Metazoa: the Animals

```
LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```

The diversity of Animal life (collagfe by Panda3, Wikipedia)

Metazoa: Contents

Part 1: Alphabetical Listings

A. Glossary of terms and abbreviations.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

B. Taxon Index: alphabetical list of taxa.

C. References: literature citations by author.

Part 2: Systematic Listings

A. Taxonomy

Metazoa - Linnaean classification

B. Dendrograms ("Cladograms")

Metazoa - Overall dendrogram

B. Descriptions

Units marked with an asterisk are placeholders and contain little material. These units will be expanded in due course.

Animalia (Metazoa)*: brief introduction to the animal kingdom
Porifera: the humble sponges, the earliest and most primitive forms of multicelluar animals
Radiata*: animals with radial symmetry, this is just a short unit
Cnidaria*: jellyfish, corals, hydrozoans. An ancient and important group of primitive animals. Corals as reef builders have a particularily rich fossil record
Bilateria: animals with bilateral symmetry, with a head or front and back, and left and right side (lost in some forms, e.g. echinoderms). Includes a discussion on protstome phylogeny
Spiralia: better known as Lophotrochozoa, one of the largest and most diverse clades of animal life. In this unit ancestral Cambrian forms are discussed. The following five or six units are also spiralian
Mollusca*: a very diverse assemblage of mostly generalised spiralians; include chitons, clams, snails, octopii, and many more. Their hard shells have enabled them to leave an extensive fossil record. A large number of subdirectories here but our coverage is currently rather spotty
Annelida*; segmented worms, a more diverse group than most realise. Include tube worms, earthworms, leeches, and many others. The minor phyla Sipuncula and Echiura are related
Brachiopoda*: yet another spiralian taxon, this was an abundant group of Palaeozoic filter feeders, now much reduced. The phoronida may be shellless brachiopods
Polyozoa*: include the Bryozoa and related taxa, may or may not be reated to brachiopods.
Platyzoa*: flatworms, rotifers, gastrotrichs, and other odds and ends, probably an artificial assemblage of assorted miniaturised or simplified spiralians. No fossil record
Chaetognatha*: "Arrow worms", a small group of uncertain affinities, include some conodonts.
Ecdysozoa: "moulting animals", a major group, sister taxon to the Spiralia. This unit includes a general introduction and a review of a number of wormlike and microscopic phyla (Kinorhyncha, Loricifera, Priapulida, Nematoda, Nematomorpha, and Tardigrada) as well as the extant onychophora and paleozoic lobopods and protoarthropods. Also discussion on general ancestry and evolution of teh group
Arthropoda*: animals with a jointed exoskelton, the most speciose phylum of ecdysozoa: trilobites, spiders, crustacea, myriapods, insects and more. AS with mo;l;luscs, this unit includes many subdirectories spotty coverage
Deuterostomia: major group, includes vertebrates, echinoderms, and a number of minor taxa. Discusison here also covers a number of enigmatic Paleozoic forms
Echinodermata*: deuterostomes with secondarily radial symmetry: starfish, sea urchins, crinoids, etc. Extensive fossil record
Hemichordates and *Chordates* are covered in the next main unit (Vertebrates)

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Metazoa: the Animals

```
LIFE
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`--+--Archaea
   `--Eukarya
      |--Chlorobionta
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         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```


Editor's note

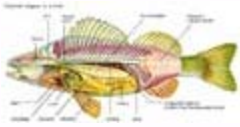
This page is in the process of being revised, but is posted as is for now as a holding page and to provide links to other pages. Because Palaeos com is still under construction and major revision, not all links given here work. MAK120115

Quick Links to Major Animal Groups

Arthropods: insects, crustaceans, scorpions -- the most successful metazoans. 

Brachiopoda: they look like mollusks, but they're not. 

Bryozoa: advanced, encrusting reef-builders. 

Chordata: mostly, the Vertebrates. 

Cnidaria: Radiate animals -- jellyfish and corals. 

Echinoderms: our cousins, the sea urchins, sand dollars, starfishes and so on. 

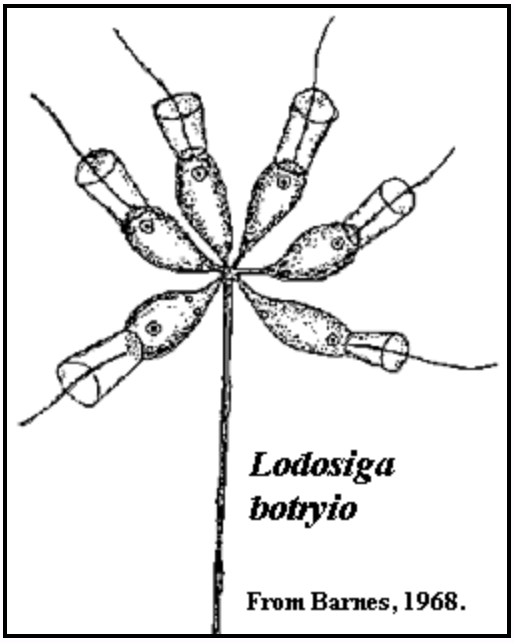
Mollusca: clams, oysters, and the like. 

Porifera: sponges. 

Halkieriida sometimes bizarre worms near the root of the Spiralia. 

Tardigrada: "water bears." 

Evolution of the Metazoa

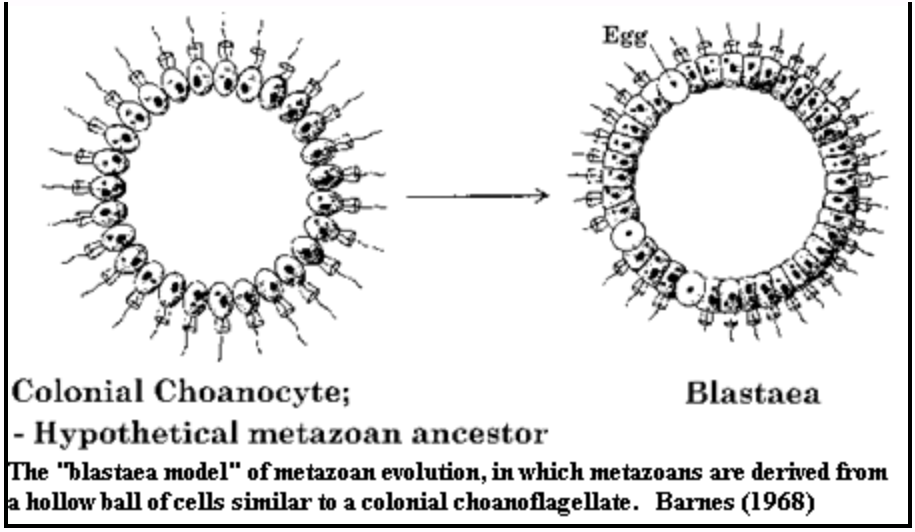


The Animal Kingdom (Metazoa) is usually considered to include multi-cellular, heterotrophic eukaryotes in which (unlike Plants) the cells are without cell walls. Everything from sponges and jellyfish to insects and vertebrates is belongs in "Metazoa", and considered to have evolved from a single unicellular choanoflagellate ancestor, sometime during the Ediacaran period.

From a simple colonial choanoflagellate, animals developed through increasing grades of specialization and complexity: first sponges, then coelenterates, and finally bilateral animals (possessing a head and distinct right and left sides). A recent interpretation of this monophyletic animal kingdom theory is the phylogenetic scheme of Wainright et al. 1993 shows choanoflagellates contained within the monophyletic assemblage Metazoa (= "animals"), and Fungi as the closest sister group to Metazoa. We thus conceive of Metazoa as the sister group of the Fungi, and use the term phylogenetically to mean toads > toadstools.

The problem here is that, although choanoflagellates seem clearly related to sponges, it is not clear how closely related sponges are to the rest of the Metazoa. It is also difficult to see how such a locally organized organism as a sponge (essentially nothing but a glorified colonial protozoan) can develop into an organism with a specific body structure and internal organs. The most widely held theory seems to be that a colonial choanoflagellate evolved into a hollow spherical ball of cells, the blastula, which constitutes the earliest embryonic stage of development, and even occurs in sponges. The 'blastula model' of metazoan evolution goes back to the famous 19th century German Darwinist Ernst Haekel.

However, it is not certain that such a blastaea animal ever even existed. The theory that "ontogeny recapitulates phylogeny," championed by Haekel



The "blastaea model" of metazoan evolution, in which metazoans are derived from a hollow ball of cells similar to a colonial choanoflagellate. Barnes (1968)

(according to which the growing embryo passes through all its past evolutionary stages - e.g. the early human fetus possesses gill slits and a tail), was enormously popular for some time.

All we can say for certain is that, some time during the Late Proterozoic era, an unknown protozoan (or protistan) organism developed into a tiny colonial form, which eventually became the common ancestor of the Metazoa. The actual nature of this organism is not known, as it was soft-bodied and left no trace. It used to be thought that sponges evolved from a different single celled organism to higher animals (in which case the Metazoa are a polyphyletic taxon), but recent molecular phylogenetic evidence indicates this is not the case.

Phylogenetic Organization of Metazoa

The base of the animal tree is moderately non-controversial. Animals are closely related to a particular group of protists, the choanoflagellates. The first metazoans were probably sponges, Porifera. Sponges are multicellular animals with specialized cell types, but no specialized tissues. The different cell types are intermingled, and one part of a sponge looks rather like another. The Porifera are probably paraphyletic. That is, all other animals are probably descended from something we would probably think of as a "sponge." In that sense, all animals may be members of the Porifera. However, we will use the term only as it applies to sponge-like animals. More generally, animals without strongly differentiated tissues are sometimes referred to as Parazoa, since there are probably animals other than sponges with this grade of organization, *e.g.*, the Archaeocyatha and the Ediacaran fauna.

All animals with distinct tissue types are referred to as the Eumetazoa. Phylogenetically, we might define the Eumetazoa as the crown group uniting jellyfish and silverfish. The jellyfish lineage includes the Cnidaria (jellyfish, corals, etc.) and some related types. These animals, the Radiata, seem to have derived from a single common ancestor who was not in our direct line of descent. The Radiata all have differentiated tissues, but normally nothing much more complicated than "inside" (endoderm) and "outside" (ectoderm), with some level of front-to-back specialization. From an embryological standpoint, they lack mesoderm, a tissue type which characterizes all more derived animals. Most are radially symmetrical. Their body plan is based on a cylinder open at one end, with the open end serving both for ingesting food and eliminating waste.

All other animals are Bilateria. Bilaterians undergo a more complex gastrulation and possess mesoderm. Thus, they begin with three embryonic cell types. Furthermore, they are bilaterally symmetrical. In addition to a more complex inside-outside pattern of tissues and the ancestral front-to-back organization, Bilateria have a separate top and bottom, with symmetrical left and right sides. In many worm-like forms, this top-and-bottom asymmetry is not well developed on the outside. However, the internal organization generally involves distinct dorso-ventral organization, with, for example, muscles and circulatory structures located dorsally, and the gut and a major nerve chord located ventrally. Most (but not all) also have a separate mouth and anus, so that the flow of digestion is one way.

At this point, things become much less clear. There are three groups of Bilateria which show some internal cohesion. These are the Deuterostomia (including echinoderms and chordates), the Spiralia (including annelid worms and mollusks), and the Ecdysozoa (including arthropods). Each of these groups includes some of the "minor phyla" of animals. However, a large number of mostly worm-like groups are left out of this scheme; and their positions are sometimes too vague even to guess at.

Of the three main groups, the deuterostomes probably branched off earliest, but even this has been disputed. The term "protostome" is used a good deal, particularly in the older literature, to refer to the lophotrochozoans, ecdysozoans, and everyone else who exhibits a particular pattern of early embryonic development. For our purposes, we will treat

the deuterostomes as the earliest-branching clade and use the term "protostome" to refer to the crown group of bugs + slugs (Ecdysozoa + Lophotrochozoa). Other than the most well-established members of the two protostome groups, all other animal phyla will be treated as Bilateria *incertae sedis*.

With that said, our tree looks like this:

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

```
^ METAZOA (= toads > toadstools)
|--? Choanoflagellata
`--¶ Porifera (paraphyletic)
   |--^ RADIATA
   `--o EUMETAZOA (= jellyfish + silverfish)
      |--* Cnidaria
      `--o BILATERIA (including ?some/all "Acoelomates") (= starfish + silverfish)
         |--^ DEUTEROSTOMIA (= starfish > silverfish)
         |  |--@ Chordata (notochord present, or ^: movie stars > sea stars)
         |  `--o Echinodermata (Disaster + Pisaster)
         `--+--? (minor phyla)
            `--o PROTOSTOMIA (= bugs + slugs)
               |--^ ECDYSOZOA (bugs > slugs)
               |  |--* Bryozoa ?
               |  `--? Arthropoda
               |     |--* Crustacea
               |     `--* Insecta
               `--^ LOPHOTROCHOZOA (=Spiralia)(slugs > bugs)
                  |--?
                  `--¶ "Halkieriida" (paraphyletic basal lophotrochozoans)
                     |--* Annelida
                     `--+--* Mollusca
                        `--* Brachiopoda
```

See the dendrogram page for a more detailed coverage.

Most of the "Halkeriids" are probably closer to mollusks than to annelids.

Descriptions

Metazoa Haeckel 1874 = Animalia

Range: Fr Ediacaran

Phylogeny: Eukarya **:::** Stem Metazoa **:**Fungi + * **:** paraphyletic Porifera **:::** Eumetazoa

Characters: develop from a blastula, cellular to organ-systems grade, food ingesting without chloroplasts, subdivided on grade of organization, symmetry, and coelomic development

Comments: The Animal Kingdom. Strictly speaking, Animalia Linnaeus 1758 has priority. However on the one hand "animal" tends to be associated in the minds of the average person with vertebrates, , and specifically, mammals , whereas "metazoan" is a nice, neutral-sounding technical term, free of colloquial nuances. In older science textbooks Kingdom Animalia traditionally also includes the heterotrophic (animal-like) protsits. Hence we have adopted Metazoa defined in terms of Whittaker & Margulis's five kingdom model, with multicelluarity as the arbitrary

dividing line between paraphyletic protista and multicelluar animals. MAK120423

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Radiata

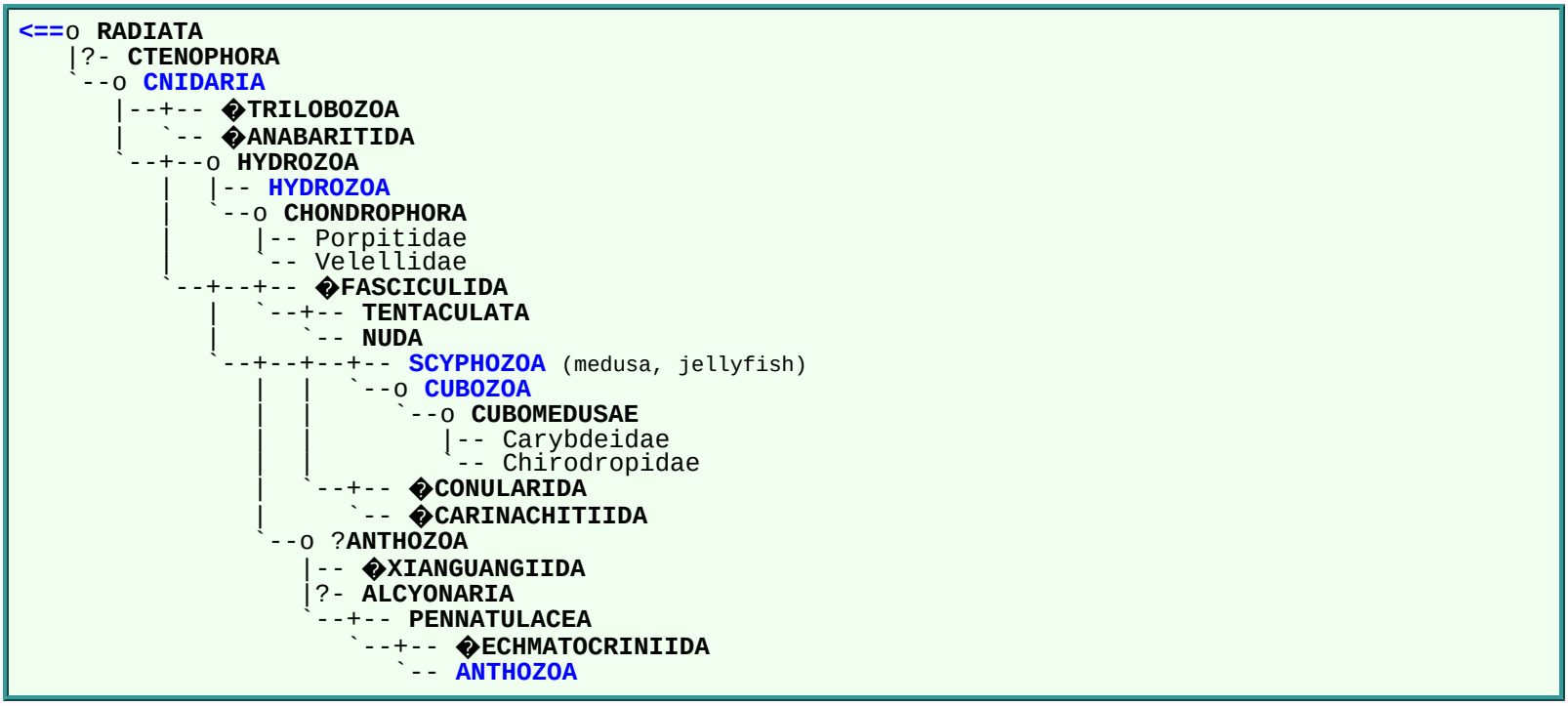
Animals with Radial Symmetry

```
Metazoa
|--Porifera (paraphyletic?)
`--Radiata
   |--Cnidaria
   `--Bilateria
      |--Deuterostomia
      `--Protostomia
         |--Ecdysozoa
         `--Lophotrochozoa
```


