrically folded.

The hemichordates are the most symmetrical of the deuterostomes. The gut is coiled asymmetrically but unlike other deuterostomes the direction of asymmetry differs between individuals. Directional asymmetries are few and relatively small - the protocoel pore is typically on the left. Boorman & Shimeld (2002). *Rhabdopleura* is something of an exception - in this genus, the right feeding arm is usually longer than the left, the single gonad is on the right, the mouth is on the left and the anus is on the right. Jefferies (1986).

In echinoderms the larva is initially bilaterally symmetrical, only to be replaced by a whole new order of symmetry in the adult. In sea urchins the pentaradial adult body plan is laid down in a structure called the adult rudiment, which lies on the left within the larva. Boorman & Shimeld (2002); Arenas-Mena *et al*. (2000). In starfish and crinoids, the left somatocoel becomes oral and the right one aboral. In starfish, only the left hydrocoel of the larva develops into the adult water-vascular system, while the right hydrocoel disappears. Jefferies (1986). A lot of debate still occurs about the appropriate interpretation of echinoderm axes, and how (if at all) they can be compared to axes in other Bilateria. It is uncertain, for instance, if the anterior-posterior axis in other animals corresponds to the oral-aboral axis of echinoderms or the central axes of the five rays. The fossil lineage of echinoderms suggests some very odd evolutionary stages, with homalozoans representing a strongly asymmetrical stage in echinoderm ancestry (if they are indeed stem echinoderms - see later).



Assymmetrical development of the pentameral "adult rudiment" in Strongylocentrotus (urchin). From Arenas-Mena et al. (2000).

The obvious question then becomes what this all means. Why are deuterostomes such individualists? Jefferies (*e.g.*, 1986) has suggested that the asymmetry of chordates and echinoderms is homologous, and evidence that they form a monophylum to the exclusion of the more symmetrical hemichordates. This clade he named Dexiothetica after his suggested explanation for its origin - that the ancestor of the echinoderm-chordate clade underwent a 90 degree rotation so that it came to lie on its right side with the left side becoming dorsal (Greek *dexios* = right, *thetikos* = suitable for lying down). In chordates, the outer body subsequently re-oriented itself over time to become bilaterally symmetrical, but the viscera remained dexiothetic.

Jefferies' theory was strongly dependent on his interpretation of the fossil homalozoans (which he referred to as calcichordates - see later). On this page, we take the more orthodox view that homalozoans are stem echinoderms, as suggested by their possession of a calcite skeleton with a similar ultrastructure to modern echinoderms. Jefferies held this skeleton to be ancestral for Dexiothetica, and subsequently independently lost in each of the three chordate subphyla. However, this seems to require a lot of convergence, expecially if, as molecular phylogenies suggest, the hemichordates are actually closer to echinoderms. A stem echinoderm position for homalozoans seems much more parsimonious.

Could dexiothetism have still been ancestral to deuterostomes as a whole? The theory does have a certain appeal in relation to echinoderms - as mentioned before, left and right do become dorsal and ventral in echinoderm development, and the unpaired nature of the gill structures in Vetulocystidae and Cornuta at the base of the echinoderm stem offers further support (if they are correctly interpreted as such - see later). In the case of Chordata, however, if the homalozoans are not regarded as relevant to the chordate stem, the support for dexiothetism is much lower. Asymmetries in the viscera may have been an adaptation for greater complexity (a coiled heart has greater pumping ability, while a coiled gut allows for more surface area in a smaller volume. Cooke (2004). The strong asymmetry in amphioxus may be an autapomorphy of that particular lineage. Evidence is therefore equivocal as to whether dexiothetism can be regarded as ancestral for Deuterostomia, or whether chordate and echinoderm asymmetries arose independently. Among fossils that may lie along the stem group of deuterostomes, the Vetulicolia have not been recorded as showing any sign of asymmetry. However, the mostly lateral, two-dimensional preservation of vetulicolians means that this is not necessarily informative.

Studies of developmental gene expressions and their relation to deuterostome asymmetry are still at a fairly early stage. The *Nodal*-*Ptx* pathway has been identified as a major factor in establishing the left-right axis in chordates. *Ptx*, for instance, is expressed predominantly on the left-hand side of the embryo in all three chordate subphyla. However, neither Pitx or Nodal have yet been identified in echinoderms, though once again the extremely derived body plan of echinoderms makes the identification of gene functional homologies difficult. Wray & Lowe (2000). Preliminary analysis suggests *Ptx* expression is symmetrical in hemichordates, but this requires confirmation. Boorman & Shimeld (2002).

In succeeding pages, we will explore some of the strange fruits that have blossomed on the Deuterostome stem. For now, we include some other, quite different, versions of Deuterostome phylogent for comparison.

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Ambulacraria

Hemichordata + Echinodermata

```
DEUTEROSTOMIA
|--Vetulicolia
`--+--CHORDATA
   `--Ambulacraria
      |--Hemichordata
      `--+--Xenoturbella
         `--+--Vetulocystidae
            `--HOMALOZOA (grade)
               `--ECHINODERMATA
```

Deuterostomia
Vetulicolia
Ambulacraria

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The Echinoderm Stem: A World of Pure Imagination

Here at Palaeos, we point out right from the start that we are not authorities in the subjects covered, and anyone reading this site should approach its statements with all the caution of a serious burn victim re-potting cacti. Sometimes, though, a particularly abstruse topic is broached which reminds us to remind you of this rule. This is one of those times. The echinoderm stem is a repository for what are patently some of the most bizarre organisms ever to clutter the sea-bed. If, indeed, they are stem echinoderms at all. They may be derived crown echinoderms, or stem chordates, or organisms with no real connection to the echinoderms at all. Interpretations of these fossils are so varied and so divergent that one could be forgiven for failing to realize that they referred to the same animals. In the case of the Stylophora, researchers can't even agree as to which end is anterior and which is posterior.

As a result, this section is a pastiche. With so many competing theories available, I have picked and chosen as seems appropriate (or as my whim takes me), and in the process I have quite likely constructed something which no researcher has supported, and to which no-one who has actually examined the fossils in question would give the time of day. My advice is to stop reading. Go straight to the bibliography, and get your information direct from the primary literature. You'll be better off.

For those who have chosen to ignore my advice, a

few notes will be given on terminology. In light of the highly debatable nature of the echinoderm stem, I have decided to restrict the name �Echinodermata� to the crown group only, allowing me to be more explicit about the origins of characters leading towards the modern body plan. This differs from the definition (often not explicitly stated) used in many publications.

Probably the majority (including the **Treatise on Invertebrate Paleontology**) identify Echinodermata by the origin of the stereom. the calcite skeleton with an ultrastructure apparently unique to this clade. However, Jefferies (e.g. 1986) and his supporters, who place the Stylophora as the stem group of chordates, would see the stereom as plesiomorphic for a much larger clade. If defined by the stereom, Echinodermata would then include Chordata.

Another alternative is defining Echinodermata by the origin of pentaradial symmetry. However, this character is often widely altered in both modern and fossil groups of echinoderms. Also, the 2-1-2 system of ambulacra in edrioasteroids demonstrates that pentamery and pentaradial symmetry did not necessarily arise simultaneously.

� Christopher Taylor, CT050827

Image: *Carneyella*, an edrioasteroid, from the **College of Wooster, Department of Geology**.

The Monophyly of Ambulacraria

As an initial matter, the echinoderms and chordate phyla have been arranged in almost every possible phylogenetic order. Classical taxonomy was of no help, since we lacked enough data on basal deuterostomes to make even educated guesses about interrelationships. It was like trying to do a connect-the-dots picture with most of the dots missing and half the others in the wrong place. This confusion was succeeded by a large number of molecular studies reported folks who had a whole lot of dots, but were a little unclear on how to connect them. Finally -- really within the last five years -- both new fossils and great improvements in molecular techniques have allowed us to put the big pieces together with confidence. The overall picture looks like this:

```
Deuterostomia
|--Ambulacraria
|  |--Hemichordata
|  `--Echinodermata
`--Chordata
   |--Urochordata
   `--+--Cephalochordata
      `--Vertebrata
```

We are particularly encouraged by studies like Furlong & Holland (2002) who re-analyzed prior sequence work with sophisticated Bayesian techniques, and obtained the same result with a great variety of individual sequences. *See also* Winchell *et al*. (2002) (same results, concatenating different sequences). Sequence phylogenies are still hit-and-miss; but the new fossils make it much easier to assess which have hit and which have missed. ATW051025.

Arkarua: All That is Pentaradial is Not Echinoderm

Arkarua adami is a small disc-shaped fossil, about 3 to 10 mm across, known from the Ediacaran of the Flinders Ranges in Australia (UCMP). All known examples are external moulds with a five-lobed central region that led to its identification as the earliest echinoderm. However, *Arkarua* lacks a stereom or any sign of a water-vascular system.

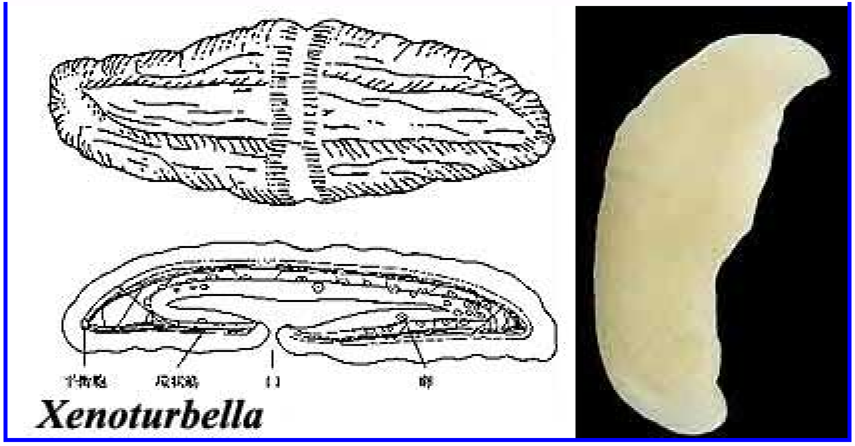
Arkarua's position as ancestral echinoderm has been widely accepted. The problem is that a number of other echinoderm stem groups (homalozoans and Helicoplacoidea) that appear to predate the origin of pentaradiality, but possess a stereom. As pointed out by Mooi (2001), this paradox has persisted because the organisms in question have rarely been compared. Those analyses that included *Arkarua* generally omitted the non-pentaradial taxa, and vice versa. There are two possible options if *Arkarua* is a stem echinoderm: (1) *Arkarua* is more crownward than the non-pentaradial taxa, and either the stereom and water-vascular system evolved independently on a number of occasions (very unlikely, as it would require the repeated appearance of an ultrastructure and a complex organ system that have not been recorded from any other clade) or *Arkarua* secondarily lost the stereom and water-vascular system (also unlikely, as it would require the complete absence of preservation of any contemporary forms retaining the stereom) (2) The non-pentaradial forms are secondarily derived from pentaradial ancestors. This latter is not impossible. Mooi (2001) suggests that unusual taxa are often placed too far down in trees by the difficulty of recognizing synapomorphies with less derived taxa. Compare, for instance, the recent transfer of Microsporidia from their originally basal position in the eukaryote tree to a much higher one within the Fungi. And some recent cladistic analyses have placed homalozoans within the echinoderm crown as derived pelmatozoans. Unfortunately any cladistic analysis is only as good as the characters it uses and the analyses in question were based on anatomical interpretations different from those favored here. The recently discovered Vetulocystidae, which lack a stereom but have a comparable organization to Stylophora, appear to support a basal position for at least some non-pentaradial taxa.

The more likely explanation is that *Arkarua*'s pentaradial symmetry is not homologous to that of echinoderms. After all, this is the single character uniting the two. *Arkarua* is therefore not here accepted as a deuterostome, and is more likely a cnidarian-grade animal or possibly even an alga.

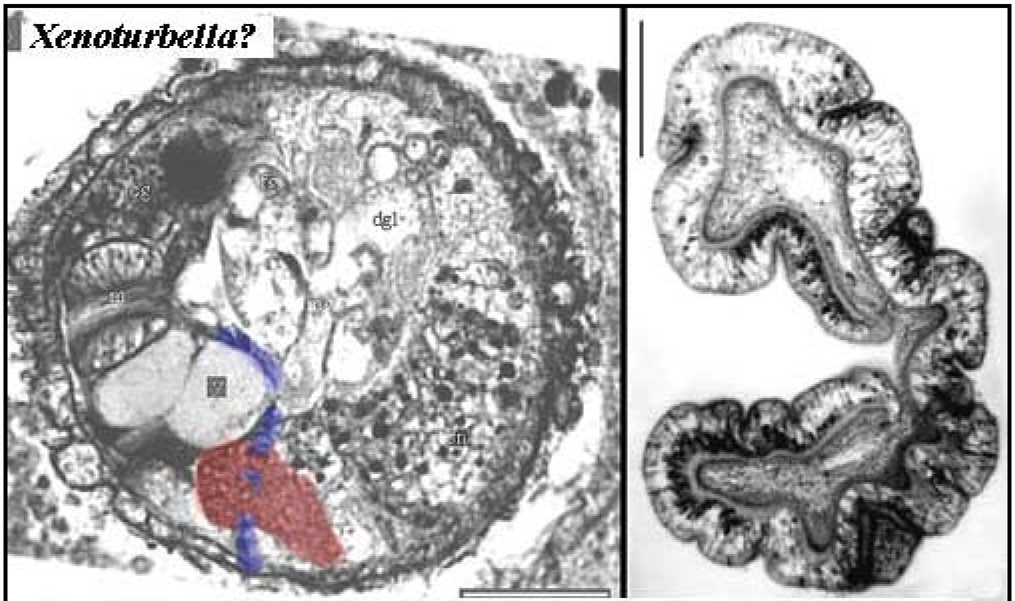
Images: *Arkarua* from the website of **Prof. Giuseppe L. Pesce**, Universit� dell'Aquila.

Xenoturbella - Back to the Basics

Xenoturbella is an odd little organism. We can't say that it has a face only a mother could love, because it doesn't have a face. Or a brain. Or appendages. Or even a through gut, just a blind *cul-de-sac*. *Xenoturbella* is a completely unassuming little blob that seems to want nothing more in life than to wallow in the mud of the North Sea. For systematists, its extreme simplicity and hence shortage of obvious synapomorphies with any other taxa have made it into something of a nuisance. Generally it has



been lumped with the Acoelomorpha, which also lack a through gut. Nevertheless, differences in anatomical structure of most organs made this a very uneasy arrangement. Haszprunar *et al*. (1991). So *Xenoturbella* was for the most part effectively swept under the rug until 1997, when two studies announced that it was a mollusk. Gee (2003); Bourlat *et al*. (2003). Not only did molecular analysis place it among bivalves, but bivalve eggs and larvae were found within specimens. It was thus inferred that *Xenoturbella* began life as a typical bivalve, but over the course of development all features indicative of its origin were lost. The problem was that such a total obliteration was in stark contrast to the apparent normality of the molecular data. Indeed, the *Xenoturbella* sequences actually nested within the genus *Nucula*, a basal but fairly unremarkable bivalve - the SSU rDNA sequence was identical to that of *N. sulcata*.