Polyorchis pencillatus - Red Eye Medusa
Phylum Cnidaria - Class Hydrozoa - Order Anthomedusae - Family Polyorchidae

Included here are invertebrates with *radial symmetry*: all longitudinal planes are equal around central body axis. They are also diploblastic (possessing only two germ layers, an ectoderm and endoderm, but, unlike the Bilateria, no mesoderm. Only two phyla belong here - the Cnidaria and Ctenophora

Radiata after Conway Morris, 1993



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Fautin, DG & SL Romano (2000)

Hou & Bergström, 1997

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Metazoa: Classification

```
LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```


Some Linnaean Lists

The classification of the animal kingdom according to major ctegories goes back to Aristotle and, more recently, Linnaeus, but it was on in the 19th century that scientists like Lamarck (who developed invertebrate zoology), Cuvier, and Haeckel developed the idea of major groups or phyla. Similarily, the relation of the colemate phyla was determined by the most apparent similarities. For Lamarck and Haeckel the idea of evolution in the conbtext of a linear chain of being, was central. Haeckel's famous "Ascent of Man" tree (and numerous and somewhat less anthropocentric 20th century versions thereof) presented the idea of progressive evolutionary stages, with protozoa at the bottom, then sponges jellyfish, and flatworms, then higher invertebrates, and finally at the top something like mammals and butterflies, reflecting anthropomorphic preferences, e.g. cuddly (mammals) or aestheric appeal (butterflies), with man ubiquitously placed at the summit (either alone or with other higher forms of vertebrate and invertenrate life). More sophisticated five and six kingdom models of life (including a rational arrangement of animal phyla) were presented by Margulis and Schwartz (1982) and Cavalier-Smith (1998) respectively, and these represent the most sophisticated developmen to date of the Linnaean paradigm.

From the 1990s onwards, molecular phylogeny and cladistics revolutionised our understanding and classification of the animal kingdom, and replaced the rank-based system with a branching tree-based model. However, The details of the branching pattern (the phylogenetic hypotheses) differ according to different researchers and analyses, and there are still a large number of unknown connections. Furthermore, most of the invertebrate zoology literature still use the traditional Linnaean scheme for higher-level classifications. Accordingly, it is useful to include a few of these schemes as a point of reference. In the the Animal Kingdom has traditionally been classified into about three dozen phyla, which have been grouped into larger categories:

The following is adapted from Margulis and Schwartz, 1982 and still represents very much the standard biology textposition view

Kingdom **ANIMALIA** - Develop from a blastula, cellular to organ-systems grade, food ingesting without chloroplasts, subdivided on grade of organization, symmetry, and coelomic development.

Subkingdom **PARAZOA** - Cellular (multi-cellular) grade, no tissues, organs, digestive tract or mouth.

Phylum **Placozoa**

Phylum **Porifera** - porous with one to many internal cavities lined with choanocytes; (the sponges).

Subkingdom **EUMETAZOA** - Tissue to organ-system grade, with mouth and digestive tract.

Branch **RADIATA** - Radial to modified radial symmetry, tissue grade organization with incipient organs, diploblastic, mesenchyme of ectodermal origin, digestive cavity the sole body cavity, no anus.

Phylum **Cnidaria** - Symmetry radial, biradial, or radio-bilateral, mouth usually encircled by tentacles armed with *nematocysts*; (the coelenterates, jellyfish).

Phylum **Ctenophora** - Symmetry biradial, eight radial rows of ciliated swimming plates, tentacles when present not encircling mouth, no nematocysts.

Branch **BILATERIA** - Primary bilateral symmetry, secondarily modified to pentameral or radial, organ-system grade of organization, most triploblastic with well-developed mesoderm of endodermal origin, most with body cavity other than the digestive cavity, anus typically present.

[*note: the following traditonal division of Bilateria into Acoelomata, Psuedocoelomata, and Coelomata is now known to be invalid, see discusison under Ecdysozoa*)

Grade **ACOELOMATA** - No coelom, region between digestive tract and body wall filled with mesenchyme or mesoderm, if segmented youngest segments nearest head.

Phylum **Mesozoa**

Phylum **Platyhelminthes**

Phylum **Nemertina**

Phylum **Gnathostomulida**

Grade **PSEUDOCOELOMATA** - Body cavity a pseudocoel (remnant of blastocoel, not lined with mesoderm on both sides), triploblastic.

Phylum **Gastrotricha**

Phylum **Rotifera**

Phylum **Kinorhyncha**

Phylum **Acanthocephala**

Phylum **Entoprocta**

Phylum **Nematoda**

Phylum **Nematomorpha**

Grade **COELOMATA** - With a true coelom and well-developed mesoderm.

Series **Protostomia** - Blastopore becomes mouth, typically *schizocoelous* with *spiral* cleavage.

Phylum **Bryozoa** (Ectoprocta) - Colonial lophophorate, *oligomerous*.

Phylum **Phoronida** - Solitary lophophorate with worm-like (vermiform) body, *oligomerous*.

Phylum **Brachiopoda** - Solitary lophophorate with bivalve shell, *oligomerous*, enterocoelous.

Phylum **Mollusca** - *Pseudometamerous*, reduced coelom, visceral mass covered by a body fold, the mantle, which secretes a calcareous shell of one or more pieces.

Phylum **Priapulida** - Marine worms, some consider pseudocoelomate; no fossil record.

Phylum **Sipuncula** - Marine worms, amerous; no fossil record.

Phylum **Echiura** - Another amerous worm.

Phylum **Annelida** - *Metamerous*, segmented, vermiform, without jointed appendages.

Phylum **Tardigrada** - small (<2mm) worm-like, meiofaunal, no fossil record.

Phylum **Pentostomata** - "Tongue worms", parasitic, no fossil record. [*note: now known to be a specialized side-branch of arthropods*)

Phylum **Onychophora** - *Metamerous*, segmented, uniramous unsegmented appendages, waxy cuticle.

Phylum **Arthropoda** - *Metamerous*, segmented; uniramous or biramous jointed (segmented) appendages.

Series **DEUTEROSTOMIA** - Blastopore becomes anus, typically *enterocoelous* with *radial* cleavage, and *oligomerous*.

Phylum **Pogonophora** - "Beard worms", sessile deep-sea worms that build chitinous tubes, some large forms inhabit hydrothermal vents.

Phylum **Echinodermata** - With secondary, pentamerous radial symmetry; water vascular system; calcareous endoskeleton of mesodermal origin.

Phylum **Chaetognatha** - "Arrow worms" and conodonts; without gill slits or endoskeleton; "teeth" of calcium phosphate (apatite).

Phylum **Hemichordata** - With gill slits and nerve chord; no notochord.

Phylum **Chordata** - "Vertebrates"; gill slits, nerve chord and notochord; endoskeleton of mesodermal origin.

Cavalier-Smith (1998) is predictably idiosyncratic yet insightful. His including Porifera under Radiata did not catch on and feels less useful than Margulis and Schwartz's distinction of Parazoa and Eumetazoa. On the plus side the old Acoelomata, Psuedocoelomata, and Coelomata are rejected in favour of more recent taxa such as Lophozoa (= Lophotrochozoa = Spiralia) and the important molecular phylogenetic revealed Ecdysozoa:

```
Kingdom Animalia
   Subkingdom Radiata
      Infrakingdom Spongiaria
         Phylum Porifera
      Infrakingdom Coelenterata
         Phylum Cnidaria
      Infrakingdom Placozoa
  Subkingdom Myxozoa
  Subkingdom Bilateria
    Branch Protosomia
     Infrakingdom Lophozoa
        Phylum Bryozoa
        Phylum Kamptozoa
        Phylum Mollusca
        Phylum Brachiopoda
        Phylum Sipuncula
        Phylum Annelida
        Phylum Nemertina
     Infrakingdom Chaetognathi
        Phylum Chaetognatha
     Infrakingdom Ecdysozoa
        Phylum Arthropoda
        Phylum Lobopoda
        Phylum Nemathelminthes
     Infrakingdom Platyzoa
```

```
        Phylum Acanthognatha
        Phylum Platyhelminthes
    Branch Deuterostomia
     Infrakingdom Coelomopora
        Phylum Hemichordata
        Phylum Echinodermata
     Infrakingdom Chordonia
        Phylum Urochorda
        Phylum Chordata
Subkingdom Mesozoa
```

A preferable model would combine the above two classifications, along with taxa based on the research of recent workers such as Dunn et al. 2008 and Edgecombe et al 2011 MAK120421

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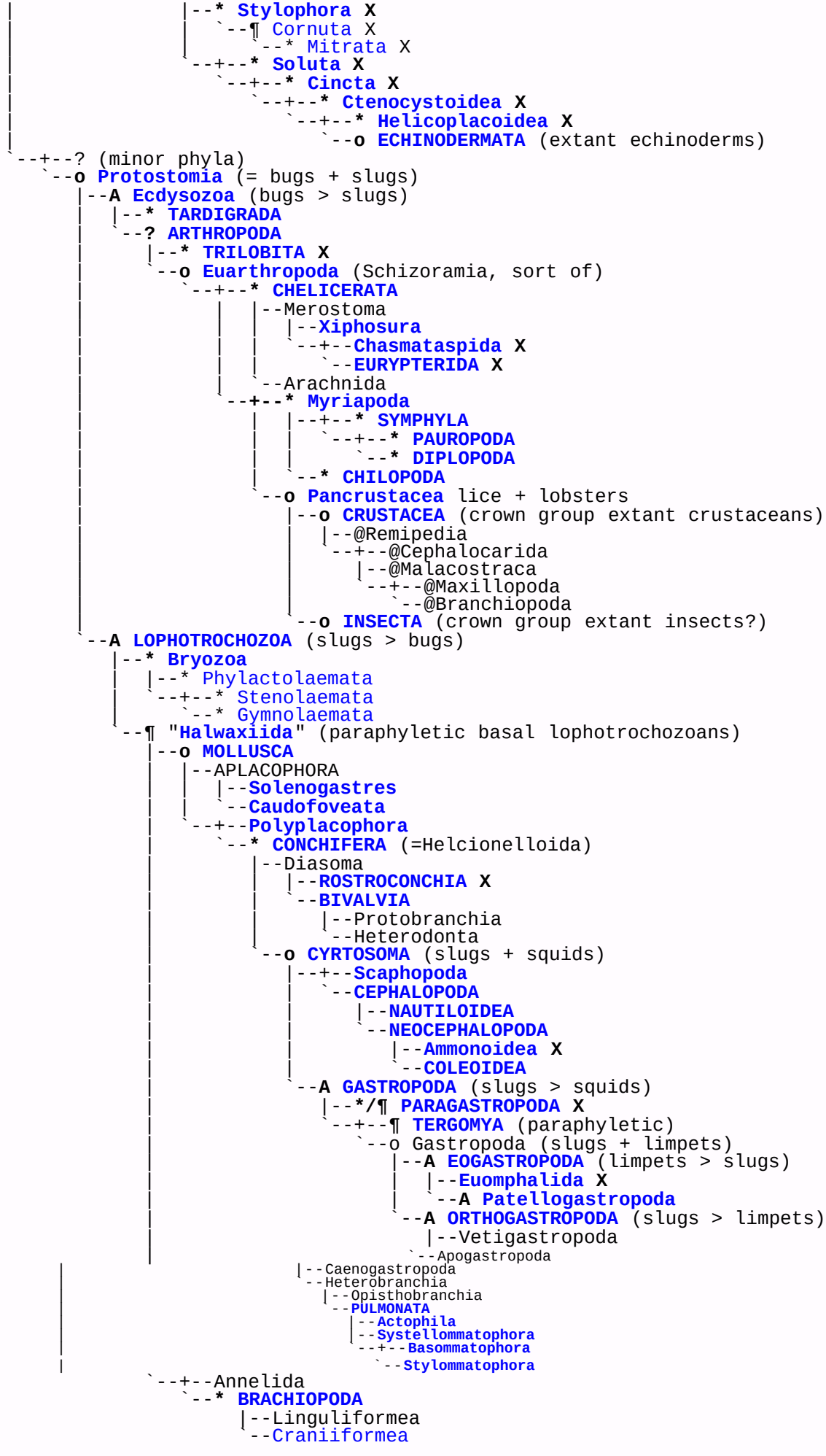
Metazoa Dendrogram

```
LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```

This claodogram is intended to give only a broad outline. Even then, it is severely underinclusive. The plan is to fill it out gradually as we explore, or re-explore, metazoan phylospace to a level approximating the superclass or subphylum of Linnean phylogenies.

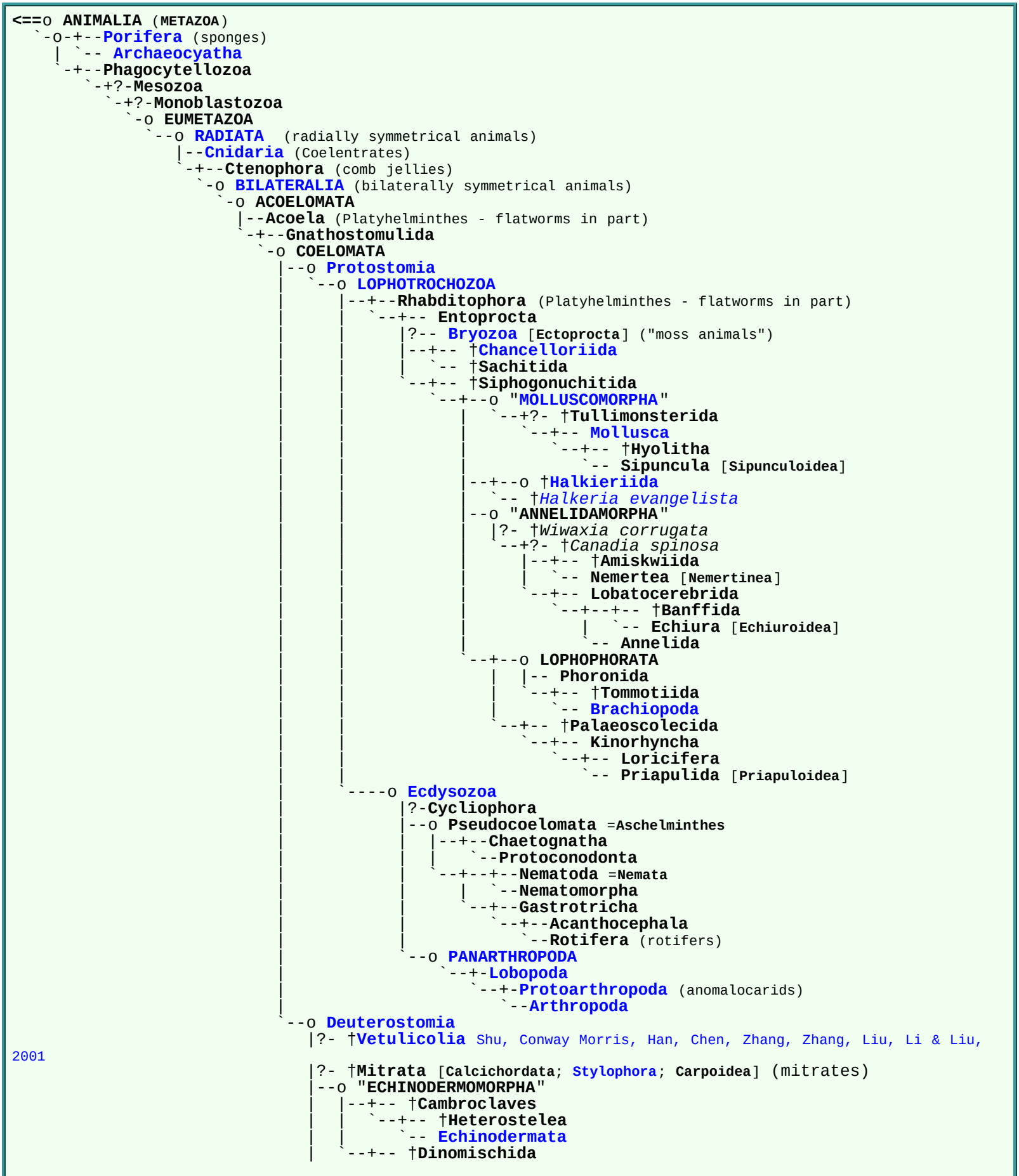
o : crown group
A : stem group
¶ : paraphyletic basal radiation
@ : apomorphy-based clade
* : similarity-based (classical) taxon
? (or blank) : basis uncertain

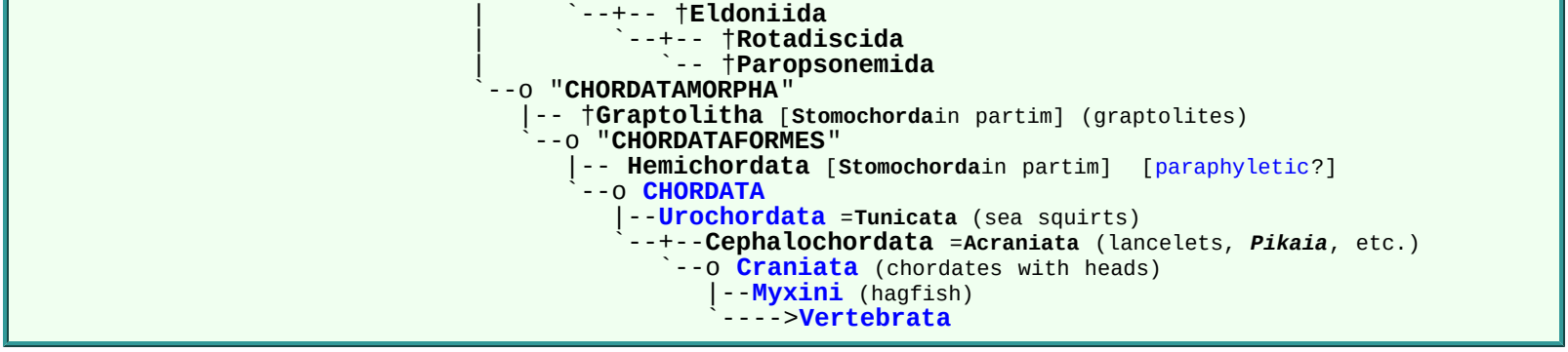
```
A METAZOA (= toads > toadstools)
|--? Choanoflagellata
`--¶ PORIFERA
   |--*Archaeocyatha X
   `--+--?(?A)Calcarea
      `--+--? Hexactinellida
         `--+--? Demospongiae
            `--o Eumetazoa (= jellyfish + silverfish)
               |--* CNIDARIA
               |  |--A Anthozoa
               |  `--+--? Hydrozoa
               |     `--+--+--? Scyphozoa
               |        `--? Cubozoa
               `--o Bilateria (including ?some/all "Acoelomates") (= starfish + silverfish)
                  |--A DEUTEROSTOMIA (= starfish > silverfish)
                  |  |--* Vetulicolia X
                  |  `--+--@ CHORDATA (notochord present, or A: movie stars > sea stars)
                  |     `--o Ambulacraria (hemichordates + echinoderms)
                  |        |--? Hemichordata
                  |        `--+--* Vetulocystidae X
                  |           `--o HOMALOZOA (grade, redefined here as Rhenocystis + Echinus)
```



For purposes of comparison, we include the following:

Metazoan Phylogeny after Conway Morris (1993) and Peterson & Eernisse (2001)





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A B C D EF G H IJ K L MN O P Q RS T U VW X Y Z

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Hox Genes

This is where we take up subjects that are too big for a glossary and aren't conveniently handled as part of some particular taxon. These are usually subjects in biochemistry or cell biology. It is annoying to have to break off from doing taxa, so this section will never amount to much.

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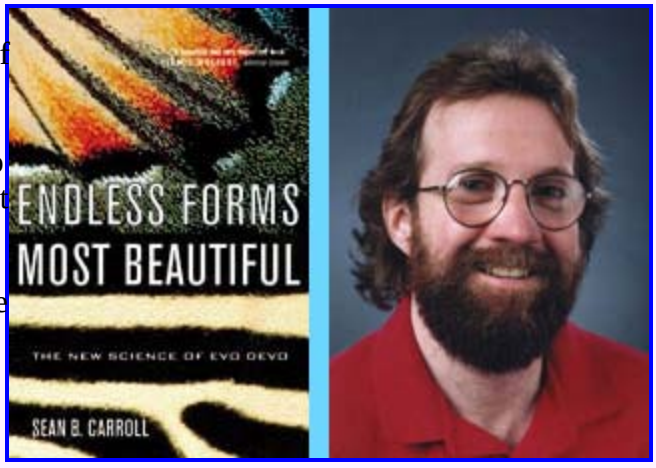
Why We Care About Hox Genes

A Really, Really Superficial Introduction to Evo-Devo

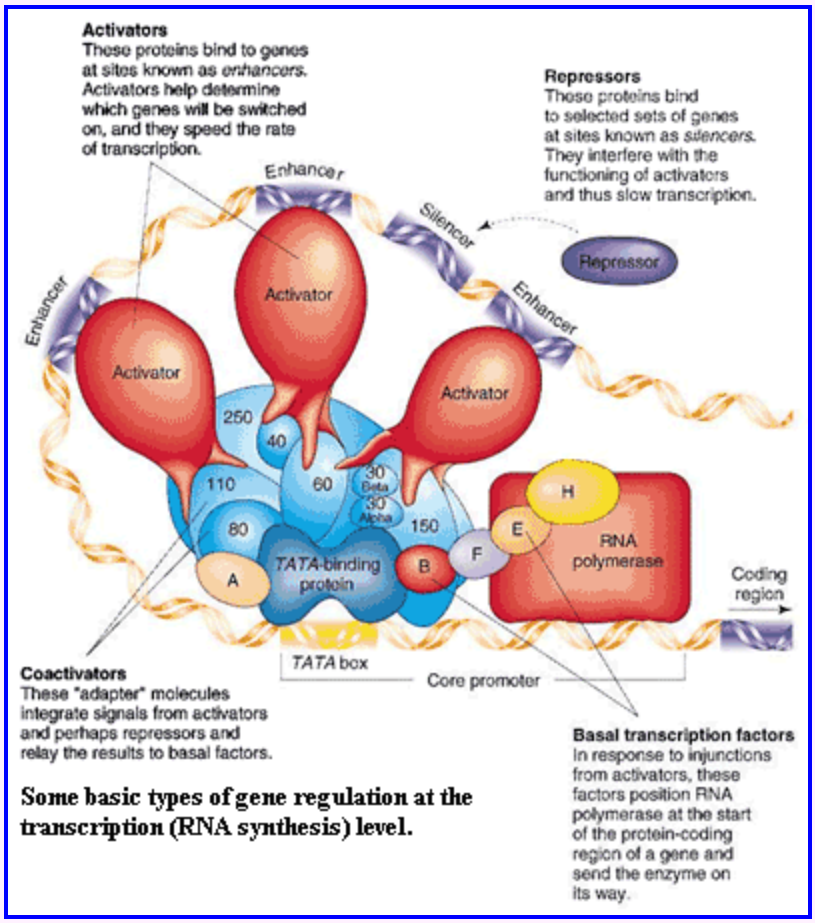


The story of evo-devo is told, in very readable form, in Sean Carroll's (2005) recent book on the topic. Buy this book. If possible, do not bother finishing this essay. Just get the book. You don't even have to look it up: here's the link to the Amazon.com page. The rest of this discussion is mostly our clumsy attempt to explain what we learned there and elsewhere on this topic. Don't waste your time on it. Buy the book.

Evolutionary developmental biology, "evo-devo," starts from the obvious: organisms get to be what they are through development as embryos, larvae, or whatever we label the stage(s) between fertilized egg and adult. Some embryos -- usually a minority – will complete the process and become reproducing adults. However, almost nothing which happens after the embryo becomes an adult can have much effect on the biology of the organism. That's what "adulthood" means. Of course, natural selection continues throughout life; but what is *selected* are the characteristics acquired during development.

Development is how we become what we are. It follows that, if we want to know how evolution makes changes, the proper focus is comparative embryology. If we want to get to the mechanics of these changes at a really fundamental level, then we must focus on comparing the way in which genes are regulated in the embryos of different organisms.

In fact, we can (as opposed to Kant) go a little further on pure reason. In animals, every cell has essentially the same complement of genes, and essentially all of those genes have some kind of homologue in every other animal. What separates us from chimpanzees can't be the miniscule differences in the sequences of the basic enzymes and structural proteins. The key is the regulation of those genes in the embryo. Carroll (2005a). One recent study could be read for the proposition that, even in protein-coding regions of DNA, the evolution of DNA sequence is primarily driven by the requirements for regulating when and where each gene is expressed (i.e. transcription and post-transcriptional processing in the nucleus), rather than by the biological function of the gene product. Parmley *et al.* (2007).



Some basic types of gene regulation at the transcription (RNA synthesis) level.

That's all off topic and rather too abstract. The point is that, even in the simplest organisms, genes don't just crank out RNA at random -- particularly in the embryo. Gene expression has to be carefully controlled. It must occur only at the right time during development and only in the right places -- just the right genes to make a leg, in the right sequence, in only the right places on the body, in the correct orientation, and hooked up correctly to the various nerves, muscles, blood vessels, and glands which integrate the leg with the rest of the adult organism. How is it done?

Evo-devo is still sketching the broadest outlines of the answer, but amazing progress has been made in the last decade. The best-understood part of the story -- arguably the *only* understood part of the story -- is anteroposterior axis "patterning" by hox genes. In other words, we're starting to get answers to the following fundamental question: how does an embryo tell its head from its ass? Of course, many adults never do seem to get this right. Fortunately, embryos rarely get involved in politics or religion, so they usually do a much better job than adults. Not only do embryos eschew these inherently inversionary activities, but they also have a special set of genes, the *hox genes*, which help them along.

Hox genes are a subset of the *homebox genes*. Some of you will doubtless attempt to claim that you've never heard of hox genes. We are not so gullible as to believe this. Yet it is possible – just – that you have temporarily mislaid this information, along with the birthdays of your parents and the name of your cat. We will mumble about them for a bit and perhaps you will recall what you have learned from some more reliable source.

Our approach uses three iterations. First, we offer some definitions and a few sentences of completely over-simplified noise -- the traditional high-school textbook stuff, without the (often very useful) diagrams. Next, we take a very brief look at some general biochemical facts about hox genes (You didn't think we were still talking about your cat, did you?). Then, having had about all the organization we can possibly stand, we will go back to doing things in the more customary **Palæos** fashion. That is, we will take a long, meandering stroll through the metazoan cladogram, and point out some of the interesting sights along the way. Finally, if we have arrived at any conclusions in the process, we will probably state them. If not, we will end more or less abruptly: like this.

In researching this section we ran into an unreasonably large proportion of exceptional papers -- too many to praise individually. This field has not only attracted some of the brightest and best, but some very engaging writers as well. We have marked a few of these papers with one or two asterisks when cited. Most can be found on the web.

First Iteration

Nomenclature

Hox Genes: The hox literature is filled with bad nomenclature, starting with the term "hox" itself. A *hox gene* originally referred to any gene coding for a protein with a particular DNA-binding motif, the *homeodomain*. At the time, this was a small family, clearly identified with *homeotic mutants* of the fruit fly *Drosophila*. We'll explain the term *homeotic* later. Unfortunately, it turned out that the class of genes coding for homeodomain-containing proteins was vastly larger than the family of genes involved in homeotic mutations. As a result the term "hox" became utterly ambiguous. It could mean all genes which coded for homeodomain-containing proteins, or just the ones implicated in homeotic mutations. Watch out for this in the literature. We will use *hox* to mean the small set of genes involved in the homeotic mutations and their closest relatives **[11]**. If we mean homeobox genes in general, we will say so. Recently, writers have introduced the term *Hom* to refer just to the homeotic (hox) genes. This terminology has not really caught on. We hope it will, but it hasn't. In any case, the numerical designations for hox genes are *hox1*, *hox2*, etc. For historical reasons, we're stuck with that system.

Numerical	*Drosophila*	Abbreviation	Notes
Hox1	*labial*	*lab*	**Beginning of anterior class** (and ANTP complex in *Drosophila*)
Hox2	*proboscipedia*	*pb*	
Hox3	*(Zerknüllt, Bicoid)*	*(zen, bcd)*	**Hox3 class**. Hox3 is probably its own "upper middle class" homology group. *Drosophila* has two hox3 homologues, but neither is homeotic.
Hox4	*Deformed*	*Dfd*	**Beginning of middle class**
Hox5	*Sex combs reduced*	*Scr*	Insects have a "hox 5½," *fushi tarazu (ftz)*, which is not homeotic
Hox6	*Antennapedia*	*Antp*	Hox6-8 are homologues of *Antp,Ubx* and *AbdA* as a group. That is, all 6 (and *ftz*) derive from a single "lower middle class" gene in *Urbilateria*.
Hox7	*Ultrabithorax*	*Ubx*	Beginning of UBX complex in *Drosophila*
Hox8	*Abdominal A*	*AbdA*	
Hox9	*Abdominal B*	*AbdB*	**Begining of posterior class**
Hox10, 11 ...			No arthropod homologues -- or (more exactly) *AbdB* is homologous to all posterior hox.

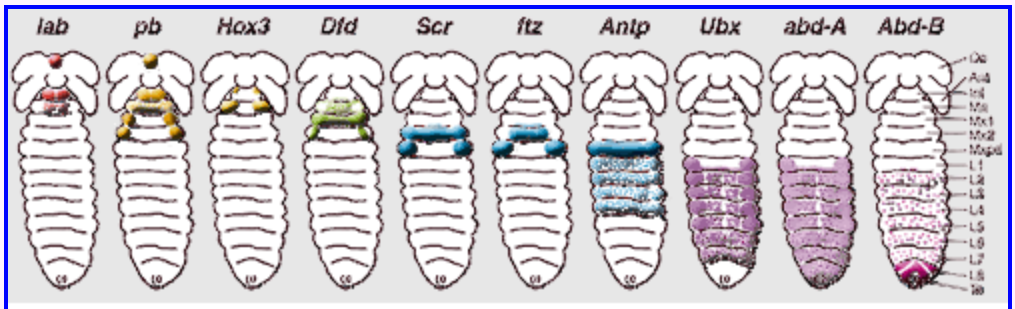
Notation: Historically, it was also customary to use the same name for a gene and the protein it coded. The gene was italicized. The protein was not. This sounds easy, but in fact the convention is cumbersome. Also, we are often sloppy and say things like "thoracic *hox4* regulates limb differentiation." The truth is that, most of the time, we don't know whether or not hox4 is actually expressed in the thorax. Perhaps it is expressed elsewhere, and the hox4 mRNA or hox4 protein is transported to the thorax. We originally tried to stick to the old convention, because it promotes rigorous thinking; but it simply gets too awkward.

Fly names: When hox genes were first discovered in *Drosophila*, no one knew how, or even whether, the genes were related. Each hox gene was given a name by the discoverer of the corresponding mutant *phenotype*. Later, when it became clear what was going on, and hox-like regulation was investigated in other animals, things had become more organized. Hox genes were then given numbers. However, there are one hell of a lot of fruit fly workers out there, and the old names are widely used. Get used to them. In any case, as indicated in the notes to the table, the homology with vertebrate hox genes is not always exact. Thus, when speaking of lophotrochozoans in general, and arthropods in particular, it is actually more accurate to use the fly names.

Abbreviations: Also, the fly abbreviations all have initial capital letters except lab, pb, zen/bcd, and sometimes abdA. Use of abdA vs. AbdA is wildly inconsistent. We assume that this practice also has some obscure historical justification. Then again, it may be deliberate perversity. Fruitfly workers tend to enjoy that sort of thing. In any case, we've decided to jettison the capital letters along with italics unless we are giving the exact name of a particular gene in a particular organism (which we almost never do).

Homology classes: It is often convenient, and sometimes essential, to treat hox genes in groups. Conventionally, there are three or four *homology classes*: anterior, posterior, middle/central, and hox3. The reasons for this will become obvious as we go along. Molecular biologists tend to use the term *orthology* instead of *homology* because they don't understand what *homology* means. If you think we're simply being rude, see 14.2. Paralogy, Homology (Wikipedia), or Homology in Molecular Phylogenetics. The last one almost has it right. If you care, see the glossary entries. For practical purposes, *paralogous* genes are homologous genes in the same organism. *Orthologous* genes are homologous genes in different organisms. We tend to use *homologous* in both cases.

The Short Version



Hom gene expression during the extended germ-band stage in embryos of the centipede Lithobius. Adapted from Hughes & Kauffman (2002).

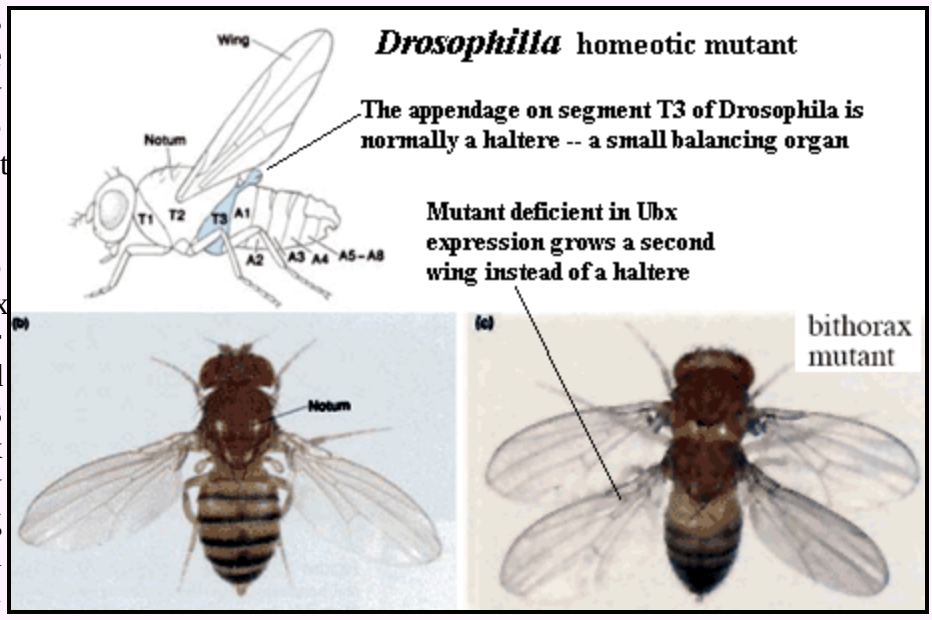
We'll postulate an ideal hox animal with none of the complications found in real animals -- call it *Hoxazoon*. *Hoxazoon* has a dozen or so hox genes. An ideal hox system has the following properties.