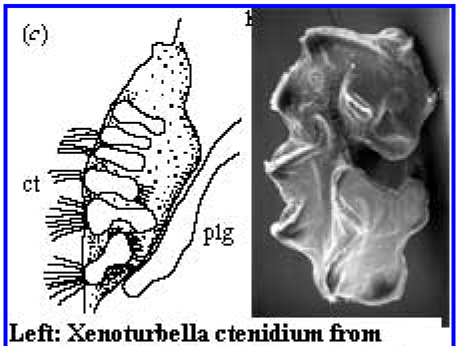
Early and late embryos of Xenoturbella according to Israelsson (1999). Red structure is unlabelled in original and may be ctenidium. Blue line is pleural ganglion.

In 2003, Bourlat and co-workers gave an explanation for this paradox -- the sequences came not from *Xenoturbella*, but from *Nucula* larvae that it had ingested. *Xenoturbella* is not a mollusk, but a molluscivore. Bourlat et al. identified another sequence that appeared to come directly from *Xenoturbella*, as shown by its amplification from specimens with the gut removed. These sequences grouped with the deuterostomes, specifically with the Ambulacraria. Unlike the mollusk hypothesis, this result was not entirely novel. Reisinger had suggested in 1960 that Xenoturbella might be derived from a neotenous deuterostome larva based on features of the nervous system, the enteropneust-like epidermis and the spermatozoa. Haszpruar *et al.* (1991). Bourlat *et al*. suggested a position as the sister group of Ambulacraria to be more likely than one within it due to codon usage. For instance, the ATA codon codes for methionine as in most metazoans, rather than isoleucine as in Ambulacraria.

The characters shared by Ambulacraria and chordates suggest that *Xenoturbella* is secondarily simplified, rather than representing the ancestral form for deuterostomes. Such secondary simplification is unusual in a free-living organism. It is more common in parasitic forms. How *Xenoturbella* managed to lose many of the features its ancestors undoubtedly had is completely unknown.

Additional note: Christopher Taylor's discussion of *Xenoturbella* was sufficiently intriguing that we decided to poke around a bit further. One further objection to ambulacrarian status for *Xenoturbella* comes from the embryological work of Israelsson (1999). Israelsson, working with rare and difficult material, it should be noted, found that embryos *associated* with *Xenoturbella* were of a perfectly normal trochophore type. This is exactly what one might expect of mollusks in general, and of *Nucula* in particular. However, specimens undergoing transformation at several months of age apparently lose all of the complexity and internal organization which they developed as embryos. *See* images.

Israelsson was not able to obtain free-living larvae at some intermediate stage. Judging from the embryo, they would be indistinguishable from other molluscan larvae. This data, Israelsson argues, clearly shows that *Xenoturbella* is a degenerate mollusk. Yet it also makes it quite difficult to explain why *Xenoturbella* develops all these molluscan bells and whistles in the first place.



Left: Xenoturbella ctenidium from Israelsson (1999). Right: auricularia larva of Stichopus (Holothuroidea)

Israelsson's remarks suggested that it might be a good idea to look harder at his images. As shown above in red, there is a curious, unlabelled mass associated with the pleural ganglion. With not too much imagination, it could be mistaken for a smaller version of the late-stage *Xenoturbella* larva on the right of the image, also from Israelsson (1999). The two images are almost exactly to scale, with scale bar = 500� in both.

A close reading of the paper suggests two alternate possibilities. First, this mass might be an early manifestation of the foot muscle. However, if we correctly interpret Israelsson's figures, the unlabelled mass is located almost directly *opposite* from the foot muscle at this stage of development. Second, the unlabelled mass might be the ctenidium (gill). Its relationship with the presumed pleural ganglion is about right. However, it looks nothing like Israelsson's line drawing of the ctenidium. (Just for fun, we have also pointed out the slight resemblance between this structure and the auricularia stage of holothurian [Echinodermata] development. Although not visible in the photograph, the auricularia also has ciliated bands like the ctenidium.)

So where does this leave us? Granted, this is all a bit of a shot in the dark, but there is a third possibility. Perhaps the unlabelled mass is actually the early developmental stage of *Xenoturbella*, while the rest is -- just as it appears -- an embryo of *Nucula*. That is, perhaps *Xenoturbella* develops as an endoparasite of *Nucula* embryos. In that case, we would suppose that *Xenoturbella* injects its own eggs *inside* the growing embryos of *Nucula*. The *Xenoturbella* embryo then consumes the *Nucula* embryo from within. It emerges into the environment as a very simple planktonic worm, feeds (not necessarily on *Nucula*) and grows. Eventually, it captures more *Nucula* embryos of its own, and continues the cycle.

This hypothesis explains much that is otherwise obscure. For example, *Xenoturbella* looks like a highly simplified parasitic form because, developmentally, it ***is*** a highly simplified parasitic form. The non-parasitic adult form is only a bridge between parasitic developmental forms. Free embryonic forms of *Xenoturbella* are never found because no such embryos exist except inside *Nucula* embryos. Similarly, larval forms of *Xenoturbella* are never found because development is direct. Fertile eggs of *Nucula* are routinely found in the gut of adult *Xenoturbella* for the very good reason that *Xenoturbella* cannot reproduce without them. We might conclude, then, that *Xenoturbella* is neither mollusk nor molluscivore, but an obligate developmental parasite of bivalves. ATW050828.

Christopher adds: Another possibility to explain the simplicity of *Xenoturbella* that might be more likely (though really equally hypothetical) is that it has gone through a size squeeze at some point in its ancestry. In other words, at some point an ancestral deuterostome became really small, probably as a member of the meiofauna, and lost a number of complicated organ systems as a result. Compare what happened to the Kowalevskiidae among the Urochordata (loss of endostyle, heart, and spiracles; body form strongly simplified, with very short life cycle). *Xenoturbella* then once again became bigger, but with a simplified organ system. However, short of actually finding micro-xenoturbellids, it would be very difficult to test this idea. CT050901.

Images: *Xenoturbella* diagram from the **University Of Tokyo School of Science**. Photo inset from **BBC News, 030821**. *Stichopus* larva from **Marine Invertebrate Larvae: a Study in Morphological Diversity**, by Prof. Thurston Lacalli (Univ. Saskatchewan). All other figures from Israelsson (1999).

Links: Clade Ambulacraria - Cladification - Systema Naturae 2000 (Taxonomicon entry); Bayesian phylogenetic analysis supports monophyly of ambulacraria and of cyclostomes; Evaluating Hypotheses of Deuterostome Phylogeny and Chordate Evolution with New LSU and SSU Ribosomal DNA Data (two molecular studies supporting the monophyly of Ambulacraria); Folie 1 (biochemical study of phylogeny, focusing on *Xenoturbella*); Pharyngula--Spectacular echinoderms from the Lower Cambrian (summary of Shu *et al*., 2004 from Pharyngula); Ancestral echinoderms from the Chengjiang deposits of China (full text of Shu *et al*., 2002). A phylogeny of the hemichordates based on morphological characters (Cameron, 2005 -- really nice paper, but restricted to living taxa); Animal phylogeny and the ancestry of bilaterians- inferences from ... (full text of Peterson & Eernisse, 2001). ATW060104.

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Vetulicolia

```
DEUTEROSTOMIA
|--Vetulicolia
|  |--+--Xidazoon
|  |  `--Didazoon
|  `--+--Pomatrum
|     `--Vetulicola
`--+--CHORDATA
   `--Ambulacraria
      |--Hemichordata
      `--+--Vetulocystidae
         `--HOMALOZOA (grade)
            `--ECHINODERMATA
```

Deuterostomia
Vetulicolia
Ambulacraria

Dendrogram
References

In 2001, Shu *et al.* suggested that a small group of Cambrian animals which they named Vetulicolia represented the stem group of modern deuterostomes. Vetulicolia possess a distinctly bipartite body plan with a voluminous anterior section bearing five pairs of lateral openings (interpreted as gills) and a seven-segmented �tail�. The gut runs to the posterior end of the tail. The junction between the two sections is constricted in the genera *Xidazoon* and *Didazoon*, which have an oval-shaped anterior bearing a large mouth with a strengthened rim, and a leaf-shaped tail. The genus *Vetulicola* has a more rectangular anterior with a �carapace� of four rigid cuticular plates. The posterior section is slender, strongly cuticularised and placed dorsally. The whole animal bears a superficial resemblance to a phyllocarid crustacean which lead to *Vetulicola* being originally regarded as an arthropod. However, the complete lack of appendages, the gill openings and the four-plated nature of the carapace are distinct from all known arthropods. Finally, the genus *Pomatrum* has an anterior like *Didazoon* and *Xidazoon*, but a slender tail like *Vetulicola*.

The position of vetulicolians relative to other deuterostomes is still contentious. Shu *et al.* did not identify anything resembling a notochord, which may indicate a position outside the deuterostome crown. However, they identified a dark ventral structure in the anterior part of *Xidazoon* and *Didazoon* as a possible endostyle, a structure currently known only from chordates. Vetulicolians bear a superficial resemblance to a tunicate �tadpole� larva, and also to the divided �somato-visceral� animal hypothesized by Romer as the ancestor of vertebrates. Shu *et al.* (2001). Lacalli (2002) suggested that the vetulicolian cuticle was homologous to the urochordate tunic.

Other fossil animals may be assignable to the Vetulicolia or their near relatives. The worm-like

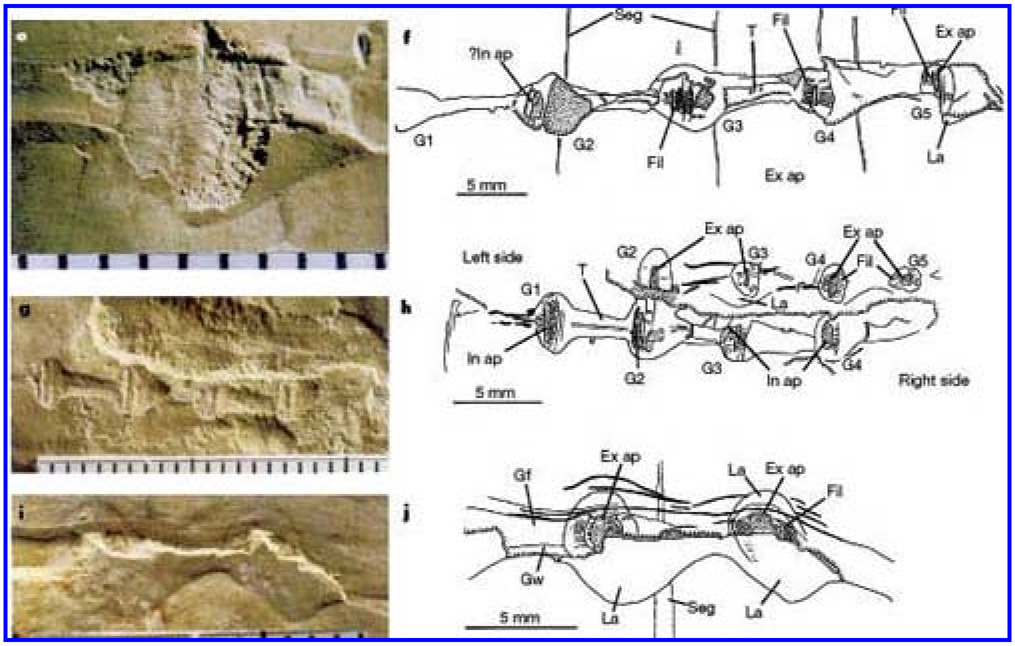
Three vetulicolians. Front to back: Vetulicola, Xidazoon, Didazoon

Banffia resembles Vetulicolia in its bipartite body, as does the recently described *Skeemella* (Briggs *et al.*, 2005), both from the Cambrian. Both these genera, however, have considerably more segments in the posterior section (43 in *Skeemella*) and no sign of gill openings. Briggs *et al.* argued on this basis that the assignment of vetulicolians to deuterostomes was probably unjustified. It is possible, of course, that these two genera are not related to Vetulicolia, or that they are further down on the deuterostome stem and predate the origin of gill openings.

When *Xidazoon* was first described as an unplaced problematicum (Shu *et al.*, 1999) it was compared on the basis of the rim of plates around the mouth to the �agnathan� *Pipiscius* from the Carboniferous Mazon Creek of Illinois. Other features such as possession of gill rays would retain *Pipiscius* in the chordates.

Finally, the Burgess Shale problematicum *Nectocaris* resembles *Vetulicola* in its possession of an arthropod-like carapace with a chordate-like tail and no appendages.

The Yunnanozoa are another group of Cambrian animals known from the Chengjiang Lagerstatte of China. Two genera are known, *Yunnanozoon* and *Haikouella*. Like vetulicolians, they have a bipartite body plan with a gill-bearing (six pairs) anterior and a segmented posterior. Unlike vetulicolians, the segmented section overlays the slender canoe-shaped anterior to a significant degree. The two sections are connected by a median zone which apparently had a thinner cuticle, probably allowing the anterior region to expand and contract in height. The gills were external and an outwardly- and downwardly-directed �skirt� surrounded the anterior section. Yunnanozoans have generally been regarded as chordates, and Dzik (1995) identified structures on the head of *Yunnanozoon* with a notochord running ventrally to the �muscle blocks� (the posterior segments). These structures were not identified in *Haikouella* by Shu *et al.* (2003), and Dzik's �eyes� probably correspond to the front of the skirt around the anterior. Other authors identify both a dorsal and a ventral nerve cord, which might support a position closer to hemichordates.



Images: *Vetulicola* from 岐阜大学教育学部 理科教育講座地学教室 (Gifu University Department of Education Science Education. Geography Classroom). Three vetulicolians from the **Internet Museum of Natural History**. *Vetulicola* gill structures from Shu *et al.* (2001).