1) **Genetic colinearity:** All of the hox genes are found on one chromosome, one after the other, separated only by promoter/repressor regions. Hox1 is located on the 3' end of the cluster (*i.e.* "first"), while hox14 is on the 5' end ("last").

2) **Anatomical colinearity:** During development, the *Hox* genes are expressed in the same order along the anterior to posterior axis: hox1 toward the front of the head, hox14 at the tail end, as in the figure from Hughes & Kauffman (2002)*.

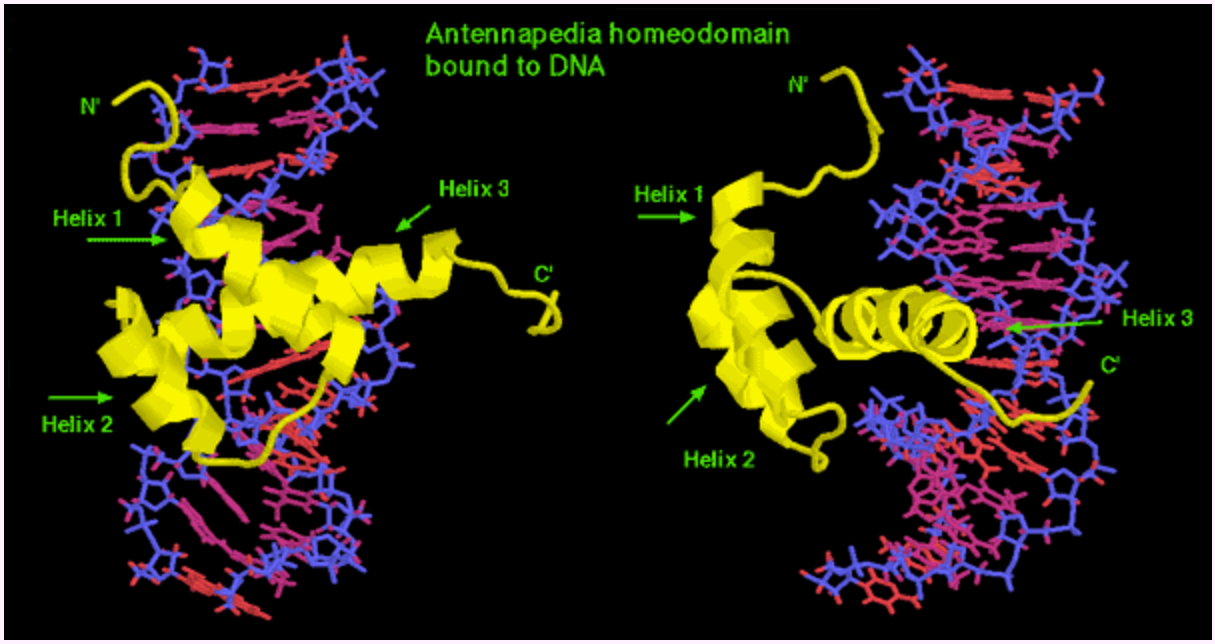
3) **Temporal colinearity:** Generally, hox genes are also expressed in the same sequence in time -- hox1 first, hox14 last.

4) **Evolutionary Conservation:** Hox genes are quite highly conserved. In some cases, the mouse and fruit fly genes are practically identical. That's what makes it possible to use the same names for these genes in different animals without much loss of information.



5) **Homeotic transformation:** You have doubtless been told by someone that the hox genes are responsible for "anteroposterior patterning" of the embryo. Although we used that language ourselves in the last section, it is actually a poor choice of words. What hox genes actually do is this: they allow embryonic development to progress using something close to an object-oriented programming language. Many high-level developmental signals are calls to an abstract class (e.g. a class of limbs). The object (the limb) is actually built using some subclass. The particular methods and data inherited by the subclass are specified by other inputs -- the developmental "context." This is where the hox genes come in. The particular combination of hox genes expressed in the target location specify what *kind* of object gets made: arm, leg, or even an intermediate form. The hox genes thus specify the particular methods and attributes included in the object.

As shown in the image, a homeotic mutant has the wrong pattern of hox expression and therefore gets the wrong kind of limb. Since JAVA programming may also be unfamiliar territory, we'll back away from the analogy; but it's a much more powerful powerful metaphore then "patterning" if you happen to have some experience in that area.



These five properties greatly simplify the machinery needed to develop an embryo. In essence, some master timing switch sends a message: "build me an appendage." That's *all* it needs to say. In a crustacean, for example, the cells receiving that same message will make a *maxilliped*, *pedipalp*, bristle, or whatever. The choice depends on which hox genes are active in the area. The message doesn't have to include detailed instructions about what kind of appendage to make or how to make it. The target cells respond to the message based on context -- the hox "code." This allows development -- and sometimes evolution -- to proceed in a simple, modular way.

The general tells his adjutant, "get me a car." Depending on where they are and what unreasonable time frame the general has imposed, the adjutant decides what depot to call. He calls the sergeant at the depot and orders a suitable car. The sergeant decides what's available, and tells off a private to drive the car to the general. The private decides whether the car needs gas and how to get to the general. At each step, the instructions are simple and efficient, with execution dependent on context. The hox "code" provides that context. Unless something goes seriously wrong, the code ensures that the fruit fly grows a pair of halteres, rather than a second pair of wings. The general departs in a conveyance appropriate to his exalted rank (perhaps a *Hom*-V), rather than a water buffalo.

This idealized, linear version of hox regulation is not at all unique. Embryonic development, computer programming, and military structure are all methods for organizing incredibly complicated systems to acheive precise, predictable results in all kinds of unpredictable circumstances. The same basic elements are present in sophisticated versions of each: carefully graded decision-making heirarchies, modularity, error-checking and reporting, feedback loops, and some limited number of single-function specialist units.

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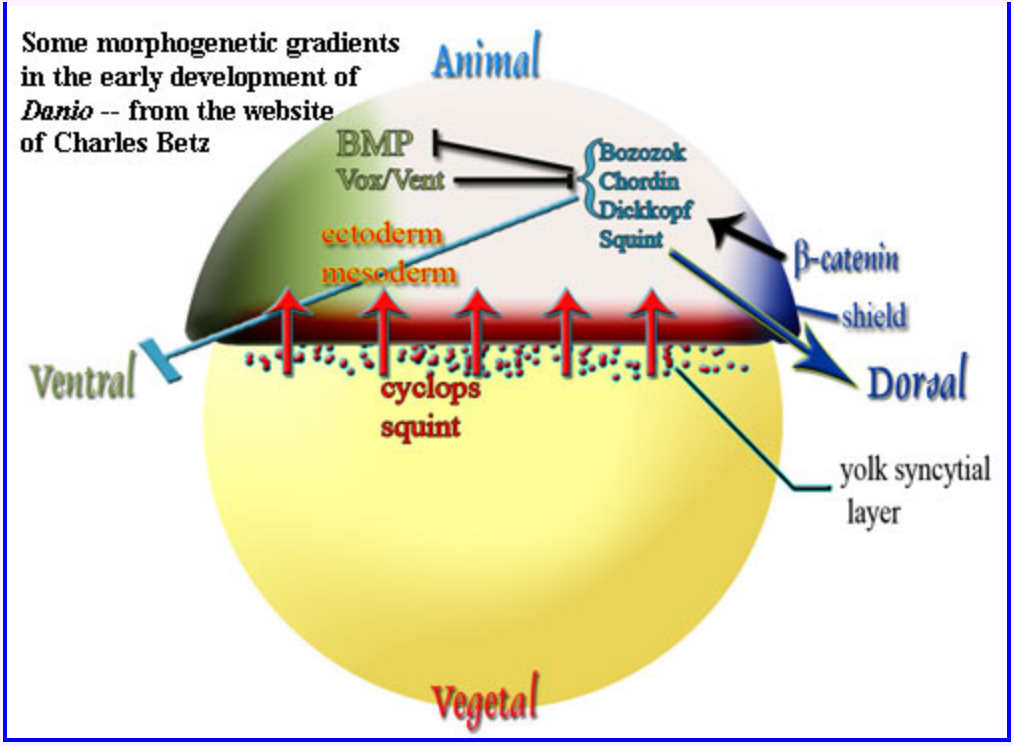
Hox Genes - 2

Second Iteration

But *Why?* ... Some Unanswered Questions

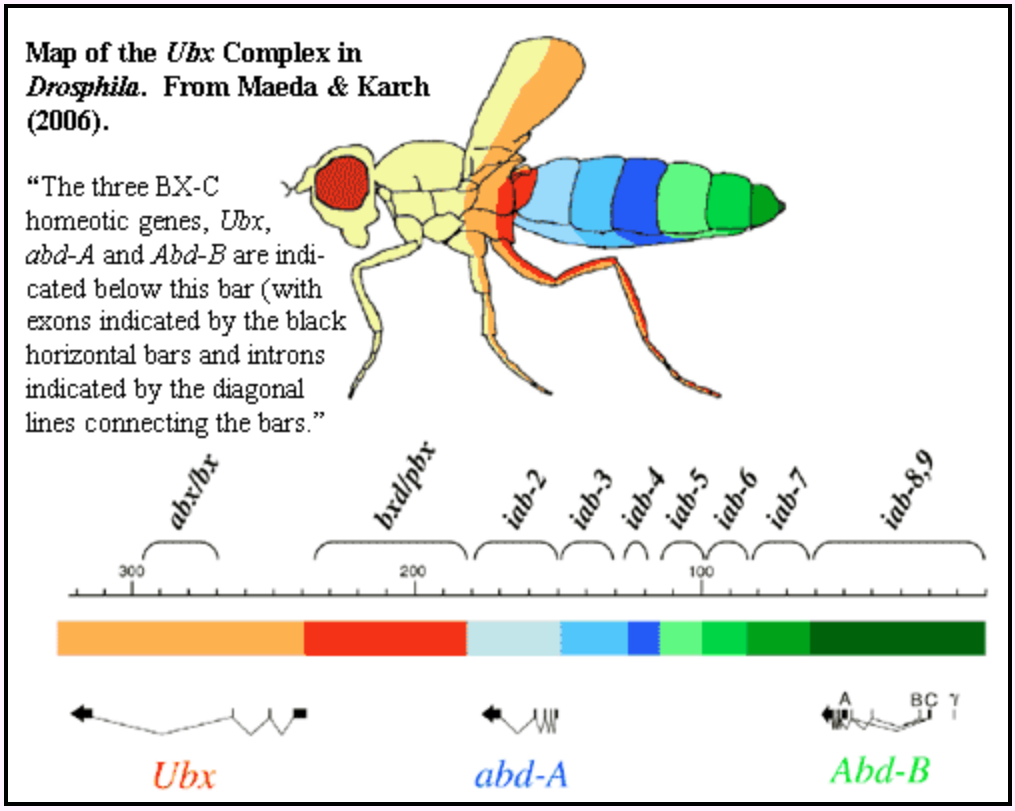
That's the idealized version. Real organisms, like real military organizations and real computer programs, tend to operate in ways which deviate from their original designs. So, before getting into specifics, we might look a little harder at the biochemical context. First, what exactly is a homeodomain anyway? Fortunately, we don't have to explain this. Pharyngula has a nice short discussion of the homeodomain. He uses language more efficiently than we do, so we will refer you to his discussion -- in particular the "Homeobox and Homeodomain"



heading.

Hox genes are but one family of what Carroll (2005) aptly calls *toolkit genes*. These all code for relatively small, simple proteins with a DNA-binding domain (homeodomain, "zinc finger," or something more exotic) which function as messengers during development to control the transcription of whole batteries of genes. The reason Carroll uses the toolkit analogy is that these transcription factors are used to regulate different groups of genes in different organisms. He comes close to arguing that toolkit genes are completely general signals which have no inherent information content.

Carroll doesn't actually go this far, because there is a really odd consistency in the functional role these genes play. The best-known example is perhaps the non-hox homeodomain protein *pax-6*. Pax-6 regulates entirely different sets of genes in chordates and arthropods. However, in both cases, it is plays a critical role in eye formation. The same applies to *tinman* and heart development. For that matter, the hox genes have some of the same peculiarity in that they rarely change order **[1]**. It's easy to "explain" all this consistency by assuming that all these functional associations are simply inherited from the last common ancestor of cows and crustaceans ("*Urbilateria*"). That's exactly the argument we made elsewhere, and that's probably all there is to it. But, if we accept that argument, it would mean that our last common Great-Grandmother with clams and shrimp was a *lot* more complex than is generally believed. Thus, we may shortly have to choose between the received teachings of biochemistry and phylogeny. That is, either *Urbilateria* was very complex and some morphologically simple bilaterian animals are probably outside the crown group Bilateria, or the *Hox* genes have a really peculiar biochemical link to specific body functions. This could go either way, but our current suspicion is that the guys in the lab coats are going to win, and we're going to have to adjust our phylogeny. *See* Ryan *et al.* (2007) (highly evolved anthozoan homeodomain system, discussed later), Chen *et al.* (2004)* (*Vernanimalcula*: in our own, distorted view, a possible stem group bilaterian **[2]**).



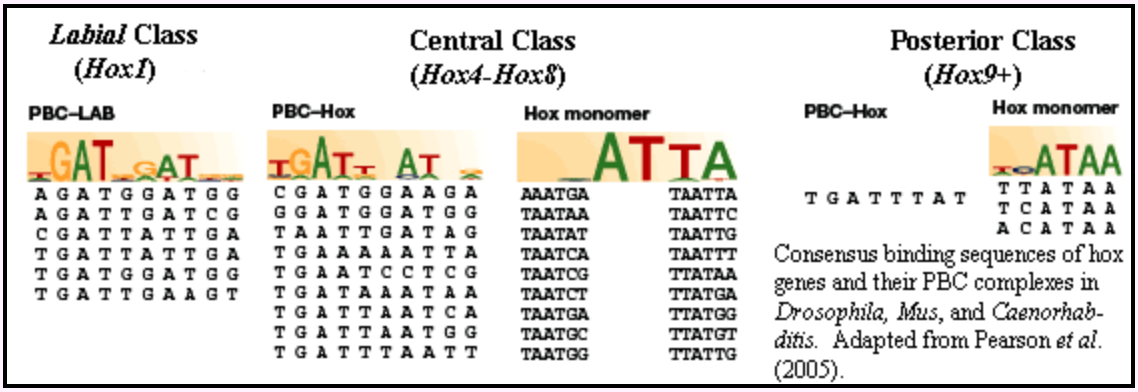
In this same vein, let's ask a more fundamental question. Why bother with this elegant, but recondite, system? Why didn't evolution just come up with a simple gradient of front to back, based on (for example) the progress of

gastrulation? Morphogenetic gradient fields are very old stuff. See review by de Robertis *et al*. (1991). Alternatively, why require the embryo to do all this hard work in the first place, when mom could easily set up the pattern during egg development? A maternally, established gradient seems to be the way it's done in some cnidarians. Momose & Houliston (2007). In fact, that's arguably how anteroposterior "patterning" is actually accomplished in *Drosophila* itself -- with a maternal *bicoid* gradient, before the embryo expresses hox. **[12: update]** In fact, in baby *Drosophila*, Mom even takes care of segment formation. The embryo later has to override the maternal "parasegments" in order to set up its own segmentation pattern. Maeda & Karch (2006).

Why bother? We have no answer for this question, and we will return to various aspects of the problem repeatedly. We thought perhaps that evolution of the hox system had something to do with segmentation **[3]**. However, bilaterian segmentation post-dates *Urbilateria* and was independently invented at least three times. Seaver (2003)* (discussed elsewhere). Another bad idea was that the regulation of hox genes was somehow unique and important to the properties and evolution of the system. In fact, it turns out that the regulation of hox expression is quite complex, variable and -- most importantly -- it didn't immediately suggest any easy turns of arm-waving rhetoric with which to ornament this discussion. *See* Maeda & Karch (2006)* for a far more determined, more well-intentioned, and almost successful, attempt to make this subject comprehensible. In addition, hox genes are apparently subject to multiple levels of regulation, including post-transcriptional regulation, like any other gene. Pearson et al. (2005).

How the Hox System Regulates Other Genes

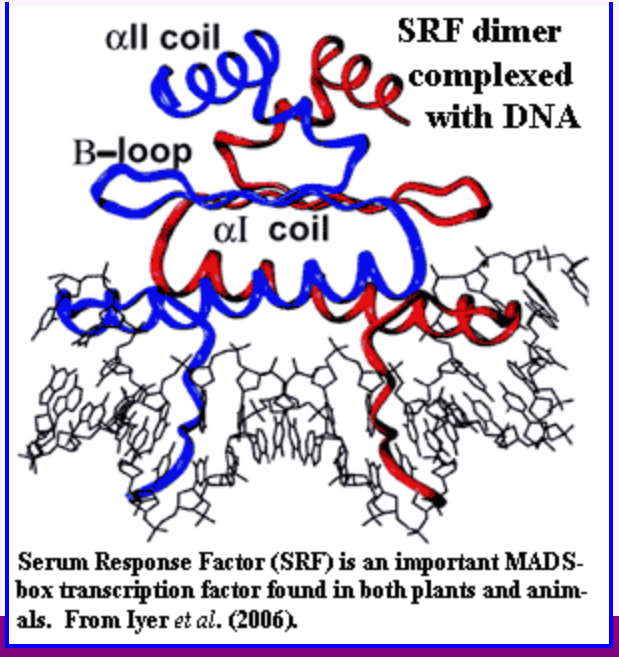
So what, exactly, does the hox system regulate and how? Again, understanding of this area has not yet reached the point at which a few sentences would suffice to summarize a fundamental principle. We're still at a point where some individual cases are understood, but we don't have a handle on any common mechanisms tying them together.