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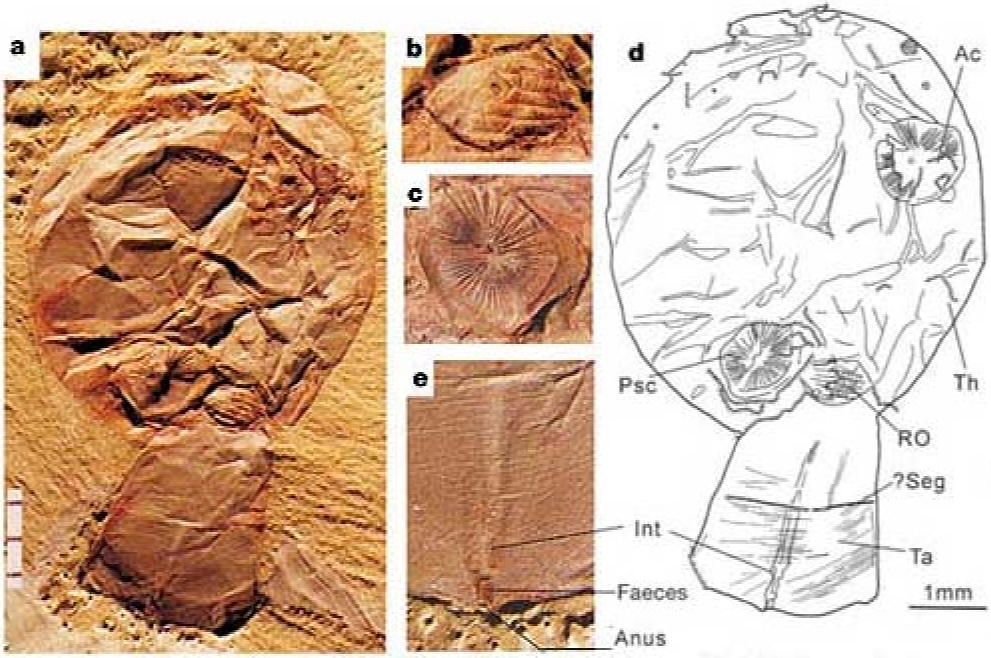
Vetulocystidae

```
DEUTEROSTOMIA
|--Vetulicolia
`--+--CHORDATA
   `--Ambulacraria
      |--Hemichordata
      `--+--Vetulocystidae
         |  |--Vetulocystis
         |  `--Dianchicystis
         `--HOMALOZOA (grade)
            `--ECHINODERMATA
```

More Hints from Chengjiang

Dendrogram
References

More Hints from Chengjiang



Vetulocystis from Shu *et al*. (2004). Ac is the putative mouth, RO the respiratory organ, and Psc a possible exhalant or excretory exit.

The Vetulocystidae are a very recently described family of two species from the Chengjiang Lagerstatte of the Lower Cambrian of China. Shu *et al*., 2004. The authors interpreted them as an anatomical link between the Vetulicolia on one hand and the homalozoans on the other. Like Vetulicolia, they have a distinctly bipartite body plan. The anterior section is globular and bag-like. The posterior tail is truncated -- in *Vetulocystis catenata* it is broad and expands posteriorly, in *Dianchicystis jianshanensis* it is tapering. Weakly developed furrows crossing the tail were regarded as segment boundaries like those of Vetulicolia, but this should be regarded as far from definite.

Three prominent openings are present on the anterior part (the "theca"). Two cone-shaped orifices are present in the right antero-dorsal and left postero-dorsal quadrants which the authors interpreted respectively as the mouth and anus. A right postero-dorsal lenticular structure with prominent ridges was interpreted as a respiratory organ, and at least one specimen indicates a lamellate structure to this suggesting gills. The specimens are irregularly wrinkled, indicating that the cuticle was not sclerotised and there was no stereom.

The superficial similarity of these creatures to Stylophora is readily noticeable, more specifically to Jefferies' (1986) reconstruction of cornutes. Both show a right anterior mouth and posterior gills, with a posterior tail. The Vetulocystidae therefore supply corroborating evidence for this reconstruction. The tail of *Vetulocystis* also preserves a median tubular structure that Shu *et al*. suggested might be an intestine, though they admit that this is inconsistent with identification of the posterior cone as an anus. The tail structure may represent a notochord-like organ, which would also be consistent with Jefferies' Stylophora reconstruction.

The Vetulocystidae probably led sedentary lives on the sea-floor as filter-feeders drawing water into the mouth and expelling it through the anus or gills. The function of the tail is difficult to imagine - it seems too short and the wrong shape to function well as a propulsive organ nor does it resemble a holdfast. Perhaps it was used to dig the animal into the sediment (thanks to David Marjanovic for suggesting this).

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Deuterostomia Dendrogram

```
Metazoa
|--Porifera (paraphyletic?)
`--+--Radiata
   `--Bilateria
      |--Deuterostomia
      |  |--Vetulicolia
      |  `--+--Chordata
      |     `--Ambulacraria
      |        |--Hemichordata
      |        `--+--Vetulocystidae
      |           `--Homalozoa (grade)
      |              `--Echinodermata
      |
      `--Protostomia
         |--Ecdysozoa
         `--Lophotrochozoa
```

Dendrogram

o : crown group
^ : stem group
� : paraphyletic basal radiation
@ : apomorphy-based clade
* : similarity-based (classical) taxon
? : basis uncertain or not yet established

```
o BILATERIA (including ?some/?all "Acoelomates") (= starfish + silverfish)
|--^ DEUTEROSTOMIA  (= starfish > silverfish)
|  |--* Vetulicolia X
|  |  |--+--Xidazoon X
|  |  |  `--Didazoon X
|  |  `--+--Pomatrum X
|  |     `--Vetulicola X
|  `--+--@ CHORDATA (notochord present, or ^: movie stars > sea stars)
|     `--o Ambulacraria (hemichordates + echinoderms)
|        |--? Hemichordata
|        `--+--Xenoturbella
|           `--+--* Vetulocystidae X
|              |  |--Vetulocystis X
|              |  `--Dianchicystis X
|              `--o HOMALOZOA (grade, redefined here as Rhenocystis + Echinus)
|                 `--+--* Stylophora X (or possibly �)
|                    `--+--* Soluta X
|                       `--o ECHINODERMATA (living echonoderm crown group)
`--PROTOSTOMIA
```

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Deuterostomia References

```
METAZOA
|--PORIFERA  (paraphyletic?)
`--+--RADIATA
   `--BILATERIA
      |--DEUTEROSTOMIA
      |  |--Vetulicolia
      |  `--+--CHORDATA
      |     `--Ambulacraria
      |        |--Hemichordata
      |        `--+--Vetulocystidae
      |           `--Homalozoa  (grade)
      |              `--ECHINODERMATA
      |
      `--PROTOSTOMIA
         |--ECDYSOZOA
         `--LOPHOTROCHOZOA
```

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Ambulacraria.

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Echinodermata

Cambrian to Recent

The echinoderms (or "spiny skins") are a diverse group of completely marine animals. They are known from the Cambrian to the Recent and are found in shallow marine waters as well as the deep abyssal plains.

They have a soft body encased in a hard rigid shell or exoskeleton (called a *test*) made of individual plates (or *ossicles*). made up of numerous thin plates. Many echinoderms have spines covering their test (e.g. the sea urchin). This group includes such familiar sea-shore creatures as starfish and sea urchins, as well as a number of less known types, and a whole range of paleozoic forms that are no longer around. there are some 6000 recent species, distributed among five classes. But these are only a small fraction of the number and diversity of types that lived in past ages, especially during the Paleozoic era when the group was at its height.

The most distinctive thing about echinoderm appearance is their pentameral - that is, a five fold - radial symmetry. In other words, their body is structured on a five-fold plan, with rays or arms in fives or multiples of five, as shown for example with the familiar starfish with its five arms.

Echinoderms also have a complex and unique water-vascular (or *ambulacral*) system; a hydrostatic skeleton of internal water-filled canals. This evolved originally as a food collecting and transporting device, but in some echinoderms like starfish and sea urchins is used primarily for movement by means of suckered "tube feet". It can also be used to grip objects and even in the case of starfish apply tremendous force to price open clams, upon which those animals feed.

Echinoderms larvae have bilateral symmetry (having a definite front and rear) while as adults this is lost. This shows that they evolved from normal ancestors and only secondarily reverted to radial symmetry.

Many early echinoderms were not pentameral at all, and had strange armoured shapes. Some types were able to crawl by nudging themselves along the sea floor with a sort of "tail".

Strange as it may seem, echinoderms are actually distant cousins of vertebrates. Both share a common type of embryonic development, and are grouped under the infrakingdom Deuterostomia.

Classification

Phylum Echinodermata

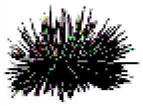
Subphylum Blastozoa

..........Class Eocrinoidea (Cambrian - Silurian, 30-32 genera)
..........Class Parablastoidea (Ordovician, 3 genera)
..........Class Rhombifera = Cystoidea in part (Ordovician - Devonian, 60 genera)
..........Class Diploporita = Cystoidea in part (Ordovician - Devonian, 42 genera)
..........Class Blastoidea (Silurian - Permian, 95 genera)

Subphylum Crinozoa

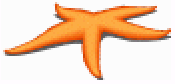
..........Class Crinoidea - sea lilies (Cambrian? Early Ordovician - Recent, 1005 genera)
..........Class Paracrinoidea (Ordovician - Silurian, 13-15 genera)

Subphylum Echinozoa



..........Class Echinoidea (Sea Urchins) (Ordovician - Recent, 765 genera)
..........Class Holothuroidea (Sea Cucumbers) (Ordovician - Recent, 200 genera)
..........Class Edrioasteroidea (Early Cambrian - Carboniferous, 35 genera)
..........Class Edrioblastoidea (Ordovician, 1 genus)
..........Class Helicoplacoidea (Cambrian, 3 genera)
..........Class Cyclocystoidea (Ordovician - Devonian, 8 genera)

Subphylum Asterozoa (= Stelleroidea)



..........Class Asteroidea - starfish - (Early Ordovician - Recent, 430 genera)

..........Class Ophiuroidea - Brittle Stars -(Ordovician - Recent, 325 genera)

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Echinodermata: Glossary

aboral side. The side of the body opposite the mouth is called the **aboral side**. This is normally dorsal.

The **ambulacra** are located in the middle of each arm along a features called the **ambulacral groove**.

The **ambulacral groove**. In many echinoderms, this groove carries small captured food particles to the mouth of the organism, although in some types the feature has been altered to serve other functions.

ambulacral system: same as the water vascular system.

arms. long, flexible mobile limbs - usually containing a feeding groove

brachioles Delicate arm-like appendages coming off their ambulacra in stalked echinoderms like Blastoids.

calyx At the top of this stem of echinoderms like Crinoids and Cystoids is the main part of the animal, a cup-shaped body, to which arms are attached.

columnals. stacked, articulated plates that make up the stem.

crown. The calyx and the arms together are sometimes referred to as the crown.

madreporite, a structure located on the aboral surface, in some species looking rather like a drain cover in a sink. The madreporite is a perforated platelike structure which acts as the inlet for the water vascular system.

oral side. The side with the mouth in echinoderms is defined as the **oral side**. Depending on the group, the oral side can point up or down. In starfish it points down, in crinoids up.

ossicles The numerous small plates that constitute the echinoderm skelton. These ossicles are composed of a form of calcium carbonate known as calcite.

pinnules Small, feather-like structures on the arms which form the filtration fan which stalked echinoderms (crinoids, cystoids, and blastoids) use to feed. The pinnules which are used to filter small food particles from the water.

stem. The calyx is usually connected to the bottom via a **stem**. The stem is either circular or pentagonal (five-sided) in section and composed of numerous disc-like plates called **columnals**. Stemmed forms frequently have a **holdfast** composed of small, polygonal plates, although some species wrapped their stem around other organisms, and thus didn't need a holdfast.

test: many echinioderms to have fused calcite ossicles forming a rigid, external skeleton referred to as a test.

water vascular system. The water vascular system maintains communication with the surrounding sea water through a group of pores in the **madreporite**. It serves for food transport in some forms, but has been adapted to assist in locomotion and as a kind of internal, hydrostatic skeleton.

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```
<==o ECHINODERMATA
   |--+-- �CYSTOIDEA
   |  `-- �BLASTOIDEA
   `--+-- CRINOZOA (merilijat)
      `--o ELEUTHEROZOA
         |--o �EDRIOASTEROIDEA
         `--+?- HOLOTHUROIDEA
            `--+--o ASTEROZOA (merit�hdet)
               |  |--o STELLEROIDEA
               |  |  `--o SOMASTEROIDEA
               |  |     `--o GONIACTINIDA
               |  |        `-- Platasteriidae
               |  |-- ASTEROIDEA
               |  `-- OPHIUROIDEA
               |?- [�]CONCENTROCYCLOIDEA
               `?-+-- �OPHIOCISTIOIDEA
                  `--o ECHINOZOA
                     `-- ECHINOIDEA
```

References & Links

Conway Morris, S., 1993: The fossil record and early evolution of the Metazoa. --Nature, vol. 361, 21 January,pp. 219-225

The Tree of Life site has an excellent cladogram and discussion of the relationships of Echinodermata, both living and extinct. It differs in a number of respects from our arrangement. TheBerkeley UCMP page has yet another arrangement -- a bit more like our own but probably somewhat out of date. Mikko Haaramo's cladogram – from which ours is derived -- may be found at Echinodermata. For those determined Linneans out there, the California Academy of Sciences maintains a Linnean scheme at Classification of the Extant Echinodermata. Finally, Tom Holtz has a good discussion of the issues in his course notes at GEOL 331 Lectures 32-33- Echinodermata. ATW050801.

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Subphylum Asterozoa

(Ordovician-Recent)

starfish and their relatives

Starfish and brittle stars, as they are popularly called, are members of the group called organisms called the Stelleroidea or Asterozoa which are characterized by a flexible star shaped body which has a central disk with five or more radiating arms. Each **arm** contains a radial branch of the **water vascular system**, which supports numerous paired **tube feet** which extrude through the underside of each arm, alongside the **ambulacral groove**. (feeding groove). The mouth is located on the underside of the disk, in the center where the radiating ambulacra intersect.

Complete fossil starfish are usually quite rare. Most fossil starfish consist of scattered individual plates or segments of arms. This is because the skeleton is not ridged, as in the case of echinoids (sea urchins), but is composed of many small plates (or ***ossicles***) which quickly fall apart and are scattered after death and the decay of the soft parts of the creature.

Asteroidea - true starfish

Ophiuroidea - brittle stars.

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Class Asteroidea

true starfish

(Ordovician-Recent)

The asteroids or true starfish usually have five arms, although some species have more. Unlike the ophiuroids, there is no sharp distinction between the arm structure and the central body structure, and the internal body parts extend into the arms.

Starfish move along the sea-floor or climb rocks using the numerous small tube feet which are present on the underside of their bodies. These tube feet are also used for burrowing and manipulating prey.

Most starfish are voracious hunters, preying on other animals, particularly clams, corals, other echinoderms, or anything else unlucky enough to cross their path. Some asteroids can extrude their stomach through their mouth, killing and partially digesting their prey outside their body. Asteroids are among the most active echinoderms.

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Palaeos **ECHINODERMATA**

Παλαιός

ECHINODERMATA **OPHIUROIDEA**

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Palaeocoma egertoni

Palaeocoma egertoni
A Jurassic brittle star.
Early Jurassic of Bridport, Dorset, England.
from Hans' Paleobotany Pages

Class Ophiuroidea

(Ordovician-Recent)

Ophiuroidea contains two large clades, the Ophiurida (brittle stars) and Euryalida (basket stars). Many of the ophiuroids are rarely encountered in the relatively shallow depths normally visited by humans, but they are a diverse group. Some 1500 to 200 species exist today, and -- because many species live at considerable depth -- these numbers probably fall quite short of the actual living diversity of this taxon.

Range/ Location: Ophiuroids can be found in all of the major marine

Basket star

provinces, from the poles to the tropics. In fact, crinoids, holothurians, and ophiuroids rule the floor of the deep oceans at depths below 500 metres. Basket stars usually confined to the deeper parts of this range. Ophiuroids are known even from abyssal (> 6000m) depths. However brittle stars are also common, if cryptic, members of reef communities, where they hide under rocks and even within other living organisms. A few ophiuroid species can even tolerate brackish water, an ability otherwise almost unknown among echinoderms.

The ophiuroids diverged in the Early Ordovician, roughly 500 million years ago. Their fossil record is weak, since brittle stars (as their name implies) tend to break apart easily.

Disk and internal organs: Like all echinoderms, the Ophiuroidea possess a calcium carbonate (calcite) skeleton. In ophiuroids, the calcite ossicles are fused to form armor plates (collectively, the *test*).

Ophiuroid internal anatomy

Of all echinoderms, the Ophiuroidea may have the strongest tendency toward 5-segment radial (*pentaradial*) symmetry. The body outline is similar to the Asteroidea, in that ophiuroids have five arms joined to a central disk (*calyx*). However the central body disk in ophiuroids is sharply marked off from the arms. The disk contains all of the viscera. That is, the internal organs of digestion and reproduction never enter the arms (in contrast to Asteroidea).

The mouth is rimmed with five jaws. Behind the jaws is a short esophagus and a large, blind stomach cavity which occupies much of the dorsal half of the disk. Ophiuroids have neither an intestine nor an anus. Digestion occurs within 10 pouches or infolds of the stomach. Gas exchange and excretion occur through cilia-lined sacs called bursae; each opens onto the interambulacral area (between the arm bases) of the oral (ventral) surface of the disc. Typically there are 10 bursae, and each fits between two stomach digestive pouches.

The sexes are separate in most species. Gonads in the disc open into the bursae. Gametes are then shed by way of the bursal sacs. Many species actually brood developing larvae in the bursae. The ophiuroid coelom is strongly reduced, particularly in comparison to other echinoderms. The nervous system consists of a main nerve ring which runs around the central disk. At the base of each arm, the ring attaches to a radial nerve which runs to the end of the limb. Ophiuroids have no eyes, as such. However, they have some ability to sense light through receptors in the epidermis.

Arms: Both the Ophiurida and Euryalida have five long, slender, flexible whip-like arms, up to 60 cm in length. They are supported by an internal

Ophiurid arm cross section. from Biodidac.

skeleton of calcium carbonate plates that referred to as *vertebral ossicles*. These "vertebrae" articulate through ball-in-socket joints, and are controlled by muscles as shown in the figure. The body and arms are also bear calcite plates and delicate spines. Euryalids are similar, if larger, but their arms are forked and branched. Ophiuroid podia generally function as sensory organs. They are not usually used for feeding, as in Asteroidea.

The vessels of the *water vascular system* end in tube feet. The water vascular system generally has one *madreporite*. However, some forms have none. Suckers and ampullae are absent from the tube feet.

Ophiuroids can readily regenerate lost arms or arm segments unless all arms are lost. Ophiuroids usethis ability to escape predators, like lizards who automize, or deliberately shed, part of their tails to confuse pursuers.

Locomotion: Brittle stars use their arms for locomotion. They do not, like starfishes, depend on tube feet. Brittle stars move fairly rapidly by wriggling their arms which are highly flexible and enable the animals to make either snake-like or rowing movements.

Trophic: Many ophiuroids are scavengers or detritivores. Small organic particles are moved into the mouth by the tube feet. Ophiuroids may also prey on small crustaceans or worms. Basket stars, in particular may be capable of suspension feeding, using their mucous covering the branched arms to trap plankton and bacteria. ATW040801.

Links:

Class Ophiuroidea: brief discussion

The Ophiuroidea: the UCMP page. This a good one.

BrittleStars: emphasis on diversity of living species

ADW- Ophiuroidea- Classification: Best on the Web

Class- Ophiuroidea: a few images without text, but contains hard-to-find image of a complete basket star

Ophioderma Laboratory Exercise: more on brittle star anatomy

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Class Blastoidea

(Cambrian - Permian)

The Blastoidea are echinoderms with a long stalk with a head or theca at the top. The fragile and slender arms or brachioles attach near the mouth of the individual The grooved ambulacral areas extend away from the mouth along the sides of the theca. They had a complex internal respiratory system which differentiates the blastozoan classes from other echinoderms. The morphology of the blastoids and other blastozoans has led some workers to suggest that the blastozoans lacked tube feet, and thus possibly a water vascular system - another feature which would differentiate them from all other echinoderms. However, this theory is still controversial.

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Class Eocrinoidea

Early Cambrian to Silurian

Gogia spiralis
later Early Cambrian

The Eocrinoids ("dawn crinoids") are among the earliest groups of echinoderms. They had a vase-shaped body (calyx), covered by plates. the plates were symmetrical and bore ridges which meet up with the ridges of other plates, giving a geometrical pattern. Each of the five topmost plates bears a bifurcated brachiole (a slender arm-like food-gathering structure, like the similiar structures in cystoids).

Early eocrinoids, such as *Gogia spiralis* shown above, were attached to the bottom by a plate-covered thick stem or holdfast. Later eocrinoids evolved a long stalk with columnals, like crinoids and blastoids.

Although the thecal plates are of crystalline calcite (as with crinoids), Eocrinoids are actually more closely related to, and indeed ancestral to, various groups of Blastoids. The group therefore did not die out in the Ordovician or Silurian, but rather continued through its descendents up until the Permian

Links

The Eocrinoidea

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Class Crinoidea

(Cambrian? Ordovician-Recent)

The popular names for crinoids are "sea lilies" (for fixed crinoids) and "feather stars" (for free-swimming crinoids). There are several hundred species of stalked and unstalked crinoids inhabit the modern world's oceans, but this is just a tiny fraction compared to their abundance in past ages. The stalked forms inhabit the deep oceans, while stalkless forms are commonly found in shallower depths (including the shallows of coral reefs).

Crinoids have a cup-shaped head (the calyx) to which are attached long, branching **arms**. The food is transferred down the arms to the mouth by tube feet located on the pinnules and arms. The calyx is usually connected to the bottom via a **stem.**

There are usually five or a multiple of five arms, which may be repeatedly branched. Grooves in the arms channel food to the mouth, which is located in the centre of the calyx. Both the mouth and the anus are on the oral side of the calyx. Some paleozoic crinoids developed a symbiotic relationship with gastropods which would sit on the crinoid anus and feed on the shit (which was obviously rich in nutrients).

There are over a thousand known genera, mostly fossil forms

Evolutionary History

Organisms that have been identified as Crinoids first appeared in the early in the middle of the Cambrian period, although Conway Morris suggests these may actually be an extinct group of Cnidarians. Undoubted crinoids are known from the Ordovician period, by which time they had already become abundant and important. They became so numerous during the Palaeozoic era that their remains often form vast thicknesses of limestone. These great crinoid gardens probably lived in shallow water. The group as a whole suffered a major crisis during the Permian period when most of the crinoids died out, with a few surviving into the Triassic period. During the Mesozoic era there was another great radiation of the crinoids, with more modern forms possessing flexible arms becoming widespread. In the Cenozoic they again declined, and most species live in very deep water

Most Paleozoic crinoids lived attached to the sea-floor by a flexible stem, which may be either cemented to the sea-floor, or have a root-like system buried into the sediment. Fossil crinoids have stems ranging in size from a few centimetres in length to as much as 21 metres.

Some crinoids, such as Pentacrinites shown in the illustration at the left, seem to have lived attached to floating driftwood and complete fossil colonies are often found. Sometimes the driftwood to which they were attached became waterlogged and sank to the bottom, taking the attached crinoids with it. The stem of *Pentacrinites* can be several metres long.

Pentacrinites fossilis
Lower Lias. (Jurassic)
Lyme Regis, Dorset,
England.

Classification

Detailed classification of the crinoids is based primarily upon the arrangement of the plates within the calyx, the number and branching pattern of the arms, and the external surface detail of the calyx. Internal features of crinoid anatomy, such as the nervous and respiratory systems, are also important

Subclass Camerata (Middle Ordovician - Permian)
Subclass Inadunata (Early Ordovician - Late Permian)
Subclass Flecibilia (Middle Ordovician - Late Permian)
Subclass Articulata (Triassic - Recent) The only living subclass of crinoids.

```
<==o CRINOZOA
   `--o CRINOIDEA
      |-- †DISPARIDA
      `--+-- †"Four-circlet crinoids"
         `--+-- †CAMERATA
            `--+-- †FLEXIBILIA
               `--+-- †CLADIDA
                  `-- ARTICULATA [ICZN rules, article 1 b4]
```

Reference(s):

iNet: Tree of Life --http://tolweb.org/tree/

Parker, S. P. (ed.), 1982: Synopsis and classification of living organisms. Vols. 1 & 2 --McGrew-Hill Book Company

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Homalozoa

```
DEUTEROSTOMIA
|--Vetulicolia
`--+--CHORDATA
   `--Ambulacraria
      |--Hemichordata
      `--+--Vetulocystidae
         `--HOMALOZOA
            |--Stylophora
            `--+--Soluta
               `--+--Cincta
                  `--+--Ctenocystoidea
                     `--+--Helicoplacoidea
                        `--ECHINODERMATA
```

Homalozoa
- A Passing Grade
- "Haplozoa" -- A Couple of Loose Ends
- Stylophora
- Soluta
- Cincta
- Ctenocystoidea
- Helicoplacoidea
- Dendrogram
- References

Rhenocystis latipedunculata a Mitratan carpoid from the Early Devonian (Seigenian/Emsian) Hunsruck Slate /lagerstatten, Bundenbach Germany; Length about 3 cm, with a 2.5 cm "tail"

Even for a phylum as unusual as the echinoderms, the carpoids, or homalozoa as they are also known, are strange. These small (mostly only about an inch in length, although a few grew a bit larger) armoured paleozoic animals lacked the usual radial symmetry of their echinoderm cousins, which means they had a definite "front" and "rear". Even so, they resemble no animals we are familar with; their irregular flattened, asymmetric body and long "arms" and "tail" make them look more like creatures from the pages of a science fiction novel.

Homalozoans have variously been interpreted as stem-group echinoderms, stem group chordates (the calcichordates hypothesis of Jefferies), and a assemblage of groups related to Crinoids and Blastozoa. MAK120113

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"Homalozoa"

```
DEUTEROSTOMIA
|--Vetulicolia
`--+--CHORDATA
   `--Ambulacraria
      |--Hemichordata
      `--+--Vetulocystidae
         `--HOMALOZOA
            |--Stylophora
            `--+--Soluta
               `--+--Cincta
                  `--+--Ctenocystoidea
                     `--+--Helicoplacoidea
                        `--ECHINODERMATA
```

A Passing Grade
"Haplozoa" -- A Couple of Loose Ends

A Passing Grade


Anomalocystis from the Early Devonian of New York State. Yale Peabody Museum.

The Homalozoa, as that term is usually used, are plainly not a clade. Therefore, we will use the term simply to designate a grade of deuterostomes more derived than the Vetulocystidae, but outside the echinoderm crown group. In doing so, we will probably include groups which probably would not be called homalozoans in ordinary parlance -- assuming that one ordinarily cared to discuss homalozoans at all. A more conventional use of the word defines Homalozoa simply as a grade of physical organization, and composed for taxonomic purposes of the Stylophora, Soluta, Cincta and Ctenocystoidea. The four classes have little to unite them other than possession of a flattened theca and the *absence* of pentaradial symmetry. But, whatever, the definition, Homalozoait is not a terribly useful concept, since the arrangementof this area of phylospace is quite unstable at the moment, and it is impossible to say anything of interest about the difference between homalozoans and echinoderms. We simply have too little informmation about which is which.

One historical point is worth making. Jefferies, *e.g.* Jefferies (1986), argued long and loudly that some Homaloza (the Mitrata, in particular) were ancestral to the Chordata. In fact, he continues to do so. *See*, e.g., Dominguez *et al*. (2003). The group putatively related to Chordata he called "Calcichordata," the thought being that the calcium carbonate plates which characterize the homalozoans had been exchanged for apatite in chordates. While Jefferies' phylogenetic hypothesis is no longer a serious contender, many of his anatomical observations are very much in play. In any case, it is common to see the term "Calcichordata" used as a synonym for Homalozoa.

"Haplozoa" -- A Couple of Loose Ends

In 1941, Whitehouse introduced a new echinoderm subphylum Haplozoa for two genera of small fossils from the lowernmost Middle Cambrian of Queensland, Australia. Each of these fossils was placed by Whitehouse in a new class, *Cymbionites* in the class Cycloidea and *Peridionites* in the class Cyamoidea. Ubaghs (1967b).

Cymbionites is a generally hemisphaerical cup-shaped fossil with an average diameter of 12 mm. It is composed of five massive wedge-shaped plates tightly sutured together such that boundaries between the plates are often hard to distinguish. The median depression has fluted sides, and a tiny central plate is present at the bottom of the depression and surrounded by the others such that it is not visible from the exterior.

Peridionites is even smaller, less than 10 mm in its maximum diameter. It is shaped like half a lens, semicircular in side view and elliptical in apical view. it is composed of five massive plates, two large terminal plates with two smaller mediolateral plates and a median apical plate. A deep, radially fluted central cavity divides the mediolateral plates.

Whitehouse compared *Peridionites* to the dipleurula stage in echinoderm larval development, and *Cymbionites* to the pentactula stage of eleutherozoan development. He therefore suggested that "Cycloidea" was ancestral to the Eleutherozoa while "Cyamoidea" was ancestral to Echinodermata as a whole.

While some workers have supported this idea, the majority have not. Others have suggested that these genera represent an eocrinoid (both) or cystoid (Cymbionites only) in which the theca has been greatly reduced. They have also been regarded as non-echinoderms close to the origin of Bilateria, and *Peridionites* has been suggested to be a calcified benthic ctenophore.

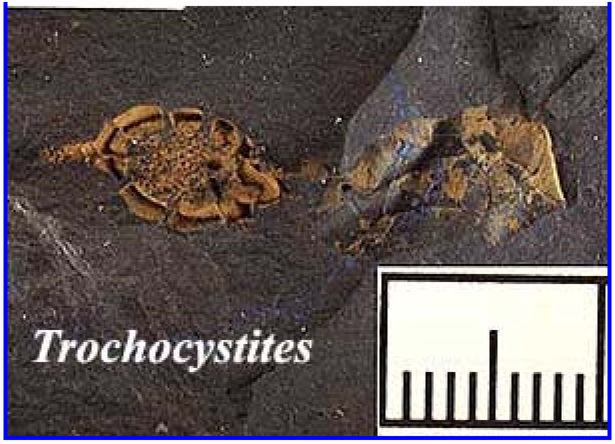
When he covered them in the Treatise on Invertebrate Paleontology, Ubaghs (1967b) placed both genera as Echinodermata *incertae sedis*. While echinoderm relationships were supported by the composition of the plates from a single calcite crystal with stereom microstructure and by pentaradial symmetry in *Cymbionites*, Ubaghs noted in regard to the various theories as to their relationships that "The temerity of some of these hypotheses contrasts with the weakness of evidence in support of them". Both *Cymbionites* and *Peridionites* simply don't preserve enough information to say much about them. The names "Cycloidea" and "Cyamoidea" are redundant with their constituent genera (and Cycloidea has been used for an order of fossil crustaceans besides) and in the absence of anything to support the two genera as closely related, the name "Haplozoa" is equally unnecessary.

Cincta