The current state of the art is described by Pearson et al. (2005). As these folks point out, one of the relatively few strong insights gained so far is that hox proteins bind to DNA as heterodimers or heterotrimers, typically cooperating with transcription factors of the pbx or hth classes (both homeodomain-containing groups). These multi-protein complexes have different sequence specificities than a simple linear combination of the individual monomers, and this creates the potential for a relatively complex, fine-tuned system of regulation based on a small number of very simple proteins.

Even with this expanded set of regulatory possibilities, we would expect that the hox system would work on a relatively high level. That is, its anticipated targets would be other regulatory genes rather than genes coding for individual enzymes and structural proteins. As it turns out, this is probably the case. Hox proteins, as expected, control the expression of a number of important transcription factors, such as *decapentaplegic* (*dpp*, governing formation of viscera), *twist* (mesoderm) and *distalless* (*dll*, appendages). Pearson *et al*. argue that hox signals also directly regulate lower-level "blue collar" genes. However, their examples are not particularly convincing.

Third Iteration: a Sprint Through the Zoo



Serum Response Factor (SRF) is an important MADS-box transcription factor found in both plants and animals. From Iyer *et al*. (2006).

Non-Animals & Sponges

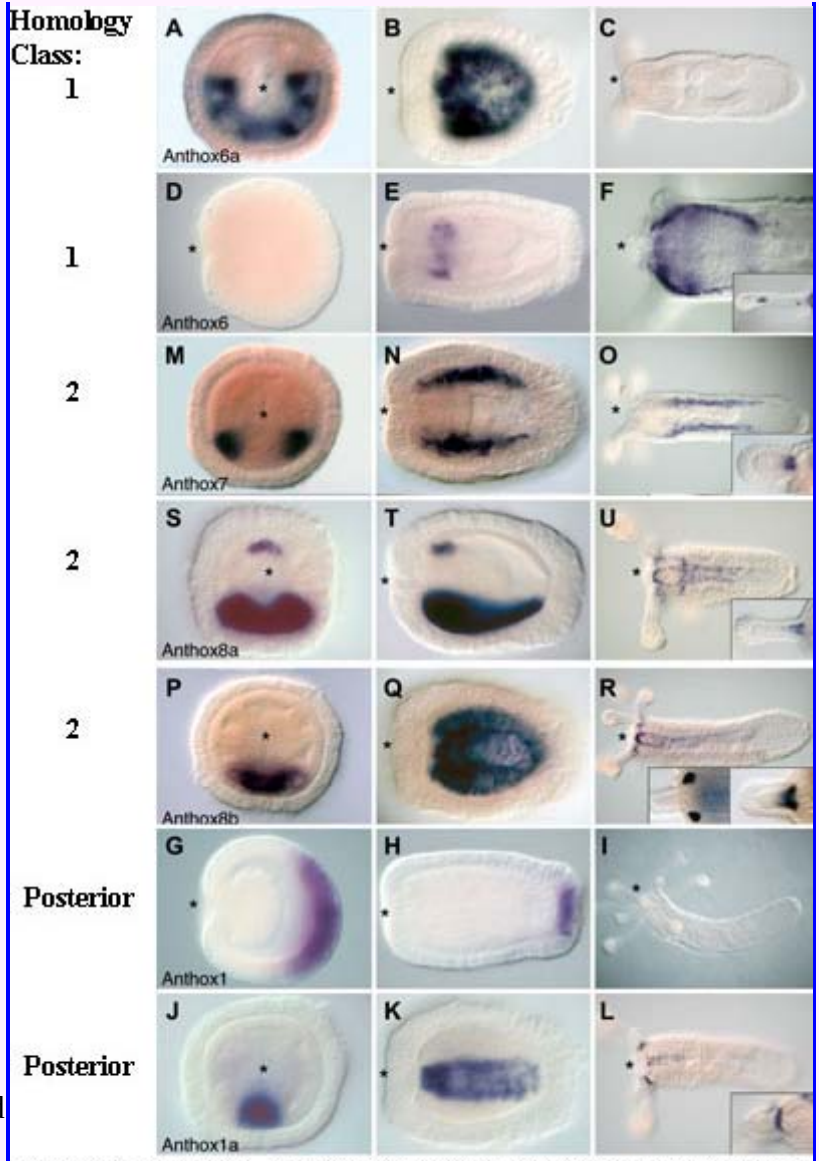
But enough of vague generalities. Let's turn to ... uh ... more specific generalities. Where do hox genes come from? The basic helix-turn-helix DNA-binding motif is about as old as DNA itself. Nelson & Cox (2005); Giraldo & Díaz-Orejas (2001). The homeodomain itself is essentially identical to the DNA-binding regions of some transcriptional regulators in bacteria. Carroll (2005). While irrelevant to the present discussion, we can't resist mentioning that plants have a system somewhat analogous to the hox system involving "MADS-box" genes, which are also descended from bacterial transcription factors. Kofuji *et al*. (2003). In fact, plants have some homeobox genes and animals use a few *MADS* genes.

Sponges and non-anthozoan Cnidaria (including Ctenophora) lack identifiable *hox* homologues, although they do possess closely-related homeobox genes. However the key property of colinearity is present only in anthozoans and bilaterians. Peterson *et al*. (2005). Despite speculations about hox gene clustering basal to the Cnidaria (e.g. Monteiro & Ferrier, 2006), "true" hox homologues are found only in certain cnidarians and in Bilateria. Brooke & Holland (2003). And, even in Anthozoa, their colinearity is not strong or consistent.

Cnidaria

That brings us up to Ryan *et al*. (2007)* who discuss the homeobox genes of the anthozoan, *Nematostella*, a sea anemone. This is probably the most interesting paper we've read in the last year. Fortunately it is readily available on line. We will only deal with the portion which relates to hox genes **[4]**. *Nematostella* has a surprising number of homeobox genes – about 130. Ryan *et al*. (2006). This is somewhat more than in *Drosophila*, which has around 100. *Id*. Of these 130, *Nematostella* has seven hox genes: two *hox1* orthologues, three *hox2* orthologues, and two posterior class hox genes. Ryan *et al*. (2007). There are no hox3 or middle class homologues.

Are the *Nematostella* hox genes collinear? Sort



Nematostella **hox genes. Mouth (blastopore) marked with '*'. Third column shows expression at planula stage. Adapted from Ryan *et al.* (2007).**

of. Maybe. First, notice that, going down the second column in the figure, the sequence *anthox6-anthox8a/8b-anthox1* makes a sort of anterior to posterior pattern -- at least "in the dusk, with the light behind her." More convincingly, going down the first column, the sequence *anthox6a-anthox7-anthox8a-anthox8b-anthox1a* makes a very good pattern along a "secondary," "dorsoventral," or (as we see it) radial axis. So, we seem to have some morphological colinearity. It's just not the kind we're used to seeing.

Genetic colinearity is a closer case. The *Nematostella* hox genes are fairly scattered, but there is one major exception. All of the hox2 homologues and one of the hox1s (*anthox6*) are tightly linked in a single cluster with several other homeodomain genes. We've run out of room here, so the image is included in footnote **[5]**. All of these genes are transcribed in the same direction except *Dmbxd* and *HlxB9*.

Although Ryan *et al.* don't go into it, the structure of this group is interesting. The hox genes are somewhat out of order, with the hox1 homologue positioned after the tightly-linked hox2 group. *Dmbxd* is a member of the dmbx class. This class is only found in cnidarians and deuterostomes. Morphologically, it is expressed at the anterior limit of hox expression. Takahashi & Holland (2004). Ryan & Co. don't test for expression of this gene, but it is genetically located in the right place, just upstream of the hox cluster. *Evx* is an *even-skipped* gene. Evx class genes, in bilaterians, are located just downstream of the hox cluster, often linked with a *caudal* element. Copf *et al*. (2003); Minguillón & Garcia-Fernandèz (2003); Minguillón *et al*. (2005). Here, the *evx* is downstream of the hox2 cluster, between them and the hox1 homologue.

Phylogeny of Selected Homeodomain Gene Families

```
Root
|--Dlx
`--+--Hlx
   |--+--Even skipped (Evx)
   |  `--Rough (ro)
```

We've droned on *Nematostella* and about this rather marginal hox system because it seems to be the most basal system which has any significant colinearity and is known in some detail. Potentially, it tells us a lot about colinearity, one of the central mysteries of hox, and about the evolution of the system. In addition to colinearity, *Nematostella* illustrates several features of the hox system which we will see repeatedly, to wit:

```
   `--+--Mox
      `--+--Gsx*
         `--+--Anterior Hox
            |  |--Hox1
            |  `--Hox2
            `--+--+--+--Hox3
               |  |  `--Xlox*
               |  `--Middle Hox
               `--+--Posterior
Hox
                  `--Caudal
(Cdx*)
```

Adapted from Ryan *et al*. (2007). The tree was constructed with a neighbor-joining technique, using homologues from *Branchiostoma* (a deuterostome), *Drosophila* (a protostome), and *Nematostella*. Each species gives the same pattern. Families marked '*' are ParaHox genes (explained below).

1. ***Duplication*:** Hox genes have a strong tendency to duplicate, often in groups (or so it is said). As Ryan *y sus compadres* discuss, the tendency is to assume multi-gene duplication events. However, their data suggest that the "hox cluster" system developed by single-gene duplications and gradual rearrangement. Certain Evil Norwegians disagree. However, since they seldom publish in open-access journals, we will spitefully refuse to cite them.

2. ***Independence of morphological and genetic colinearity*:** Although the *Nematostella* hox system has some degree of both morphological and genetic colinearity, these features show considerable independence. The posterior (*Anthox1* and *1a*) genes are not genetically linked to the others, but appear to work as part of a single morphological system. One hox1, and all hox2, homologues are collinear, but the hox1 gene is in the wrong order -- actually located after a gene (*evx*) which is usually the downstream bookend for the whole system.

3. ***Recycling:*** as the third column in the figure indicates, some hox genes are used again later in development, apparently for completely different purposes.

4. ***Evolutionary order of classes:*** Anterior class genes came first, followed by posterior class genes. The consensus view is that these were followed, later in phylogeny, by the middle class and hox3 (upper middle class) homology groups (but see phylogeny box).

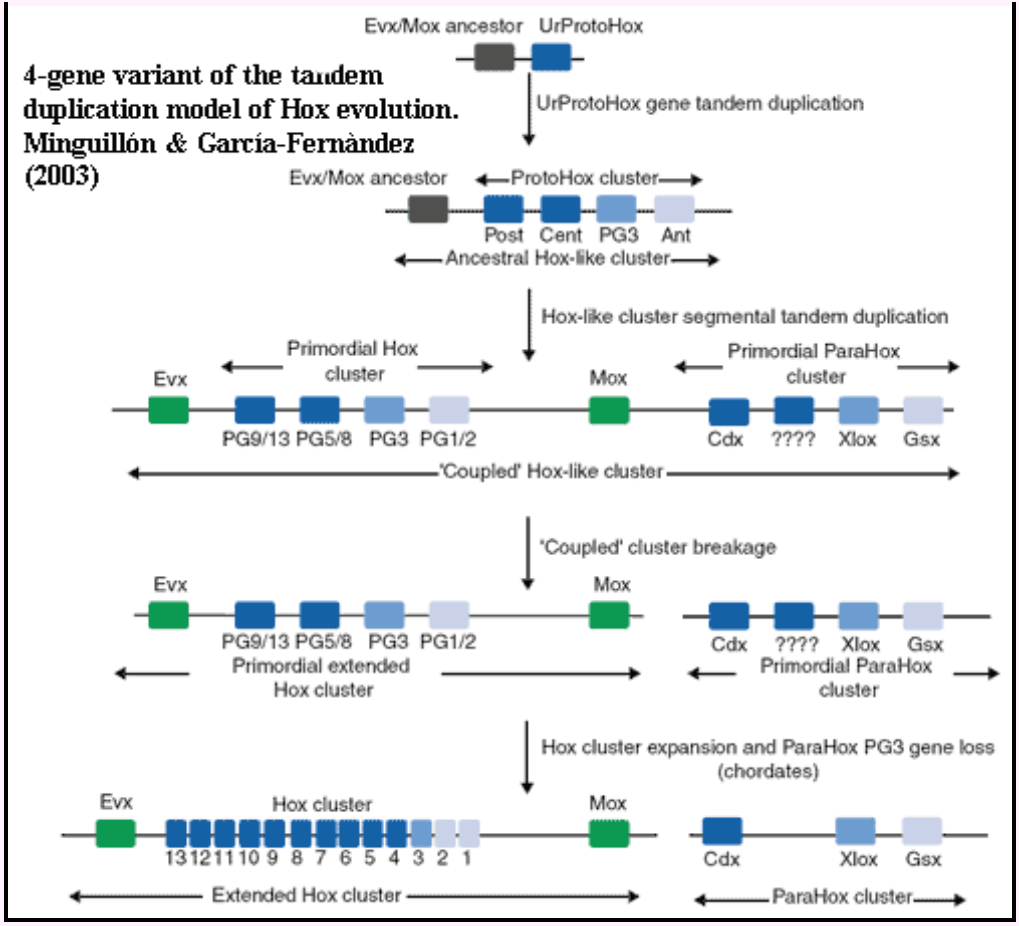
We leave the Cnidaria with an unanswered question. The homeodomain genes of *Nematostella* include several hints that the Cnidaria are paraphyletic. In fact, some features even suggest that the Anthozoa may be more closely related to deuterostomes than to protostomes, although that seems unlikely. Other work connected with Mark Martindale (Univ. Hawaii), his former student John Finnerty (Boston Univ.), and Finnerty's students (e.g., Ryan) indicates that Anthozoa are morphologically and genetically very bilaterian. See, for example, Martindale *et al*. (2004); Sullivan *et al*. (2006). Yet none of this work actually questions the monophyly of the Cnidaria. Perhaps that assumption needs to be re-examined.

Acoelomorpha

The acoelomorphs are gutless little flatworms which used to be thrown in with "Platyhelminthes" for lack of a better place to put them. That is, they were two of the many classes in the garbage taxon Platyhelminthes: Acoela and Nemertodermatida. After Platyhelminthes fell apart, these orphans were shuffled into an indifferent foster home between *Urbilateria* and the base of the protostomes, while the Authorities decided what to do with them. Recently, they seem to have been evicted from Bilateria altogether and live on the streets, as it were, unafilliated with any larger Metazoan group. Cook *et al*. (2004); Jiménez-Guri *et al*. (2006) (collectively, the "Barcelona Group"). **[6]**

The Barcelona Group previously (2004) found that the acoel *Symsagittifera* had anterior, middle, and posterior hox genes. It even had a caudal (cdx) homologue -- but lacked a hox3 class gene. This was a little odd, for reasons we'll get to in a moment. Consequently, they decided to check these results with a representative of another group of acoelomorphs, *Nemertoderma*. As a result of this work, they have changed their position and state that this group ancestrally had representatives of all four hox homology groups. This conclusion follows from their (2006) finding that the acoelomorph *Nemertoderma* has -- not a hox3 gene, but an xlox homologue.

Sadly, this forces us to get into the ParaHox genes, a task we had hoped



to avoid. Our melancholy is due to: (a) our minimal understanding of ParaHox and (b) a depressing suspicion that the underlying theory is a gross and misleading oversimplification. As we lack any inclination to get creative here, we will fall back on the mythic language of reviews and textbooks. To us, this stuff sounds a bit like a Bronze Age creation myth:

> So it came to pass that a "... ProtoHox cluster of four genes duplicated early in animal evolution, giving rise to two twin clusters. These would be the primordial Hox cluster, which expanded by *cis* duplication to eight genes in *Drosophila*, or to 13 paralogous groups in mammals, and the primordial ParaHox cluster, which lost one member and gave rise to the three-gene complex maintained at least in cephalochordates and vertebrates." [García-Fernàndez, 2005]. So that the Hox grew and became many and multiplied in the eagles of the great hills, in all the beasts of the earth, and also among the fishes of the ocean depths did they flourish.

This parody is shamefully unfair; and our (admittedly rudimentary) sense of fair play compels us to include a detailed graph of the actual model from Minguillón & García-Fernàndez (2003). The idea is that the hox and parahox clusters developed from tandem duplication of a four gene protohox cluster and its downstream evx book-end. When the double cluster split, it split unevenly. This left evx book-ends on both sides of the hox cluster. Theupstream homologue subsequently diverged to become a mox gene.

Why come up with this messy and complex model? Look back at the hox phylogeny from Ryan et al. (2007). The hox3 and posterior homology classes are both more closely related to non-hox (parahox) genes than to each other. In the Barcelona Group's experiments, this is also true of the anterior class (paired with gsx). Also, the two book-end genes, evx and mox, are closely related. Something has to explain this odd connection. The parahox model does that. If this is correct, the presence of a cdx gene in Acoelomorpha without either a hox3 or an xlox was peculiar.


***Isodiametra* (Acoela). See link for explanation of anatomy.**

But here's an alternative (which we just invented -- don't take it too seriously). Suppose there was *never* a protohox cluster. Instead, morphological colinearity came first. This made it convenient, for purposes of gene regulation, to evolve genetic colinearity. Not essential, mind you. Just helpful. What kind of genes would get recruited to this new linkage group? Clearly, if we are integrating multiple complex regulatory domains, it might be helpful if we were using duplicate spare parts. In that case, while one copy was gradually fitting itself into the complex regulatory assembly line of a hox linkage group, the other copy would still be out there doing things the old-fashioned way. That is, evolution would favor recently duplicated genes, since an embryo could often survive the sub-optimal regulation of one copy.