```
Homalozoa
|--Stylophora
`--+--Soluta
   `--+--Cincta
      `--+--Ctenocystoidea
         `--+--Helicoplacoidea
            `--ECHINODERMATA
```

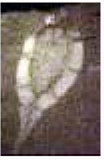
The Cincta are known only from the Middle Cambrian. They possessed a round, flattened theca with a plated stele, giving an overall shape something like a frying pan. The theca is mostly covered by small tesselated plates with a single row of large marginals. There are three openings at the front and dorsal of the theca -- a large central orifice with operculum, a smaller orifice to the right and a pyramidal orifice to the left. Under the reconstruction favoured here, the right orifice is the mouth and the left the anus, implying a U-shaped gut. The central orifice is the gill opening. A small opening behind the mouth represents the hydropore, perhaps combined with the gonopore. Dominguez-Alonso, 1999. Other authors would interpret the pyramidal opening as the gonopore, and the central and left openings would be the mouth and anus, with differing interpretations as to which was which. Ubaghs (1967a); Parsley (1999). A biramous ambulacrum is lodged in grooves recumbent on the anterior side of the theca. The two branches differ in size, and the right ambulacrum is reduced or missing in at least one genus, *Gyrocystis*. Unlike Stylophora and Soluta, the tail is simple in structure and not divisible into sections. Compared to that of other homalozoans, it appears to have been fairly rigid, though a small amount of "waggling" may have been possible. A lot of debate has occurred over whether the "tails" of the homalozoan classes are homologous, as has already been touched on in Soluta. Those who would derive them from more typical echinoderm ancestors would usually say not, regarding them as independent adaptations of radial arms. Supporters of the reconstructions used here are more likely to regard them as homologous on the basis of similarities in position and structure. Most authors do agree that the "tails" are probably not homologous with pelmatozoan stems, as they differ in structure and being lateral to the theca rather than ventral. An exception is Parsley (1999) who, using the pyramid-as-gonopore reconstruction, argued that the Cincta were derived Blastozoa and identified the cinctan stele with the blastozoan column.

In the current reconstruction, the double ambulacrum and its postion recumbent on the body rather than restricted to the arm argue for a more crownward postion for Cincta than Soluta. Jefferies (1997).



Cincta probably lay on the sediment with the theca directed downstream, where back-eddies from water flowing over the theca would provide optimum conditions around the ambulacra for filter feeding. Parsley (1999). The stele would have been used to dig into the sediment and anchor the animal in place. if the central orifice of the theca is correctly interpreted as a gill opening, water being forcibly expelled from the gill could have aided in pushing the stele back into the substrate. Jefferies (1997).

� Christopher Taylor CT050908.

Images: *Trochocystites* from Prof. Cowen's **History of Life, Fourth Edition** site. *Gyrocystis* from **Проблемы эволюции**. Not shown is a large version of this  specimen which can be seen at **www.paleontologia-hispana.com** (*Gyrocystis*).

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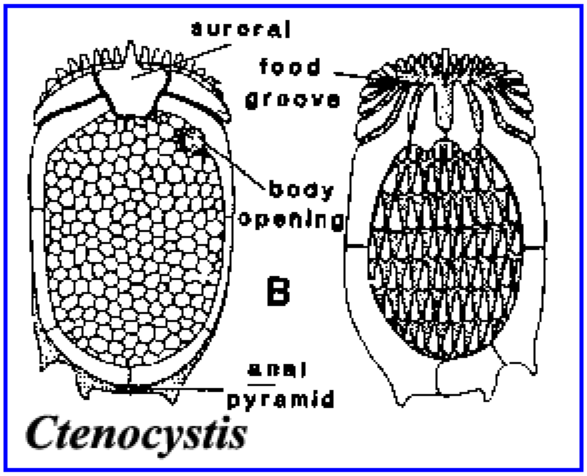
Ctenocystoidea

```
HOMALOZOA
|--Stylophora
`--+--Soluta
   `--+--Cincta
      `--+--Ctenocystoidea
         `--+--Helicoplacoidea
            `--ECHINODERMATA
```

Ctenocystoidea are a small class of bilaterally symmetrical stem echinoderms from the Middle Cambrian of western North America and Bohemia, first described in 1969. Dominguez-Alonso (1999); Parsley (1999). An undescribed form from the Upper Ordovician of Wales has also been assigned to the Ctenocystoidea, but preliminary illustrations (Dominguz-Alonso, 1999) are significantly different from other members of the class, so we'll have to wait for a detailed description before passing judgment.

Ctenocystoidea differ from the more basal homalozoans in lacking an appendage. They are distinctly flattened and rectangular to trapezoidal in dorsal view. Like Cincta, they have a central covering of small tesselated plates with a row of much larger marginal plates around the outside edge of the theca.



The most distinctive feature of the Ctenocystoidea (and the source of their name) is the ctenoid organ along the anterior margin. This is composed of two series (one each side of the mouth) of ctenoid ("comb-like") plates separated by paired rostral plates on the anterior mid-line. The ctenoid plates were dorsally articulated and so capable of slight movement. A space behind the ctenoid organ held the ambulacra. Dominguez-Alonso (1999) suggested that the ctenoid plates were covered in life by ciliary epithelium so the ctenoid organ acted as a ciliary pump drawing water into the ambulacrum.

The hydropore is located at the anterior right of the dorsal integument, while the pyramidal anus is located at the centre of the posterior margin. The mechanism by which ctenocystoids moved is problematical. Parsley (1999) suggested that the ctenoid plates may have been mobile enough to claw the animal forward. Rather more dramatically, it has been suggested that water may have been forcibly expelled through the anus, moving the animal by jet propulsion.

Ctenocystis

Dominguez-Alonso (1999). The potential here for comedic commentary being obvious, we leave it to the reader's own interpretation.

Placing the Cincta and Ctenocystoidea in the deuterostome phylogeny requires us to identify how the bilateral ambulacra of these classes correspond to the pentaradial ambulacra of crown echinoderms. Echinoderm ambulacra are identified by letters A-E, with A the anterior anbulacrum and the letters rising clockwise. In crown echinoderms, the ambulacra all run direct to the mouth, but in some pentameral stem echinoderms such as the edrioasteroid *Stromatocystites*, the B and C ambulacra fuse a short distance distally from the mouth, as do the D and E ammbulacra, forming the 2-1-2 ambulacral pattern. Jefferies (1997). In Cincta and Ctenocystoidea, the left is therefore probably the DE ambulacrum while the right is the BC ambulacrum. Dominguez-Alonso (1999) placed the Ctenocystoidea crownward of the the Cincta due to the loss of the posterior appendage and the greater symmetry of the ambulacra. We're willing to run with this hypothesis for now, but would like to point out that these are characters that could have easily appeared convergently.

Images: *Ctenocystis* line drawing from **Campbell (1987)**. Photo from **FossilsForSale.com ONLINE CATALOG**.

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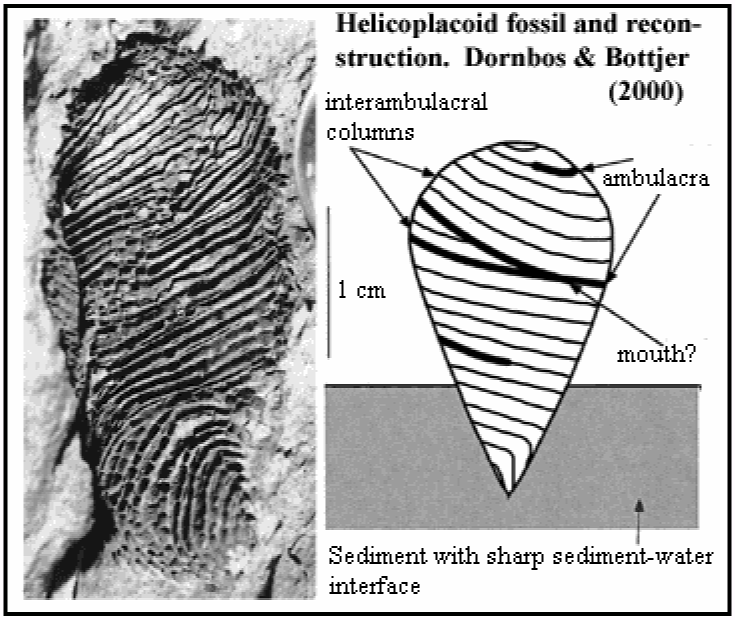
Helicoplacoidea

Armour-Plated Spirals

```
HOMALOZOA
|--Stylophora
`--+--Soluta
   `--+--Cincta
      `--+--Ctenocystoidea
         `--+--Helicoplacoidea
            `--ECHINODERMATA
```

Helicoplacoidea are known only from the Early Cambrian of western North America, no later the Atdabanian. Articulated body fossils are rare, and they are mostly known as dissociated plates. Durham (1993). Helicoplacoidea had a football-shaped body (rugby or American football, not soccer) with ambulacra running spirally down it. At the anterior end there are two ambulacra that meet partway down the body leading to a single ambulacrum posteriorly. The apparent connection of plates by soft tissue rather than direct articulations suggests that the body couldbe expanded or contracted as required.

Most authors interpret the life position of helicoplacoids as sessile, standing upright with the double-ambulacral end upwards. Some authors have argued that the flexibility of the test indicates a more vagile lifestyle in a reclined position, either on the substrate surface or burrowing. However, such a position appears inconsistent with the spiral ambulacra which obviously function to maximise exposure on all sides. The single ambulacrum does not reach the point of the downwards end, which was probably partially buried in the sediment to anchor the animal.


Helicoplacoid fossil and reconstruction. Dornbos & Bottjer (2000)

The position of the mouth is a matter of some debate. One interpretation places the mouth at the junction of the ambulacra, implying a triradial organisation as has been suggested to be the direct forerunner of the 2-1-2 organisation of the most basal pentameral stem echinoderms. *See, e.g.*, Dominguez-Alonso (1999). Durham (1993) found no sign of a structure identifiable as a mouth at this position in articulated specimens and supported an alternative position at the uppermost point, though it should be noted that no likely structure was identified there either. Even in articulated specimens, however, the loose organisation of helicoplacoids generally results in some shifting of individual plates, making interpretation more difficult. A dorsal position for the mouth does seem more likely for the sole reaspon that this is the position in almost every other sessile radial animal. The animal is then generally regarded as uniradial with the left adoral ambulacrum regarded as a branch of the main ambulacrum. One possibility which doesn't appear to have been considered is that helicoplacoids were derived from bilateral ancestors, with the left ambulacrum representing the DE branch and the right the BC. The posterior fusion of the ambulacra would then probably be unique, but surely no less likely than the secondary branching and change of direction otherwise required.

In light of this possibility, we put Helicoplacoidea crownwards of the Ctenocystoidea based on a single character, the dorsal rather than anterior position of the mouth (alternatively, a triradial reconstruction would definitely put the helicoplacoids crownwards).

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```
<==o �MITRATA [CALCICHORDATA; STYLOPHORA; CAROIDEA] (mitrates)
   |?- �Aspidocarpus bohemicus Ubaghs, 1979
   |?- �Chauvelia discoidalis Cribbs, 1990
   |?- �Ovocarpus monccereti Ubachs, 1994
   |?-o �CORNUTA
   |  |-- �Cothurnocystis
   |  `-- �Scotiaecystis
   |--o �Lagynocystidae
   |  `-- �Lagynocystis pyramidalis
   |--o �Peltocystidae
   |  `-- �Peltocystis cornuta
   `--o �Mitrocystidae
      |-- �Mitrocystides mitra Barrande, 1887
      |-- �Eomitrocystella savilli Beisswenger, 1994
      `--+--o �Mitrocystella
         |  |-- �M. incipiens
         |  `-- �M. abarrandei
         `--o �Anomalocystidae sensu Ruta, 1999 [Fig. 13b]
            |-- �Barrandeocarpus jaekeli Ubaghs, 1979; U. Dev. WEu.
            `--+-- �Kierocystis incerta Parsley, 1991; U. Dev. ENA.
               `--+-- �Barrandeocarpus norvegicus Craske & Jefferies, 1989; U. Dev. WEu.
                  `--+-- �Ateleocystites guttenbergensis Kolata & Jollie, 1982; U. Dev. CNA.
                     `--+--+-- �Kopficystis kirkfieldi Parsley, 1991; U. Dev. ENA.
                        |  `--+-- �Willmanocystis denticulata Kolata & Jollie, 1982; U. Dev. Aust.
                        |     `--+-- �Anomalocystis cornutus Hall, 1858; L. Dev. ENA.
                        |        `--+-- �Bokkeveldia oosthuizeni Ruta & Theron, 1997; L. Dev. SAf.
                        |           `--+-- �Mongolocarpos minzhini Rozhnov, 1990; U. Dev. CAs.
                        |              `--+-- �Placocystites forbesianus de Koninck, 1869; U. Dev.
WEu.
                        |                 `--+-- �Rhenocystis latipedunculata Dehm, 1932; L. Dev.
CEu.
                        |                    `-- �Victoriacystis wilkinsi Gill & Caster, 1960; U.
Dev. Aust.
                        `--+-- �Diamphidiocystis drepanon Kolata & Guensburg, 1979; U. Dev. ENA.
                           `--+-- �Enoploura popei Gaster, 1952; U. Dev. ENA.
                              `--+-- �Occultocystis koeneni Haude, 1995; L. Dev. SSA.
                                 `--+-- �Notocarpos garratti Philip, 1981; U. Dev. Aust.
                                    `--+-- �Tasmanicytidium burretti Gaster, 1983; U. Dev. Aust.
                                       `--+-- �Placocystella africana (Reed, 1925) L. Dev. SAf.
                                          `--+-- �Allenicytidium flemingi Gaster & Gill, 1968; L.
Dev. NZ.
                                             `-- �Australocystis langei Caster, 1954; L. Dev. ESA.
```

Reference(s):

Ruta, M., 1999: A cladistic analysis of the anomalocystid mitrates.
--Zoological Journal of the Linnean Society: Vol. 127, pp. 345-421

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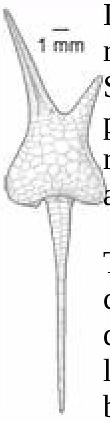
Soluta (= Homoiostelea)

```
Homalozoa
|--Stylophora
`--+--Soluta
   `--+--Cincta
      `--+--Ctenocystoidea
         `--+--Helicoplacoidea
            `--ECHINODERMATA
```



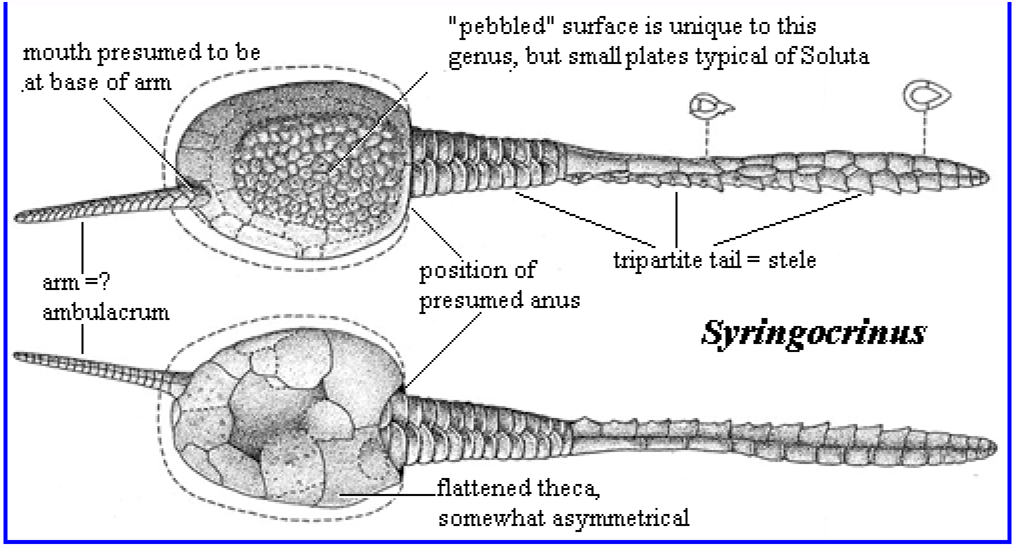
Like Stylophora, the Soluta appear to have never been overly diverse but occur over a long stratigraphic range, from the Middle Cambrian to the Lower Devonian. Caster (1967); Parsley (1997). Also like Stylophora, the main body of Soluta is an asymmetrical flattened theca. However in Soluta the theca possesses two appendages at roughly opposite ends, one significantly larger than the other. Almost all researchers agree that the smaller appendage is anterior and represents a feeding arm, while the larger appendage (the "stele") probably functioned as a propulsive tail.

The arm is generally clearly divided from the theca. It is contained by four rows of plates with the plates smaller along the dorsal side, probably indicating an ambulacrum. The exact location of the mouth is unknown, but is undoubtedly near the base of the arm. The anus was near the posterior ?right of the theca. Another opening near the arm is interpreted as the hydropore.

The stele is divided into three parts, the tetramerous proxistele closest to the theca tapering through the mesistele to the dimerous dististele furtherest from the theca. In the reconstruction used here, the stele is homologous with the stylophoran tail, as suggested by its position and tripartite division. The possession of an ambualcrum suggests a more crownward position than Stylophora.

Needless to say, other reconstructions would indicate other positions. If the stylophoran appendage is interpreted as an aulacophore, it may correspond to the solute arm rather than the stele. Caster (1967) regarded the Stylophora and Soluta as independently derived from pentaradial ancestors with the solute arm and stele both representing derived arms. Under the "calcichordate" hypothesis, some solutes were stem "Dexiothetica" while others were stem chordates less crownward than Stylophora. Jefferies (1997). This theory also differs in reversing the suggesting orientation so that the ambulacral side of the arm is ventral.

In the earliest solute genera, *Coleicarpus* and *Castericystis*, the distal end of the stele bears a



holdfast, though in juveniles only in *Castericystis*. All other solutes were free-living. They probably lay flat on the sediment, living as passive filter feeders. Later species show a tendency to reduce the size of the arm and develop a more bilaterally symmetrical theca.

Images: *Dendrocystoides* and starfish from **The Passionate Collector - George Rae Fossils**: An exhibition of fossils collected by George Rae and bequeathed to the Hunterian Museum. *Syringocrinus* adapted from two figures at **Geologic Overview of the Trenton Group** by the Harvard Museum of Comparative Zoology.

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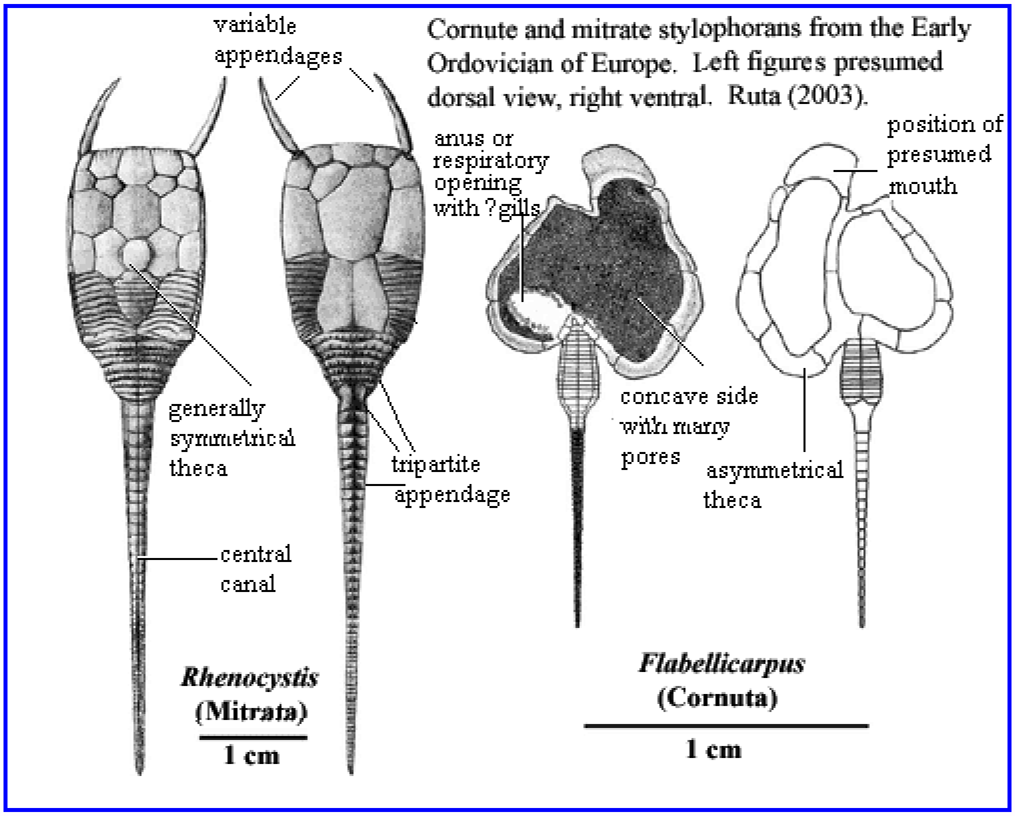
Stylophora

```
HOMALOZOA
|--Stylophora
|   |--Cornuta
|   `--Mitrata
`--+--Soluta
   `--+--Cincta
      `--+--Ctenocystoidea
         `--+--Helicoplacoidea
            `--ECHINODERMATA
```

Like a Tee-to-tum They Twirled Him



Cornute and mitrate stylophorans from the Early Ordovician of Europe. Left figures presumed dorsal view, right ventral. Ruta (2003).

The Stylophora were a not-overly-diverse but long-lived group of animals (Middle Cambrian to Middle Devonian - Ubaghs, 1967) that have probably received the most attention of the stem echinoderms, largely because of Jefferies' (e.g. 1986) suggestion that they were ancestral to the chordates according to his "calcichordate" theory. Jefferies' theory was strongly dependent on his interpretation of the fossil homalozoans, which he referred to as "calcichordates." On this page, we take the more orthodox view that homalozoans are stem echinoderms, as suggested by their possession of a calcite skeleton with a similar ultrastructure to modern echinoderms. Jefferies held this skeleton to be ancestral for Chordata, and subsequently independently lost in each of the three chordate subphyla. However, this seems to require a lot of convergence, expecially if, as molecular phylogenies suggest, the hemichordates are actually closer to echinoderms. A stem echinoderm position for homalozoans seems much more parsimonious.

Stylophora are generally united with the following three taxa - Soluta, Cincta and Ctenocystoidea - into the

Homalozoa, regarded as a subphylum of Echinodermata. However, for reasons that will be covered later, this taxon appears to be paraphyletic. The four classes have little to unite them other than possession of a flattened theca and absence of pentaradial symmetry. For our purposes, "homalozoans" are regarded as a grade only, and the Echinodermata refers to the crown group of living echinoderms.

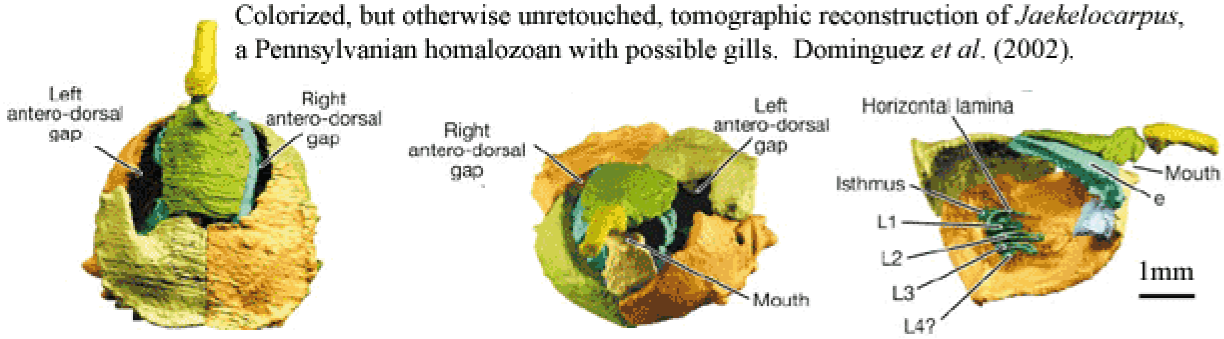
Stylophora are divided between two orders, the strongly asymmetrical Cornuta and the more bilateral Mitrata. Some authors regard certain Cornuta as forming a stem group to Mitrata, and move them over to join mitrates in an order Ankyroida. *See* results and discussion in Ruta (2003). They possess a theca which is always asymmetrical to some degree - even in those species where the external outline is symmetrical, the pattern of the plates that make it up is not. The broadest edge of the theca bears a plated appendage, and there is a major orifice on the edge opposite the appendage. The theca has two faces, one flat or slightly concave, one convex. In Cornuta there are often a number of openings on the convex surface to the left and below the appendage if the convex side is faced upwards and the appendage is pointed upwards - either a single lamellate structure or a series of pores. There are fewer pores on both faces of Mitrata, placed bilaterally. The appendage is divisible into three parts - a broad proximal section where it joins the theca then a median section tapering to narrower distal section. A canal runs through the centre of the appendage, with plates covering it.


Rhenocystis from the Devonian of Germany. This image illustrates the difficulty of deciding which end is up. From The Natural Canvas

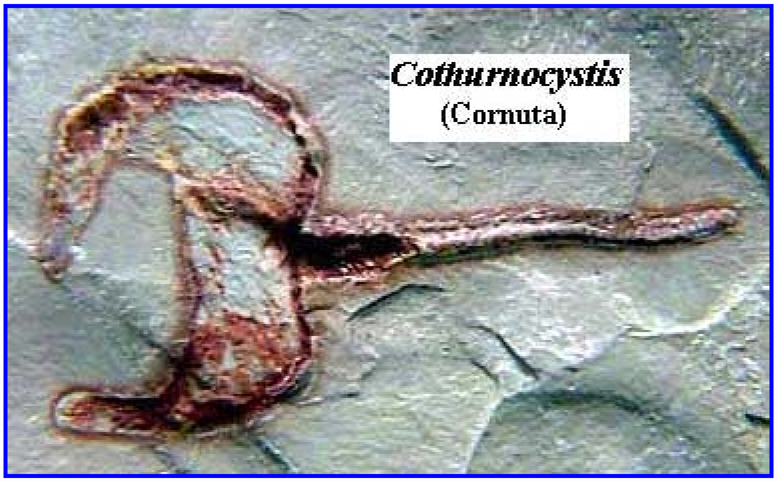
So far these are all uncontroversial features, but they are also pretty meaningless. A critical look at the previous paragraph will soon reveal that we haven't assigned a function to a single structure. Unfortunately once you start asking such questions, things start getting difficult. Almost every possible answer has been suggested at some point. To simplify matters, most reconstructions can be allied with one of two viewpoints - the "echinoderm" reconstruction and the "calcichordate" reconstruction.

In the "echinoderm" reconstruction, the theca lies with the convex side upwards and the appendage is interpreted as an anterior feeding arm ("aulacophore"). The central canal is then an ambulacrum with the plates over it able to open to expose the tube feet. The major orifice opposite the aulacophore is the anus, with the mouth somewhere near the ambulacrum. Ubaghs (1967) assumed it to be on the theca near the base, while Lefebvre (2003) placed it in the median section of the aulacophore). Various interpretations are given for the major openings on the theca as gonopores, hydropores and/or respiratory openings.

The "calcichordate" hypothesis, in contrast, reverses the orientation. The appendage is regarded as a tail, with the central canal probably containing a notochord. The major orifice is the mouth, with the anus near the tail. The minor openings in Cornuta represent the gill slits or pores, while those of Mitrata are more contentious. Dominguez *et al*. (2002) identified bilateral internal tubes in *Jaekelocarpus* (Mitrata) as paired gill slits, implying a secondary regain of bilateral symmetry in organ systems in this clade. While the Cornuta were interpreted as lying with the flat side ventrally, Jefferies suggested that in Mitrata the flat side was dorsal and the convex side ventral, while the tail was curved underneath to provide forward thrust. Support for this was seen in the common preservation of Mitrata with the tail flexed over the theca. As part of his explanation for how this inverted orientation arose, Jefferies suggested that the mitrate tail was not entirely homologous with the cornute tail, despite its similar structure, but actually with only the proximal section. At some point, he suggested, the mitrate ancestor had lost the median and distal sections of the tail, and had then redeveloped similar structures to regain a tripartite tail.


Colorized, but otherwise unretouched, tomographic reconstruction of *Jaekelocarpus*, a Pennsylvanian homalozoan with possible gills. Dominguez *et al*. (2002).

The "calcichordate" reconstruction is favoured here - as mentioned earlier, it fits better with the circumstantial evidence supplied by the Vetulocystidae. However, I am more sceptical of Jefferies' inverted orientation for Mitrata. For instance, Jefferies' reconstruction places the mouth ventrally while the more standard orientation would place it dorsally as in most other stem and basal echinoderms. Also his interpretation of tail homologies seems rather *ad hoc*. *In situ* fossils, it should be noted, are uninformative on this matter as both orientations are commonly found. Lefebvre (2003).



Note that accepting Jefferies' reconstruction of Stylophora does not require us to accept his suggested phylogenetic position for them as a paraphyletic stem to Chordata with the modern chordate subphyla arising independently from various subclades. Requiring as it does the independent loss of the stereom in at least three lineages, as well as probably independent extension of a somitic structure anteriorly in Cephalochordata and Craniata, this does not seem the most parsimonious option. It seems more likely that Stylophora represent members of the echinoderm stem branching off after the origin of the stereom but before the origin of ambulacra.