That doesn't explain the mox/evx bookends, but it wouldn't be hard to come up with some similarly*ad hox* explanations for them. We can imagine several reasons why two similar genes might tend to bracket the hox cluster.

However, we will not waste your time with these imaginings. The real point is that we can arrive at the same result, with the sub-families of hox genes each tending to be paired with a non-hox gene, as well as bookends, etc. without invoking tandem duplication events. Clearly, the data from Ryan et al. (2007) support this kind of sloppy, inelegant solution. Perhaps that's the answer. We are inclined to think that this is *still* too simple. Colinearity is, as we will see, a complex topic.

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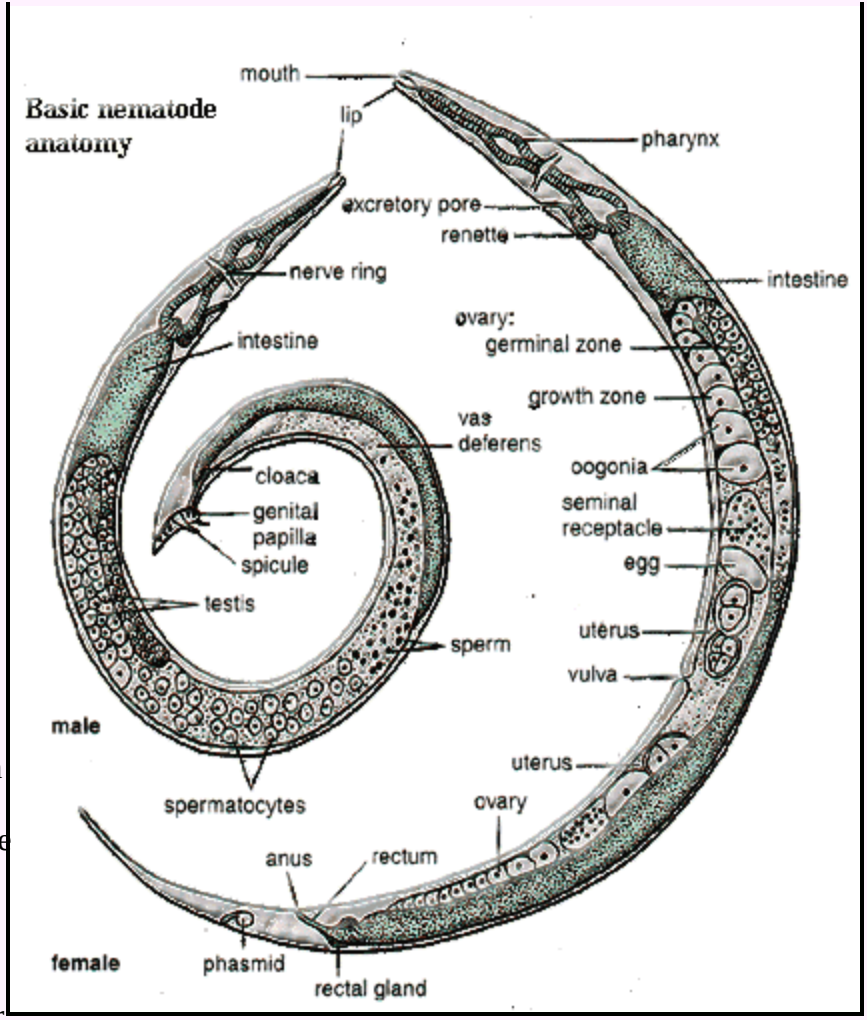
Hox Genes - 3

Bilateria

When we get to Bilateria things are much clearer. We can triangulate back from *Drosophila* and vertebrates to get a reasonable idea what *Urbilateria* had in the way of a hox complement. Certainly it had both members of the anterior homology group, i.e. hox1 and hox2. It had at least one (and probably *only* one) posterior group genes. The Standard Model asserts that it had a hox3. That's a bit less clear, but still very likely. Finally, *Urbilateria* had a startling *three* central class genes. García-Fernàndez, (2005). Look back at the homology table. If those homologies are correct, this triangulation must be correct as well. Consequently, *Urbilateria* must have had a rather highly developed system of hox genes.

Using the same technique, we can also deduce that *Urbilateria*'s hox system was clearly identified with the antero-posterior axis, rather than a complex mixture of at least two axes, as in



Nematostella. In fact, now that the confusing Acoelomorpha are removed from Bilateria, we can deduce that *Urbilateria* was a rather complex organism. Some of the morphological evidence and consequences are discussed at Bilateria (perhaps too cautiously, as matters have developed).

Some recent phylogenetic studies suggest why our last common ancestor with fruit-flies appears to be so remarkably advanced. *See, e.g.*, Rogozin *et al*. (2007); Wang & Caetano-Anollés (2006); Wolf *et al*. (2004). These papers use powerful new statistical techniques and enormous datasets. The techniques are possibly too new and undeveloped to be really reliable -- but the basic approach used in all three papers is sound: they all look for events much rarer than single-nucleotide mutations. About time. These studies suggest that the nematodes may also have to be moved out of Bilateria. If so, we will probably have to resurrect the term Platyhelminthes at least to describe a large, paraphyletic grade of "flatworms" basal to the last common ancestor of flies and fish.

At that point, the whole concept of Bilateria becomes shaky and we may revert to the old "Coelomata" terminology, as argued in Wolf et al. (2004). We'll stick with the bilaterian terminology for another year or so, but it looks like another major shake-up of the animals is almost inevitable. In fact, the hox system alone almost compels the same result. We now understand *Urbilateria*'s hox and parahox systems in some detail. But if it had a system of such complexity, can we accept that flatworms and nematodes descended from that ancestor?

Another aspect of the hox system which may be associated with the bilaterian body plan is a phenomenon we might call tagmatization; Pearson *et al*. (2005) put it like this: "In animal embryos in which mid-head and posterior abdomen can be distinguished, ‘head’ Hox genes have their initial anterior boundaries of expression in epidermal, neural and mesodermal cells of the mid-head region, and ‘tail’ Hox genes have their initial anterior boundaries of expression in the corresponding cell types of the posterior abdomen." The only citation for this remark is a 1992 paper, and a great deal has happened in the 15 years since that paper was published. We would, for example, take issue with the "posterior abdomen" part.

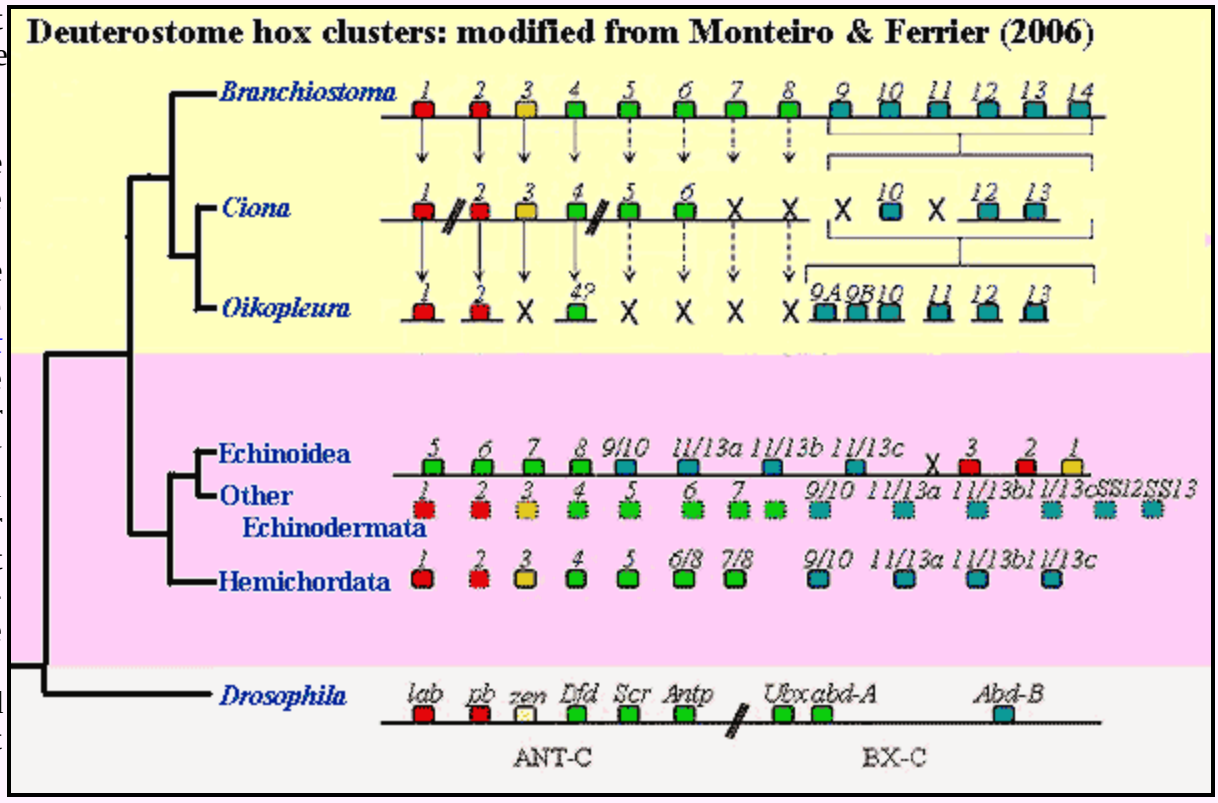
Nevertheless, it is broadly true that the anterior, posterior, and middle hox classes are often associated with major body divisions in Bilateria. And not just three divisions but, probably, five. Notice that Pearson *et al*. state that the anterior group begins in the "*mid*-head" region. All, or almost all animals with a head (and some without one)

have a very significant pre-hox region. In addition, it has recently been proposed that protostomes also have a *post*-hox region *behind* the genital area. Copf *et al*. (2003); Schramm & Koenemann (2004). What about deuterostomes? Let's have a look.

Deuterostomes and Disorganization

The most distinctive hox character of the deuterostomes seems to be the multiplication of the posterior class. Most echinoderms have six genes in the posterior class. The same applies to some vertebrates, cephalochordates and some urochordates. Despite the tendency to converge on the number six, the gene phylogenies suggest that the deuterostome posterior hox group is not the result of some massive early multiplication event. Rather, the process was more gradual and often involved the duplication of different genes in different lineages. Monteiro & Ferrier (2006). However, it is also obvious from the weird morphology of the earliest deuterostomes (Yunnanozoa, Vetulicolia) that something significant happened to deuterostome posterior morphology quite early on, presumably associated with some expansion of the posterior hox class. Shu (2005) **[8]**.

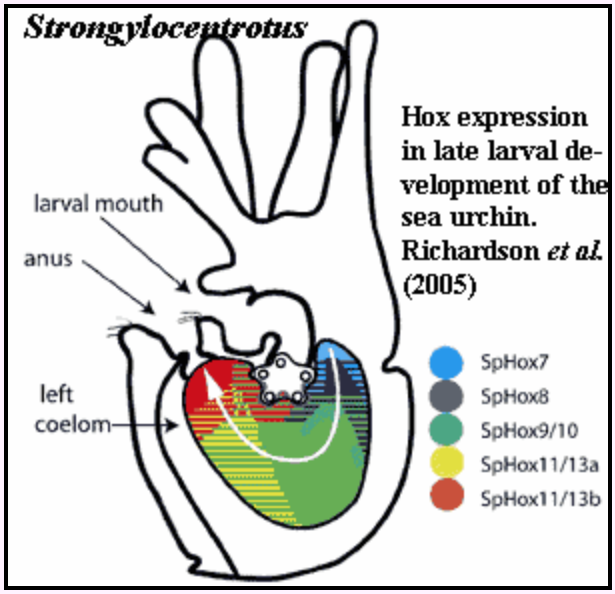
The current belief is that the gut extended all the way through the "tail" region in Vetulicolia. Shu *et al*. (2001)*. The same is true of the contemporary Vetulocystidae, whose body plan is otherwise quite different. Shu *et al*. (2004)*. So, the deuterostome posterior extension is not merely an appendage, but a distinct body region (or *tagma*). However, it may very well be a hox-related region, since the posterior hox class seems to have expanded in all significant deuterostome groups.



The Echinoidea (sea urchins) appear to be unique in having completely rearranged the linear relationships of the hox system. In the urchin *Strongylocentrotus*, the anterior class hox genes and hox3 are found (a) downstream of the posterior class and (b) in reverse order. Richardson et al. (2005) **[7]**. As you might expect, the hox1, 2, and 3 homologues are oriented backward -- but so also are hox5 and hox11/13b. The urchin evx gene is still the

downstream bookend to the system, but now located next to hox1, instead of the most posterior hox gene (here, hox11/13c).

But what does "posterior" mean to a radially symmetrical sea urchin? The answer is complex. Only two hox genes are expressed during urchin embryonic development, hox7 and hox11/13b. However, echinoid development is indirect. The sequence hox7, 8, 8/10, 11/13a, 11/13b is used, in an anatomically collinear way, and from mouth to anus, as the larva curls around the pentameric adult rudiment to form the radially symmetrical adult body. Arenas-Mena *et al*. (2000). What's more, all or almost all of the hox complement continues to be expressed in the adult.

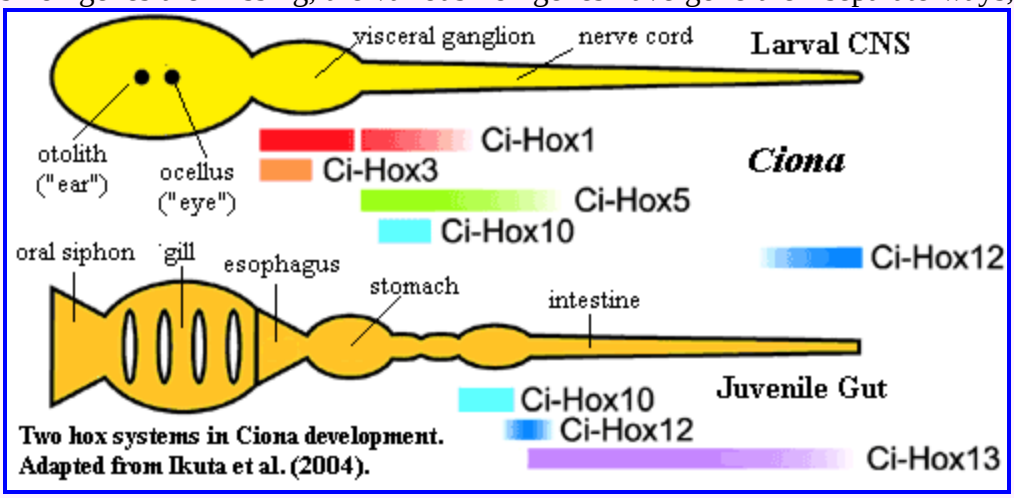


Hox expression in late larval development of the sea urchin. Richardson *et al.* (2005)

There seems to be a general tendency in the deuterostomes for hox1-3 to lie at some distance from hox5+, with hox4 variably placed nearer one group or the other. *See* several vertebrate examples in Kim *et al*. (2000). Perhaps this is related to the tagmatization of the head region in deuterostomes -- the development of the head as a very different part of the body. Yet hox3 seems to be a sort of weak link in the hox chain for all bilaterians. It simply manifests itself in different ways. In the sea urchin, a break here seems to have promoted radial symmetry. In the vertebrates, the development of the head. In arthropods -- but we are getting a head of ourselves, so to speak ...

We leave the bizarre Echinoidea with one random observation. Remember *Nematostella*, the other radially symmetrical animal we've discussed? Recall that evx was also adjacent to hox1 (but upstream) in the sea anemone, like the sea urchin. It's probably just a coincidence -- but curious all the same.

Like the sea urchins, urochordates (tunicates) develop indirectly, through a morphologically distinct juvenile stage. The tunicate juvenile is motile and has a distinctively chordate body plan. The adult is sessile and the body is laid out more along the lines of a mollusk. The hox clusters of urochordates are often said to have "disintegrated." Varying numbers of middle and/or posterior class hox genes are missing, the various hox genes have gone their separate ways, and genetic colinearity tends to be lost. These trends are taken to extremes in the larvacean *Oikopleura*, which has only one remaining middle class hox and no contiguous hox genes. However the Larvacea tend to be extreme minimalists, often dispensing with whole organ systems (heart, gills, etc.) and great swathes of DNA, in a profligate manner entirely unbecoming of a chordate. Swalla *et al*. (2000).



Two hox systems in Ciona development. Adapted from Ikuta et al. (2004).

Ciona, an ascideacean, takes a more restrained approach. Its hox genes are split up among five clusters, and a number of central and posterior elements are lost. However,*Ciona* retains a peculiar kind of morphological colinearity. Ikuta et al. (2004). As the diagram indicates, the Ikuta group argues that two separate hox programs are being run off the same set of hox genes: one establishes the larval central nervous system, while the second patterns the juvenile gut. From the figures, we speculate that perhaps there is yet a third hox program which works in the larval head at metamorphosis (see additional figure from Ikuta *et al*.).