The palaeoecology of Stylophora is nearly as contentious as its anatomy. Under the "calcichordate" model, the tail is generally assumed to be a propulsive organ, and many adherents of the "echinoderm" model also assume a locomotive function as well as a feeding one for the aulacophore. Lefebvre (2003), using the "echinoderm" model, doubted whether the aulacophore could function as such, claiming that it lacked the required flexibility and was too slender compared to the massive theca. A single slab has been found from the Devonian Hunsruck Slate of Germany which preserves specimens of *Rhenocystis* (Mitrata) in association with infaunal trails and has been cited as evidence for a vagile lifestyle (Sutcliffe *et al*., 2000), but debate continues over whether the association is valid or an artifact of preservation or preparation (Lefebvre, 2003). Some Stylophora, such as the strongly asymmetrical mitrate *Diamphidiocystis* which has the tail displaced to the right hand side of the theca and a long scimitar-shaped articulated spine coming from the posterior left corner of the theca and curved towards the tail, have morphologies that would appear inconsistent with a high degree of mobility.

Jefferies suggested that juveniles were attached to the sediment by the ends of their tails, detaching later to become free adults. The number and arrangement of the plates seems to have become fixed early in development, with the animal growing by enlargement of pre-existing plates.

� Christopher Taylor CT050908.

Images: sources as stated. *Cothurnocystis* image from **GeoTools.com**. "Moving mitrate" image of *Rhenocystis* from **Ferienland Hunsr�ck online**.

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Homalozoa Dendrogram

```
DEUTEROSTOMIA
|--Vetulicolia
`--+--CHORDATA
   `--Ambulacraria
      |--Hemichordata
      `--+--Vetulocystidae
         `--Homalozoa
            |--Stylophora
            `--+--Soluta
               `--+--Cincta
                  `--+--Ctenocystoidea
                     `--+--Helicoplacoidea
                        `--ECHINODERMATA
```

For our purposes here, we treat Homalozoa as a crown group anchored by the well-known (but not well-understood) stylophoran *Rhenocystis* and the equally well-known (but much better understood) sea urchin *Echinus*. However, the name 'Homalozoa' is never actually used in connection with living echinoderms. We are only concerned with the stem taxa. The stylophoran part of the cladogram is based largely on the supertree of Ruta (2003).

o : crown group
^ : stem group
� : paraphyletic basal radiation
@ : apomorphy-based clade
* : similarity-based (classical) taxon
? : basis not yet established

```
o HOMALOZOA (redefined as a clade: Rhenocystis + Echinus)
`--+--* Stylophora X? (may be paraphyletic)
   |  `--� Cornuta X
   |     |--Cornuthocystis X
   |     `--+--Flabellicarpus X
   |        `--@? Mitrata X
   |           |--Jaekelocarpus X
   |           `--+--Diamphidiocystis X
   |              `--+--Anomalocystis X
   |                 `--Rhenocystis X
   `--+--* Soluta X
      |  |--+--Coleicarpus X
      |  |  `--Castericystis X
      |  `--+--Dendrocystitis X
      |     `--Syringocrinus X
      `--+--* Cincta X
         |  |--Gyrocystis X
         |  `--Trochocystites X
         `--+--* Ctenocystoidea X
            |  `--Ctenocystis X
            `--+--* Helicoplacoidea X
               `--o ECHINODERMATA
```

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Homalozoa References

```
DEUTEROSTOMIA
|--Vetulicolia
`--+--CHORDATA
   `--Ambulacraria
      |--Hemichordata
      `--+--Vetulocystidae
         `--HOMALOZOA
            |--Stylophora
            `--+--Soluta
               `--+--Cincta
                  `--+--Ctenocystoidea
                     `--+--Helicoplacoidea
                        `--ECHINODERMATA
```

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Chordata : Overview

Abbreviated Dendrogram

```
Chordata
|--Urochordata
|  |--Larvacea
|  |  |--Oikopleuridae
|  |  `-+--Kowalevskiidae
|  |    `--Fritillaridae
|  `--+--Ascidiacea
|     `--Thaliacea
`--+--Cephalochordata
   `--+--Haikouella
      `--Vertebrata
```

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Introduction

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The Phylum Chordata includes the well-known vertebrates (fishes, amphibians, reptiles, birds, mammals). The vertebrates and hagfishes together comprise the taxon Vertebrata. The remaining chordates are the tunicates (Urochordata), lancelets (Cephalochordata), and, possibly, some odd extinct groups. With few exceptions, chordates are active animals with bilaterally symmetric bodies that are longitudinally differentiated into head, trunk and tail. The most distinctive morphological features of chordates are the notochord, nerve cord, and visceral clefts and arches.

Chordates are well represented in marine, freshwater and terrestrial habitats from the Equator to the high northern and southern latitudes. The oldest fossil chordates are of Cambrian age. The earliest is *Yunnanozoon lividum* from the Early Cambrian, 525 Ma (= million years ago), of China. This was just recently described and placed with the cephalochordates (Chen et al., 1995). Another possible cephalochordate is *Pikaia* (Nelson, 1994) from the Middle Cambrian. These fossils are highly significant because they imply the contemporary existence of the tunicates and craniates in the Early Cambrian during the so-called Cambrian Explosion of animal life. Two other extinct Cambrian taxa, the calcichordates and conodonts, are uncertainly related to other Chordata (Nelson, 1994).

Chordates other than craniates include entirely aquatic forms. The strictly marineUrochordata or Tunicata are commonly known as tunicates, sea squirts, and salps. There are roughly 1,600 species of urochordates; most are small solitary animals but some are colonial, organisms. Nearly all are sessile as adults but they have free-swimming, active larval forms. Urochordates are unknown as fossils. Cephalochordata are also known as amphioxus and lancelets. The group contains only about 20 species of sand-burrowing marine creatures. The Cambrian fossils *Yunnanozoon* and *Pikaia* are likely related to modern cephalochordates.

During the Ordovician Period (510 - 439 Ma) jawless or agnathan fishes appeared and diversified. These are the earliest known members of Vertebrata, the chordate subgroup that is most familiar to us. Fossils representing most major lineages of fish-like vertebrates and the earliest tetrapods (Amphibia) were in existence before the end of the Devonian Period (363 Ma). Reptile-like tetrapods originated during the Carboniferous (363 - 290 Ma), mammals differentiated before the end of the Triassic (208 Ma) and birds before the end of the Jurassic (146 Ma).

The smallest chordates (e.g. some of the tunicates and gobioid fishes) are mature at a length of about 1 cm, whereas the largest animals that have ever existed are chordates: some sauropod dinosaurs reached more than 20 m and living blue whales grow to about 30 m.

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Chordata

Urochordates

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|--Urochordata
|  |--Larvacea
|  |  |--Oikopleuridae
|  |  `-+--Kowalevskiidae
|  |    `--Fritillaridae
|  `--+--Ascidiacea
|     `--Thaliacea
`--+--Cephalochordata
   `--+--Haikouella
      `--Vertebrata
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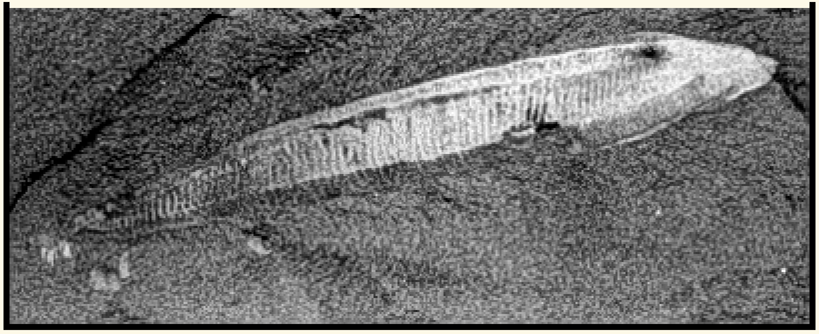
5. Oikopleuridae
6. Urochordata

Descriptions

Chordata**:** *Pikaia*.

Range: from the Tommotian, perhaps earlier

Phylogeny: *: Urochordata + (Cephalochordata + (*Haikouella* + Craniata)).

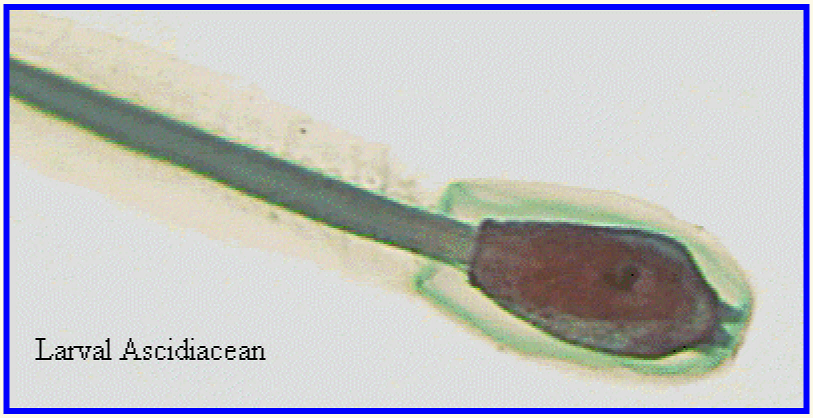


Characters: body bilaterally symmetrical; **$** single, dorsal, hollow nerve cord, usually with an enlarged anterior end (brain); nerve cord with pairs of nerves branching from it at more or less regular intervals and running to muscles; **$** pharyngeal pouches, bars and/or slits (embryologically all the same thing); body (or post cranial body if a head is present) segmented, including segmented muscles; **$** notochord, a cartilaginous rod running underneath, and supporting, the nerve cord and dorsal to gut; **$** muscular tail projecting posterior to anus; three embryonic germ layers and well-developed coelom; ventral heart, with dorsal and ventral blood vessels and closed circulatory system.

Image: *Pikaia* a possible chordate from the Early Cambrian Burgess Shale.

Note: many of these characters may not be present during some phase of the life cycle.

Links: Phylum Chordata; Introduction to the Chordata; Phylum Chordata Overview; Chordata; Chordata. The Columbia Encyclopedia, Sixth Edition. 2001; Chordata; biodidac; General Zoology - Phylum Chordata; Phylum Chordata; M17.htm; Chordate-classes; Encyclopedia.com: Chordata. ATW080123.



Urochordata**:** (= Tunicata) Tunicates. *Yarnemia*? (a pre-Cambrian form)

Range: from the Jurassic

Phylogeny: Chordata: (Cephalochordata + (*Haikouella* + Craniata)) + *: Larvacea + (Ascidiacea + Thaliacea).

Characters: Marine suspension feeders; ascidian embryo and larvacean adults have ciliated pharyngeal slits, notochord, muscular tail, dorsal nerve cord directly dorsal to notochord; dual nervous system with different nerves enervating segmented (somatic nerves) and unsegmented (visceral nerves) regions; segmented muscles (myomeres) enervated by dorsal nerve cord; locomotion by contraction of alternate sides as in vertebrates; exhibit some allorecognition (i.e. immune-type response).

Links: Urochordates; Chordata; The Urochordata; Chordata : Subphylum Urochordata; OceanLink; Kennesaw.

References: Swalla *et al.* (2000).

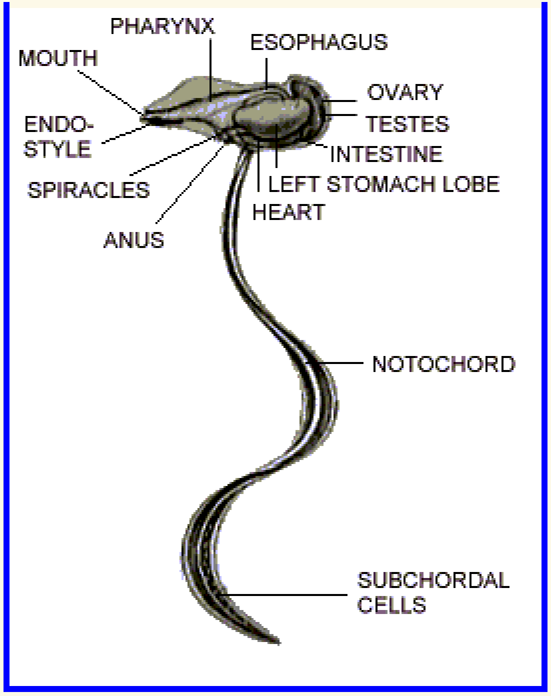
Image: © 1999 BIODIDAC and used by permission. ATW080123.

Larvacea: (= Appendicularia): Planktonic (0.5 - 5 cm) forms with adult similar to ascidiacean larvae.

Range: Recent.

Phylogeny: Urochordata: (Ascidiacea + Thaliacea) + *: Oikopleuridae + (Kowalevskiidae + Fritillaridae).

Characters: Individuals secrete acellular gelatinous "house" with incurrent, excurrent and caudal openings; incurrent duct has "screens" to keep out large particles and feeding screens or filters (again,



acellular and extrasomatic); brushes food particles into mouth with cilia; endostyle secretes mucous to trap food particles; may have pharyngeal slits (respiration?); food passes through U-shaped digestive tract and out anus and excurrent duct; anus and tail are ventro-medial; tail long, with notochord; action of tail and cilia create current for filter feeding; dorsal nerve cord present throughout life; changes in "house" relatively frequent (as short as a few hours); generation time also 1 - 2 days; largely monoecious and protandrous (see the Glossary -- that's what its there for); able to feed on nannoplankton (on the order of 1 µ); non-cellular circulatory fluid and single heart present in some forms.

Links: M20.htm; Blank (French); Nice papers on gelatinous zooplankton; gephrokapusa (image of *Oikopleura*; text in Japanese); Urochordates; Z250 (2000) - Deuterostome Clade; Earthlife.net; Larvacea.

The Earthlife site has a wonderful plain-language introduction to the Larvacea, with a good diagram. Conversely, **BIODIDAC has an excelent diagram (labelled in French), but no text. A Spineless Column by Ronald L. Shimek, Ph.D. Tunicates or Sea ... has a very nice discussion of tunicates generally. A number of sites touch briefly on the Larvacea in evolutionary context, *e.g.*.: Home page and Chordata. References to the literature are available at Pelagic Tunicate References.**

Image: ***Oikopleura*** **from MEER.**

References: Swalla *et al.* (2000). ATW080123.

Oikopleuridae: *Oikopleura*. The "complete" larvacean.

Range: Recent.

Phylogeny: Larvacea: (Kowalevskiidae + Fritillaridae) + *.

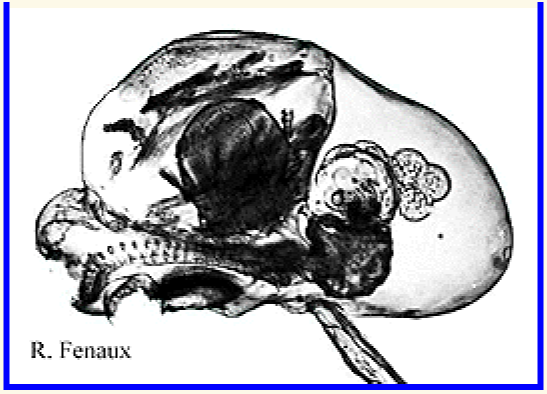
Characters: The "complete" larvacean. The other groups are presumably simplified forms which have disposed of one or more organ systems by reducing their size; very small genome size [S+01]; genes compressed, with introns and intergene regions not similar to vertebrates [S+01].

Note: Seo *et al*. (2001) expressly refuse to draw the conclusion that the genome is compacted to permit rapid reproduction, because the data is too preliminary. This is the natural conclusion to draw; but, as they note, it may also be that urochordates are less closely related to vertebrates than is normally believed.

Links: FREAKS OF NATURE (nice short description of mode of feeding, link to good photos); Study of Genetic Diversity of Eukaryotic Picoplankton (not strictly relevant, but the implications are a bit startling).

References: Seo *et al*. (2001) [S+01]. ATW050821.

Kowalevskiidae: *Kowalevskia*



Range: Recent.

Phylogeny: Larvacea:: Fritillaridae + *.

Characters: Larvaceans without endostyle, heart or spiracles; body form strongly simplified, with very short life cycle.

Links: RESUMEN; AN52. ATW080123.

Fritillaridae:

Range: Recent.

Phylogeny: Larvacea:: Kowalevskiidae + *.

Characters: Stomach strongly reduced. APW040314.

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Chordata : Chordata (2)

More urochordates, cephalochordates, and *Haikouella*

Abbreviated Dendrogram

```
Chordata
|--Urochordata
|  |--Larvacea
|  |  |--Oikopleuridae
|  |  `-+--Kowalevskiidae
|  |    `--Fritillaridae
|  `--+--Ascidiacea
|     `--Thaliacea
`--+--Cephalochordata
   `--+--Haikouella
      `--Vertebrata
```

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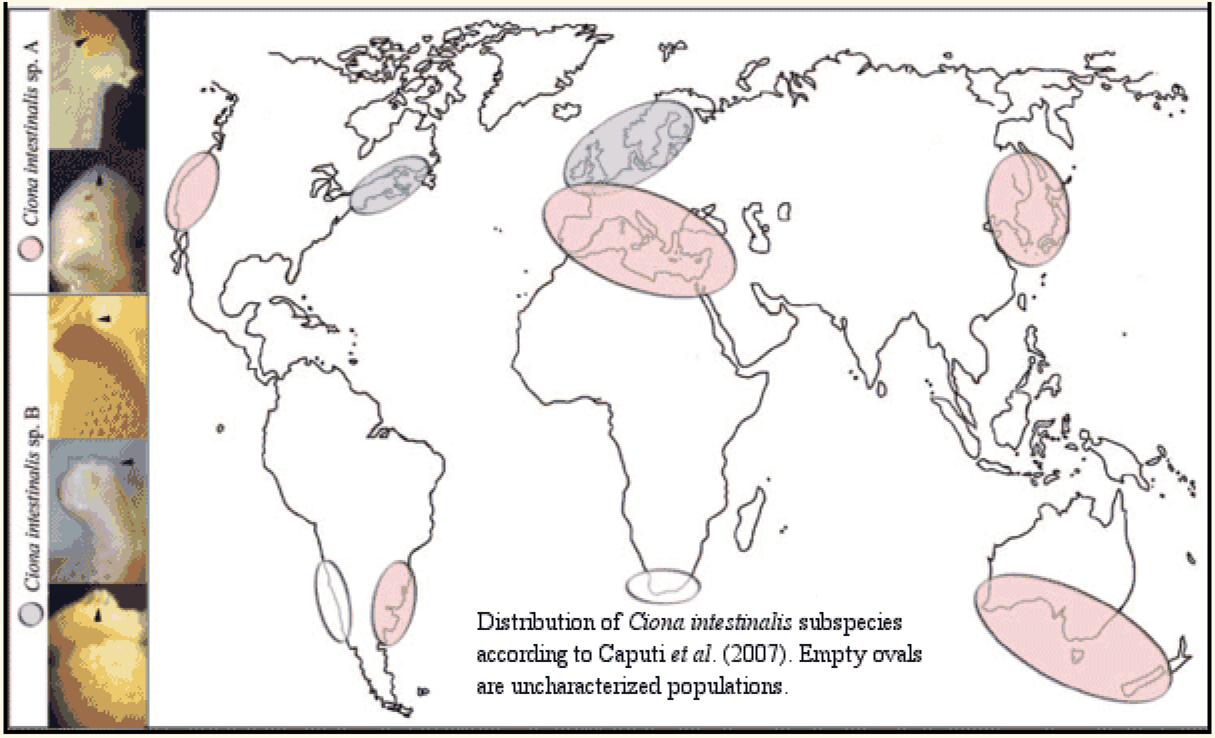
1. Ascidiacia
2. Cephalochordata
3. Thaliacea

DNA and Divergence

In 2002, the ascideacean *Ciona intestinalis* became one of the first chordates whose DNA was more or less fully sequenced. The availability of this



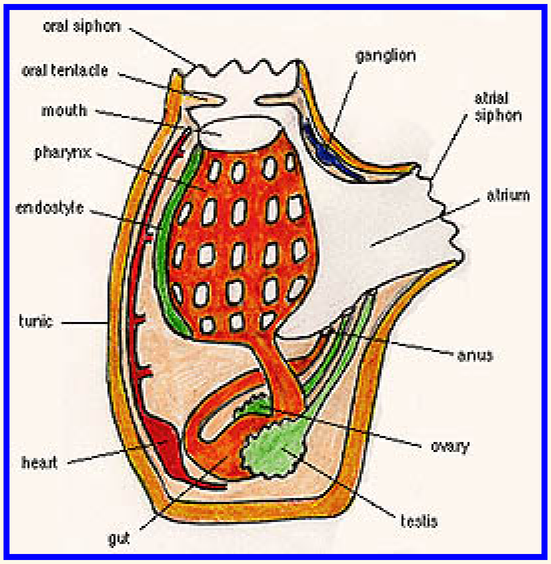
Distribution of *Ciona intestinalis* subspecies according to Caputi *et al.* (2007). Empty ovals are uncharacterized populations.

information is allowing molecular workers to develop new insights into the early evolution of the chordates. However, one of those insights is that *C. intestinalis* may not be a single species. Caputi *et al.* (2007) have learned that there are at least two major subspecies of *C. intestinalis* which cannot cross-breed successfully, although there are few obvious morphological differences. It seems likely that the published DNA sequence is entirely from Caputi's "subspecies A", since this variant is the sole type in both California and Japan, the locations where the sequencing was performed. Other subspecies, or perhaps even intermediate forms may remain to be characterized.

Recently, several species of the fruit-fly *Drosophila*, have been fully sequenced in tandem. Using these sequences, it will be possible to look closely at the types of genetic changes which are involved in the initial divergence and radiation of new species in that model system. The existence of cryptic speciation in *Ciona* will be a valuable check on these results. Earlier work in plants (*Arabidopsis*) and fungi (*Neurospora*) suggests that the types of genetic changes involved in speciation may not be universal across phylospace. That is, at the genetic level, evolution may (or may not) work in quite different ways for widely separate types of organisms.

One early lesson from these comparative studies seems to be that gene rearrangement is at least as important as gene mutation in the formation of new species. The preliminary findings of Caputi *et al*. are consistent with this pattern. However, it remains to be seen whether gene rearrangements simply cause gross errors during chromosomal exchange in meiosis, or whether they also implicate more subtle rules relating to gene regulation. ATW080123.

Descriptions



Ascidiacea: *Ciona*, *Distaplia*, *Diplosoma*. Classic urochordates with "tadpole" larvae and sessile adult.

Range: From the Jurassic.

Phylogeny: Urochordata:: Thaliacea + *.

Characters: Adult has incurrent and excurrent siphons and uses branchial filter feeding; motile larva has notochord, dorsal nerve chord, segmented muscles, and tail; solitary, social & compound forms.

Links: Ascidian Home Page for the United States; UCSC Biology 150/Urochordata: Ascidiacea (see **Image**); The Urochordata; Ascidia - Sea squirts (many, many photos); Springer LINK: Development, Genes and Evolution - Abstract Volume 209 Issue 10 (1999) pp 592-600; inventaire (French); ascidian; Filo Ascidiacea; Ascidiacea Characteristics; M20.htm; Woodbridge. APW040314.

Thaliacea: Salps. Free-living forms morphologically like Ascidiacean adults

Range: Recent.

Phylogeny: Urochordata:: Ascidiacea + *.

Characters: Free-living forms morphologically like Ascidiacean adults.

Links: Thaliacea: brief checklist; Dive Log New Zealand : Phylum Chordata. APW 040314.

Cephalochordata: *Branchiostoma* (amphioxus).

Range: from Cambrian?, from Early Permian?, Recent?

Phylogeny: Chordata:: (*Haikouella* + Craniata) + *.

Characters: Fusiform, <5cm. Brain segmented & perhaps functionally homologous to vertebrate brain; segmented muscle (myomeres) pull alternate sides, stiffened by notochord. Pharynx & gills used only for filter feeding. Circulation limited, but ventral pump & major dorsal artery. No hemoglobin; oxygen carried in solution; no kidney, but similar excretory cells. No connection between segmented & unsegmented nerves. Profound left-right asymmetry in development. Semi-sedentary filter feeder, trapping detritus in mucus; water moved by cilia – mouth and gut have little or no musculature. No paired fins, thus little or no control in 3 dimensions. Neural crest cells absent.

Links: Chordata introduction - Subphylum Cephalochordata; Characteristics; Chordata; Berkeley. APW 040314.

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Chordata : Chordata (3)

Haikouella lanceolata

Abbreviated Dendrogram

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Chordata
|--Urochordata
|  |--Larvacea
|  |  |--Oikopleuridae
|  |  `-+--Kowalevskiidae
|  |    `--Fritillaridae
|  `--+--Ascidiacea
|     `--Thaliacea
`--+--Cephalochordata
   `--+--Haikouella lanceolata
      `--Vertebrata
```

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1. *Haikouella* X

Haikouella lanceolata

Geologic Time: Early Cambrian (~525 million years ago)

Size: 16-22 mm long on a 55 mm by 50 mm matrix

Fossil Site: Chengjiang Maotianshan Shales,: Quiongzhusi Section, Yu'anshan Member, Heilinpu Formation, Anning, Yunnan Province, China.

This exceptional specimen is a multiple example of *Haikouella lanceolata*, thought by its describers to be the earliest craniate-like chordate. This fish-like animal has many similarities to the contemporaneous *Yunnanozoon lividum*, but differs in several aspects: it has a discernible heart, dorsal and ventral aorta, gill filaments (see the closeup), and

a neural chord. For all these reasons, it was identified by Chen, Huang, and Li in the seminal Nature paper (Nature 402, 518-522, 02 December 1999) as a chordate.

The debate rages on, but whatever the outcome, this creature was much like the ancestor of all the vertebrates. It derives its generic name from its resemblance to the modern day lancet Amphioxus.

Also see: Chengjiang Biota, Chengjiang Fossils, Cambrian Explosion

RGP111017

Virtual Fossil Museum

Haikouella: *H. lanceolata* Chen *et al*. 1999.

Haikouella

Range: Early Cambrian of South China.

Phylogeny: Chordata::: Craniata + *.

Characters: Body 25-30 mm, broadly triangular anteriorly, narrowly triangular posteriorly [C+99]; brain present and bi- or tri-partite, but degree of integration with cranial sensory structures unclear [C+99] (*contra* [SM03]: brain is absent); rostral "skirt" similar to larval lamprey & also present in *Haikouichthyes* [M+03]; lateral eyes or eyespots [M+03] (*contra* [SM03]: eyes are rare artifacts); ventral buccal (?) cavity with tentacular structure [C+99]; probable mineralized pharyngeal teeth [C+99]; 6 pairs of branchial arches [C+99] (*compare* [SM03]: gills are external); gill slits between arches, covered by folds of body [C+99]; unclear if gills open to exterior or atrial cavity [C+99]; notochord extending well into anterior [C+99]; dorsal nerve cord present [C+99] [SM03]; body segmented dorsally with segmental blocks of muscle fibers (hence myomeres) [M+03] (*contra* [SM03]: no evidence of "cone-in-cone" structure); muscle fibers & segmentation extend well dorsal to notochord [M+03]; about 24 myomeres not in V- or W-shape

[C+99]; postanal tail present [M+03] (*compare* [SM03]: tail is quite variable and is probably an artifact); heart, plus branchial, ventral & dorsal aortae present [C+99]; gut differentiated into esophagus, spiral mid-gut and straight intestine [C+99].

Links: Haikouella and Myllokunmingia; An early Cambrian craniate-like chordate; Titulo (Spanish); Das Kambrium (German); m-hydrate-nov99; ScienceNow; Taipei Times - archives (newspaper article on recent work); Haikouella (Wikipedia article); Chinese Science Bulletin ISSN-1001-6538 2003 Vol.48 No.8 725-735 ... (abstract of article arguing that it's a stem deuterostome).

Reference: Chen *et al*. (1999) [C+99]; Mallatt *et al*. (2003) [M+03]; Shu & Morris (2003) [SM03].

Note: The description given above is only slightly more conservative than given in the reference. *Haikouella*, unlike most other early Paleozoic species, is known from over 300 well-preserved specimens, and Chen's description therefore has very high credibility, despite the great age and small size of the organism. Chen suggests that *Haikouella* may actually *be* a craniate, and this may well be correct in the sense that it has of the features typically listed as synapomorphies of Craniata. However, it seems unlikely that it is a member of the crown group subtended by hagfish and hogs. In any case, with the addition of conodonts to the chordates and the wealth of new information from South China, it is no longer very certain exactly what the synapomorphies of Craniata are going to be. ATW040314.

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RGP111017, ATW040314

Haikouella lanceolata

Chordata : Dendrogram (Cladogram)

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|--Urochordata
|  |--Larvacea
|  |  |--Oikopleuridae
|  |  `-+--Kowalevskiidae
|  |     `--Fritillaridae
|  `--+--Ascidiacea
|     `--Thaliacea
`--+--Cephalochordata
   `--+--Haikouella
      `--Vertebrata
```

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|  |--Larvacea MH
|  |  |--Oikopleuridae •
|  |  `-+--Kowalevskiidae •
|  |     `--Fritillaridae •
|  `--+--Ascidiacea •
|     `--Thaliacea • MH
`--+--Cephalochordata • MH
   `--+--Haikouella •X
      `--Vertebrata
```

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Chordata : References

Abbreviated Dendrogram

```
Chordata
|--Urochordata
|  |--Larvacea
|  |  |--Oikopleuridae
|  |  `-+--Kowalevskiidae
|  |    `--Fritillaridae
|  `--+--Ascidiacea
|     `--Thaliacea
`--+--Cephalochordata
   `--+--Haikouella
      `--Vertebrata
```

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Swalla, BJ, CB Cameron, LS Corley & JR Garey (2000), *Urochordates are monophyletic within deuterostomes*. **Sys. Biol.** 49: 52-64.
Larvacea, Urochordata

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