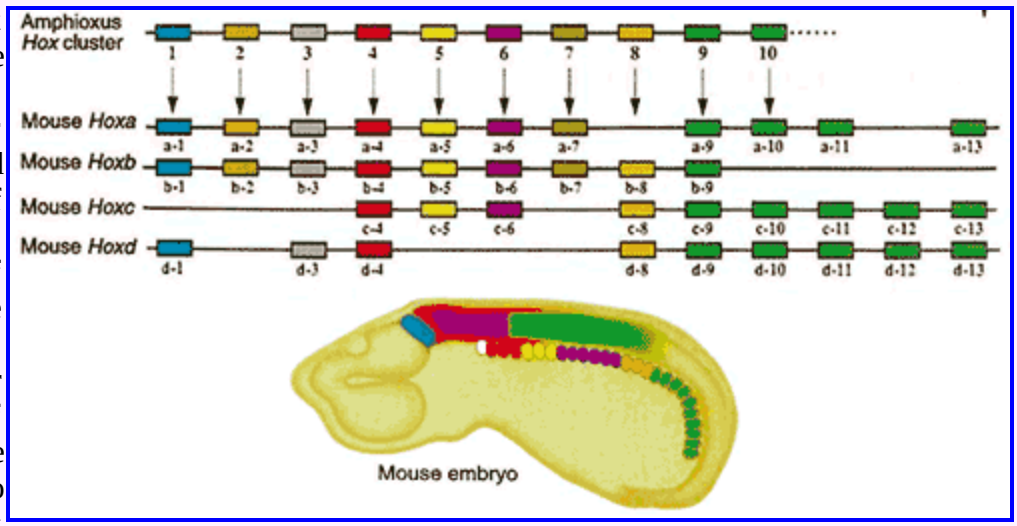
Again we find that genetic and anatomical colinearity are not tightly related. The genetic grouping (hox1, hox2-4, hox5-6, hox10, hox12-13) isn't correlated in an obvious way with any of the developmental programs. On the other hand, perhaps *Ciona* suggests something about the echinoids. It is interesting that two groups of organisms, both of which go through extremely

Ciona larvae, showing pattern of expression of hox1-5 by whole mount in situ hybridization. From Ikuta et al. (2004). Hox10 is also expressed at this stage. Scale bar = 100µ.

indirect development, both also have fractured hox clusters. As we'll see, indirect development and hox rearrangement are not Siamese twins, joined at the hip, but they are sufficiently correlated to be more than casual acquaintances. It may be a natural (but not inevitable) result of running multiple genetic programs off the same set of hox genes.

By contrast to urochordates, the cephalochordate *Branchiostoma* (= amphioxus) has the archetype of all hox systems: a single, unbroken cluster of 14 hox genes, all neatly arranged in order.

Vertebrates

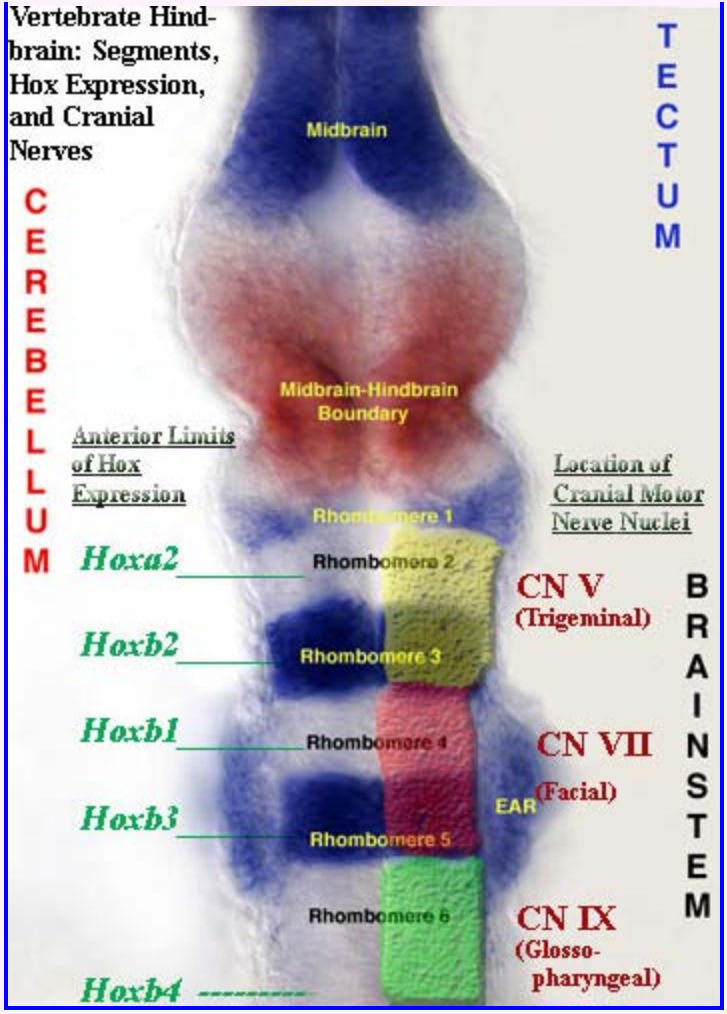


We're going to have to weasel out here. We will not attempt to cover the vertebrates in detail. This is the *In*vertebrate section of Palaeos, after all. That is a reasonable excuse – and almost credible. Can we help it if vertebrate hox systems just happen to be the most complex and difficult of the lot? Of course not! It's mere coincidence, completely unrelated to cowardice, indolence **[9]**, or other (entirely suppositional) defects of character. Nonetheless, even given the best of excuses, we're going to have to include some bullet points about vertebrates, just to avoid spiteful rumors.

1) Vertebrates have several hox clusters: We don't mean they have a single cluster which has fragmented. Vertebrates have several, more or less complete, collinear clusters of hox genes. By convention, these are referred to as hoxa, hoxb, etc. Vertebrates have four of these clusters, except actinopterygians, which have six or more. Generally, each of the *paralogous groups* will be missing a few of the individual elements. The image of the *Mus* hox system is adapted from Carroll (2005). Variations may be found wherever fine textbooks are sold.

Some workers lept from finding multiple paralogue groups to the conclusion that the entire hox system, or even the entire vertebrate genome, was duplicated in two gigantic attacks of chromosomal schizophrenia. Amores *et al*. (1998); Monteiro & Ferrier (2006). We can't say that cooler heads have already prevailed, but a far more cautious approach seems to be in the wind. Chiu *et al*. (2004); Donoghue & Purnell (2005)*.

2) The mouse image is ludicrously over-simplified: If you really want to know what the vertebrate hox expression system looks like, at least in the head region, look at Figure 4 in Kuratani (2005)*. Here's a direct link. Dr. Kuratani writes at least one review a year on this topic, and this is an easy way to keep up with what's going on. The equivalent of Kuratani's figure 4 has appeared in most of these reviews. It has become increasingly complex over the years. The actual hox expression patterns depend on dorsoventral level, on paralogue group, on germ layer, and on the nomadic migrations of neural crest cells as thasy drip down the sides of



the embryo like streams of wax from a candle.

3) Vertebrates have a large anterior hox-free zone: This zone is better known as the brain, except that hox genes are expressed in the hindbrain. Most, and perhaps all, bilaterians seem to share this hox-free brain. Arendt & Wittbrodt (2001)*. The anterior brain and sensory apparatus seems to depend on this hox-free zone. This zone is "patterned" by other homeobox genes, most notably genes of the otx and pax series. Couly et al. (2002)*; Ghysen (2003).

4) The hindbrain is a hox zone: Vertebrate hindbrain development involves a complex interaction between hox genes, mostly of the hoxb paralogy group, the "segments" of the hindbrain (*rhombomeres*), and the anatomically critical cranial motor nerves. The figure is based on an image from Prof. Andrew J. Waskiewicz of the University of Alberta, supplemented with information from Murakami *et al*. (2003)*, Carroll (2005), and Liem *et al*. (2001). Notice that hoxb2 is expressed anterior to hoxb1. As we've mentioned, such exceptions to anatomical colinearity are extremely rare.

The details vary somewhat among vertebrates (Murakami *et al*., 2003), but the general pattern is remarkably constant. Nevertheless, it is not a holdover from some primitive deuterostome segmentation pattern. The urochordates and cephalochordates show the beginnings of a vertebrate-like system of cranial nerves and midbrain structures, with some of the associated homeobox expression domains. However, neither displays hindbrain segmentation. Murakami *et al*. (2003); Dufour *et al*. (2006).

5) Vertebrate posterior hox genes are also used to mark the long axis of limbs: Hox genes are frequently re-used for other purposes, late in development. However, so far as we know, this is the only bilaterian case in which the hox *system* is used to mark out an axis other than the main anteroposterior axis of the body. The use of hox genes to elaborate the proximo-distal axis of limbs seems to be an accretion to the more typical limb-building toolkit involving the use of the dlx family of homeobox genes (e.g. *distalless* in *Drosophila*). This is particularly interesting in that vertebrate hox and dlx also work together in the branchial/hindbrain area. These dlx genes mark the dorsoventral axis, while the hox genes "pattern" the anteroposterior axis. Carroll (2005).

The lessons from vertebrates are not clear. Does the hox system have something to do with metamerism (segmentation by generation of repeated units)? If so, what relationship? Hox genes are not known to be directly involved in segmentation in any organism. In any case, segmentation proceeds (if at all) by entirely different routes in different organisms. On the other hand, a reasonably well-developed hox system may be a necessary precondition to metamerism. It is particularly interesting that the development of multiple paralogue groups seems to coincide roughly with the development of multiple, overlapping systems of metamerism. That is, most of the vertebrate body plan (the dorsal part, at least) is based on a metameric pattern of somites, mesodermal aggregates which run down the back like a double row of buttons. However, the hindbrain and brainstem area has an apparently unrelated segmentation based on metameric rhombomeres, while the gill region is subdivided yet a third way by gill arches **[10]**. What about other segmented critters?

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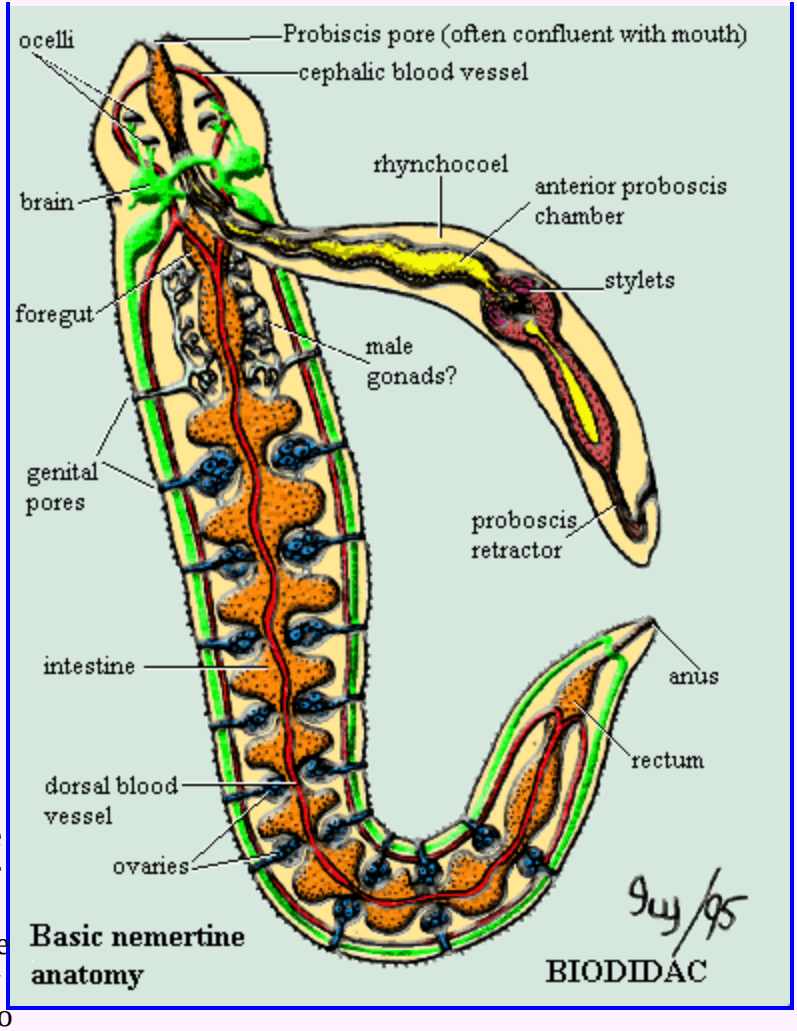
Hox Genes - 4

Slugs, Worms ...

As we've mentioned, the phylogeny of Bilateria is undergoing a sort of counter-reformation, so it is appropriate that we begin with a Diet of Worms. Actually, we have always entertained unorthodox ideas about the nemertine (= nemertean) worms. You will be thinking that no one is to be trusted who spends *any* amount of time pondering the nemertines. Perhaps you are correct. In fact, we gave up nemertines for a number of years when the winds of phylogenetics blew them away from the key position we thought they might occupy. Now, Nemertini (= Nemertea, Nemertinea, or even Rhynchocoela) may return to a place very near to *Urbilateria*.

Nemertines are long, sometimes absurdly long (30m!), non-segmented worms. They are often brightly colored and very thin -- hence the name "ribbon worm" (= "ribbonworm"). They are armed with something resembling a single enormous nematocyst, essentially a harpoon gun. Anatomically, they're rather basic except



for the rhynchocoel. For much more (and better) information, see the Nemertes site.

Kmita-Cunisse *et al*. (1998) found that the nemertine *Lineus* had (probably) a single hox cluster with six (or possibly seven) hox genes. Oddly, the *Lineus* hox genes fell into homology classes 1, 3, 4, 6, 7, and 9. The absence of a hox2 homologue is peculiar, since we know that hox2 was one of the first homology groups to evolve. In addition, Kmita-Cunisse *et al*. note that almost all of the hox protein sequences are closer to *Branchiostoma* and vertebrates than to *Drosophila*. However, these are raw "percentage identical amino acid" scores. They are not particularly meaningful where, as here, the difference is generally 1-2 residues.

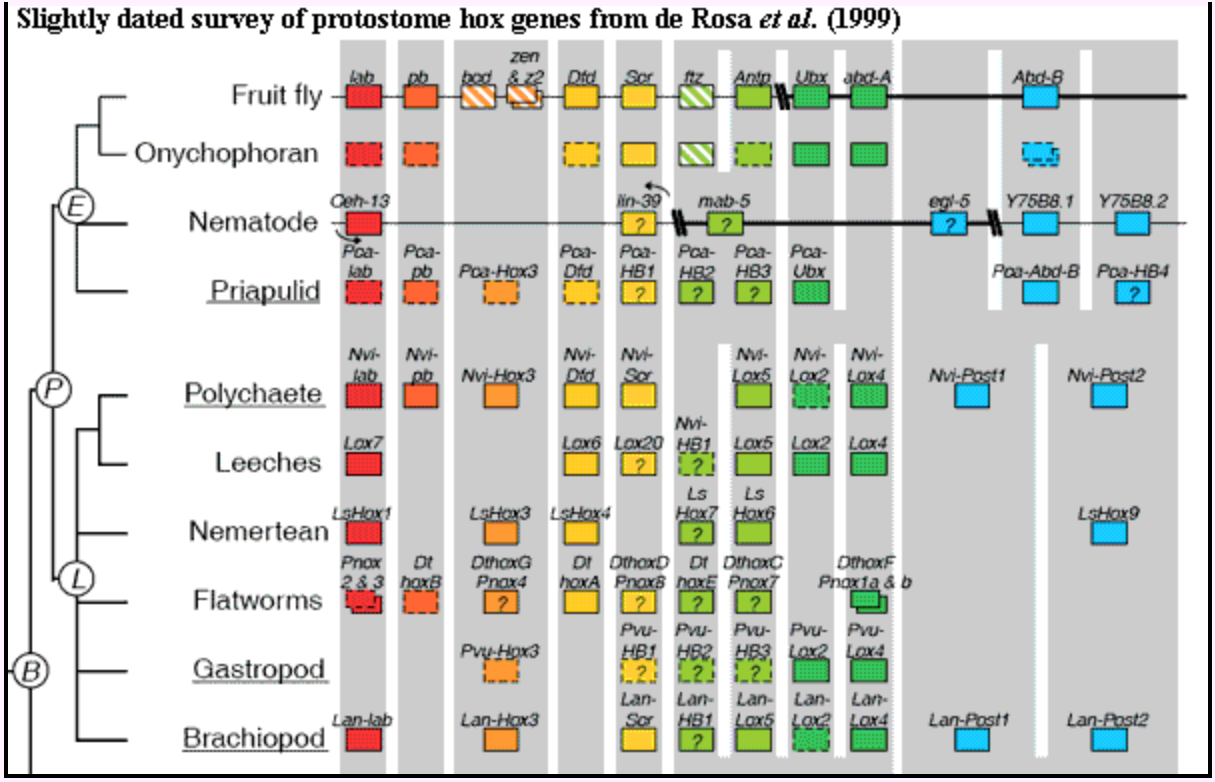
The Chaetognatha are another heretical phylum. Chaetognaths ("arrow worms") are constructed a bit like chordates who have somehow been rotated through varying angles. They have a caudal fin, but it is horizontal, rather than vertical. They have something resembling a notochord, but it is ventral. Historically, they were regarded as aberrant deuterostomes, but have recently moved in with the bugs and slugs.

Like *Lineus*, the chaetognath *Spadella* has a single, well-organized hox cluster with seven hox genes. These again include only one anterior gene, one hox3, four middle class genes, and a "mosaic gene that shares features of both median and posterior classes." Papillon *et al*. (2005).

To sum up, the two best-known lophotrochozoan hox systems seem to share the following features:

(a) absence of a hox2 homologue,
(b) middle class hox genes are numerically dominant,
(c) a maximum of 2 posterior hox, and
(d) a single hox cluster (maybe).

The pattern holds, in a smudgy kind of way, over the entire clade. Unfortunately, the exceptions are

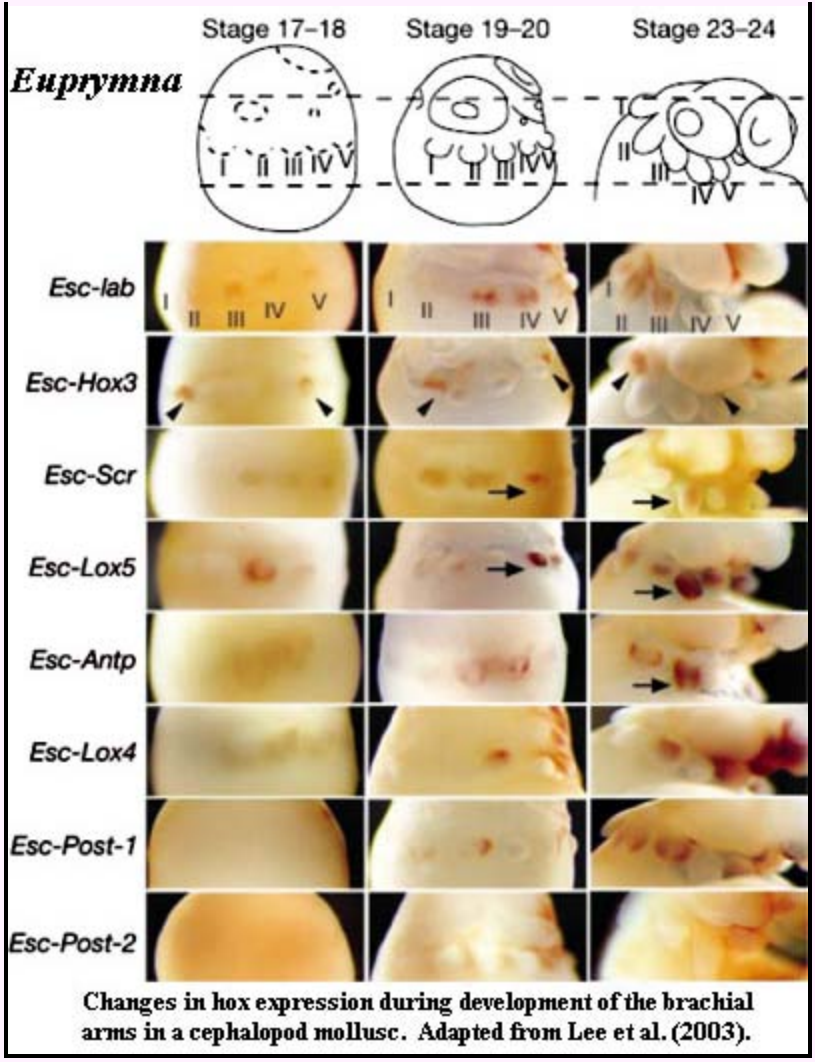


significant. As you have probably realized, precious few generalizations in hoxworld can survive contact with phylogenetics. The hox data is wrong, the phylogenies are wrong, or hox genes are oddly *homoplastic* -- probably a bit of all three.

In particular, hox2 homologues have been reported from the gastropod *Haliotis*, and several polychaete worms (*e.g.*, *Chaetopterus*). On the other hand, no hox2 homologue is known from cephalopod molluscs, the basal eogastropod (limpet) *Patella*, non-polychaete annelids (e.g., the leech *Helobdella*), or the brachiopod *Lingula*. Lee *et al*. (2003); Callaerts *et al*. (2002); Irvine & Martindale (2001); Peterson *et al*. (2000); Shankland & Seaver (2000) de Rosa *et al*. (1999). Where it does show up, the lophotrochozoan hox2 tends to be peculiar. For example, in several cases, only part of the gene was found. Callaerts *et al*. suggested the presence of an unusual *intron*, although this should only be an issue for methods which rely on expressed RNAs. In other cases, the pattern of expression is anomalous. The hox2 homologue is expressed at an unexpected point in development and in a large area not easily related to any anatomical pattern of colinearity.

The remaining characteristics are more consistent, but less distinctive. Callaerts *et al*. (2002) believe that the ancestral mollusk had five central class genes, i.e. the full complement for Bilateria. However, it is far from clear that these are the *same* five genes which were inherited by deuterostomes, or even by arthropods. We understand that more recent work may actually increase the number of basal molluscan genes, but we have no details.

The real problem with molluscan hox systems is that molluscs have completely lost interest in traditional anteroposterior colinearity. This is not very surprising, since many molluscs practice a sort of developmental yoga which inspires them to contort the body axis in ways otherwise known only to devotees of the *Kama Sutra*. Perhaps for this reason, molluscs tend to use hox systems for spatial patterning in very precise ways, often involving multiple programs, as in *Ciona*. However, unlike the urochordate case, none of the molluscan programs could reasonably be described as colinear, or even anteroposterior. In fact, some of the programs seem to involve hox combinations which change over time, as well as space.



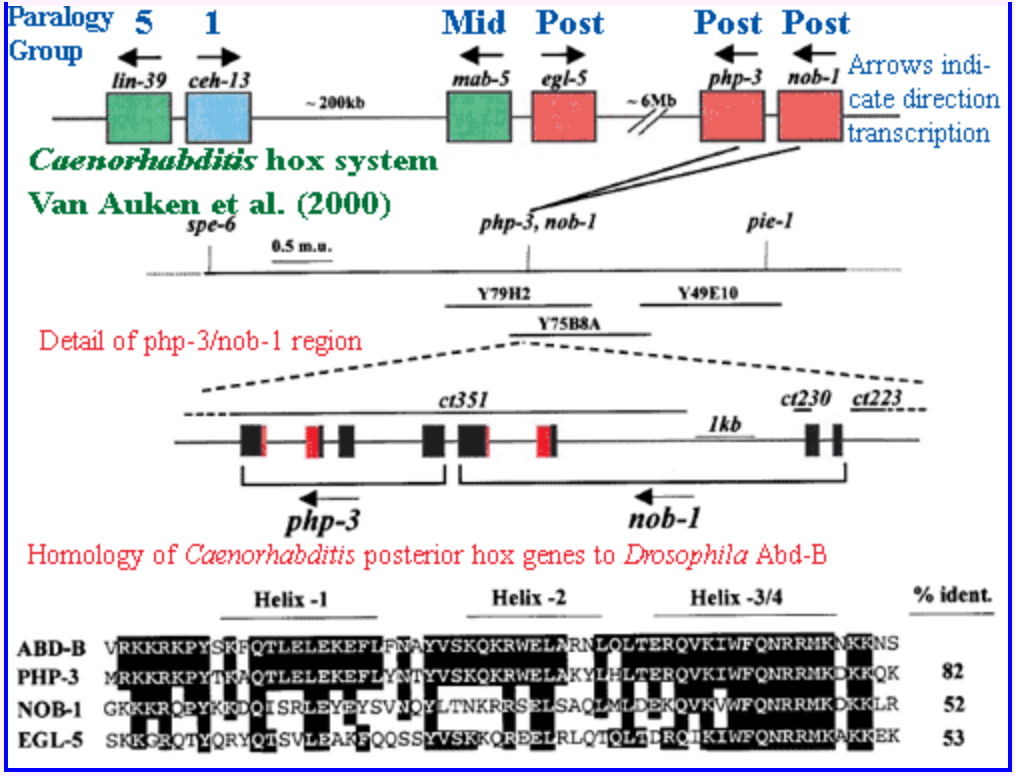
Changes in hox expression during development of the brachial arms in a cephalopod mollusc. Adapted from Lee et al. (2003).

As with the more ambitious *asana* of the *Kama Sutra*, it isn't obvious how molluscs got into this position. Pappillon *et al*. (2005) make the interesting observation that mesodermal hox expression, particularly central hox expression is related to segmentation. The correlation between mesodermal hox expression and segmentation does seem to hold for lophotrochozoans. In fact, it holds reasonably well everywhere except in the sea urchin, in which all organized hox expression is mesodermal, despite the lack of segmentation. Arenas-Mena *et al*. (2000). Saying anything this definite about hox systems causes us no end of angst. We can only state that we spent the better part of a day checking the last couple of sentences, and could find no other exception. In particular, we were unable to identify *any* taxon with metameric segmentation but without mesodermal hox expression. At the same time, none of the various known molecular systems for segmentation involve hox genes, mesodermal or otherwise. Seaver (2003).

Lophotrochozoans are very poorly known, particularly considering how common, diverse, and significant they are. The evo-devo literature about them therefore tends to resemble the state of *vertebrate* evo-devo, circa 1990, including a great many fascinating, isolated factoids connected only by gossamer filaments of speculation. We leave the subject with one of these random gleanings. Like vertebrates, the cephalopods have evolved large eyes and substantial forebrains. In vertebrates, these critical novelties are developed in a hox-free anterior zone. Notwithstanding the very different workings of cephalopod hox systems, the eyes and forebrain (i.e., the cerebral ganglion) are likewise developed in a special, hox-free anterior zone. Lee *et al*. (2003).

... and More Worms ...

We're going to rip through the rest of the animals like a kangaroo on a pogo stick. We take this shortcut for a variety of discordant reasons. First, the arthropod (and related) systems have been intensively studied and the relationship of arthropod hox systems to the arthropod body plan is very well known. Carroll (2005) explains the

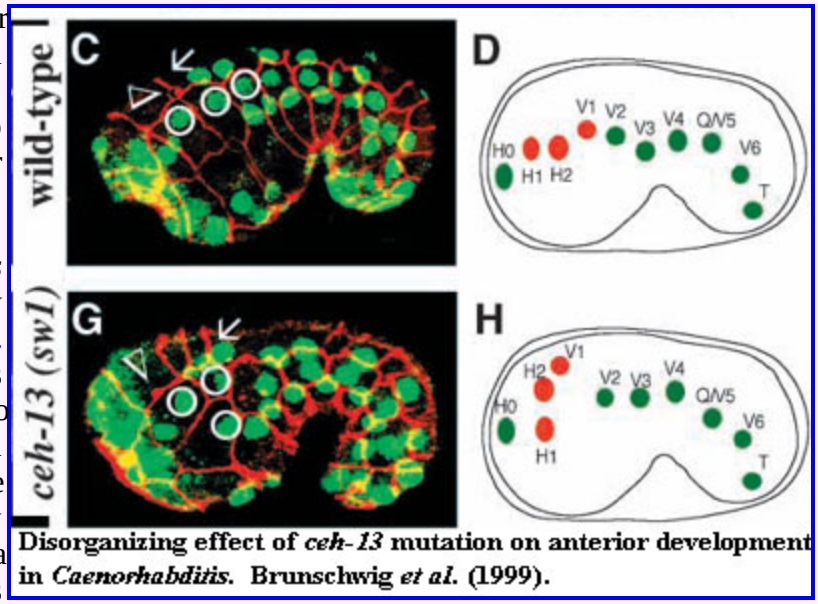


whole thing in detail. Any attempt to redigest his very accessible writing on this topic would be pointless -- and, more to the point, boring for us. Second, we took on the hox project because we found we couldn't write a section on Crustacea without a clearer understanding of hox systems. Our crustacean section will therefore cover that region of arthropod phylospace, including more basal arthropods.

That leaves us with the base of the arthropod clade and the non-arthropod Ecdysozoans. This region consists largely of nematodes and is scientifically pathological. Much of the literature in that area is based on (a) phylogenetic assumptions that are contentious (Peterson *et al*., 2005) or (b) on *Caenorhabditis*, which turns out to be somewhat aberrant, even for a nematode (*see, e.g*., Valentine *et al*., 1999).

The hox set of *Caenorhabditis* is reduced and scrambled. Cook *et al*. (2004). *Caenorhabditis* has six hox genes, plus the usual three parahox genes. Saló *et al*. (2001). They are all found on one chromosome, but in three, widely-spaced pairs. Van Auken *et al*. (2000). In fact, none of the hox genes are particularly closely spaced except the *php-3 + nob-1* pair which are separated by only about 200 base pairs. *Id*.

The homology of the nematode genes is weak in comparison to most of the others we have looked at. The hox1 homologue (*ceh-13*) is the closest to the general run of hox genes. *Lin-39* has been somewhat ambiguously described as "an orthologue of pb, Dfd and Scr." Brunschwig *et al*. (1999). That is to say, it isn't even certain whether the gene is an anterior or middle class hox. Of the posterior genes, *php-3* seems to reasonably close to the typical Abd-B gene of *Drosophila* and other ecdysozoans. The other two posterior genes are not closely related to anything, including the two characteristic posterior genes of lophotrochozoans. de Rosa *et al*. (1999).



Disorganizing effect of *ceh-13* mutation on anterior development in *Caenorhabditis*. Brunschwig *et al*. (1999).

A number of workers have argued that *Caenorhabditis* hox expression is, at least in part, anatomically colinear. Brunschwig *et al*. (1999); Wittman *et al*. (1997); Van Auken *et al*. (2000). While there is certainly something to this, we recommend a trip to WormBase, and a brief perusal of the expression patterns for any of the *Caenorhabditis* hox genes. The patterns are complex -- specific, but not easily characterized as "anterior" or "posterior," except in a rather general sense. Then again, perhaps this is actually the case with hox expression in most animals and is only obvious in *Caenorhabditis* because it is the most completely characterized animal developmental system.

At least some of the *Caenorhabditis* hox genes seem to operate by controlling cell motility and cell-cell interactions, rather than cell fates. Eisenmann *et al*. (1998) (*lin-39*) (*but c.f*. Yang *et al*., 2005); Brunschwig *et al*. (1999) (*ceh-13*); Pearson *et al*. (2003) (*lin-39* and *mab-5*). We thought that this sounded like an interesting possibility for the basal function of hox genes. Unfortunately, it turns out that*Caenorhabditis* hox are not only unusual, but relatively

unimportant. In fact loss of function mutations are lethal only for *ceh-13* (hox1) and a small proportion of *php-3* and *nob-1* mutants. Van Auken *et al*. (2000). As these authors point out, the posterior hox mutants are *hypomorphs*. That is, the posterior hox genes seem to act in a quantitative way, so that loss of function only downregulates the expression of other genes. The hox genes are not acting as on/off switches, as they often do in more conventional hex systems.

... and More ... Later

Obviously, we've left off the critical arthropods. We'll get to them, and a conclusion, after we take time out to do the crustaceans.

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Spicule Terms

LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Lophotrochozoa

Introduction

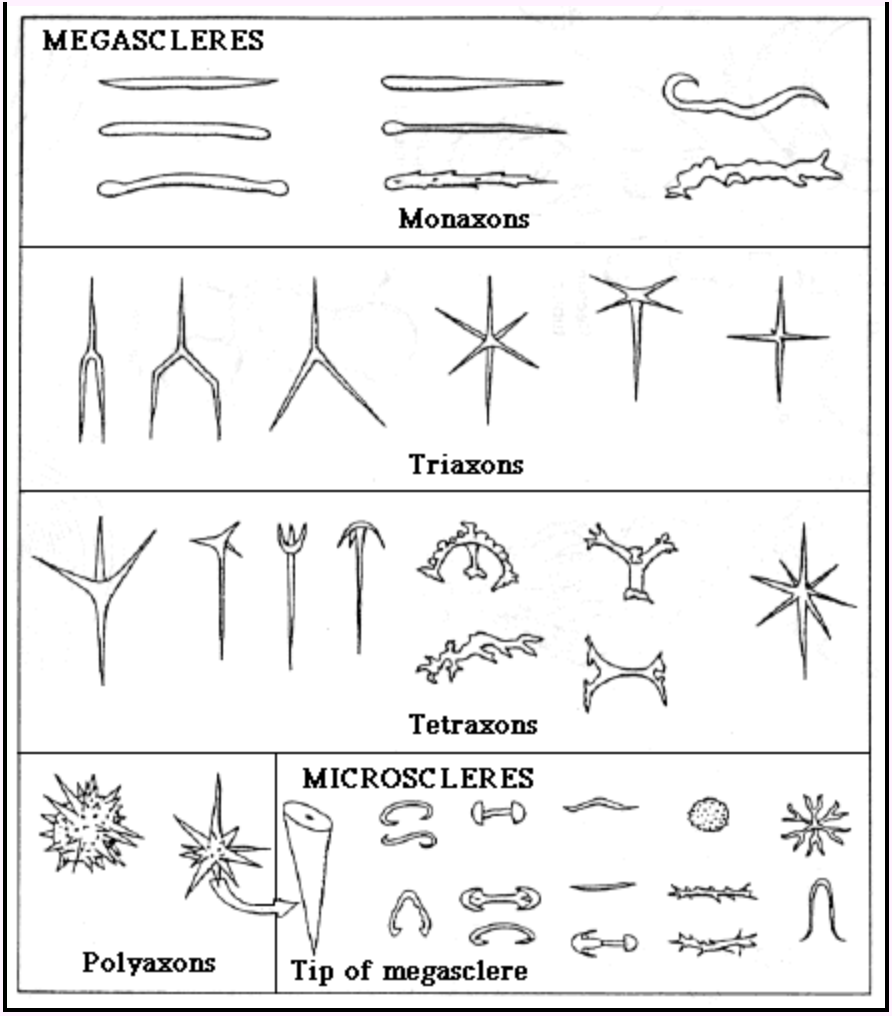
Introduction

While we were doing the research for this page, we came across a much better on-line source of information than we could ever produce. Thus, we will keep this page short, and commend any readers to **Guideline to the morphological species description for the Sponge Barcoding Database (SBD)**. That site also refers to Hooper (2000), which is an excellent source, but the web version of Hooper's work has no illustrations. The Guideline has illustrations but no written definitions. For the most part, you won't need written definitions, but they are useful for getting grounded in the system. Hence, we supply the following as a sort of introduction to the most basic terms. Another useful source for spicule terms is Andri *et al*. (2001). It is most easily used in HTML format at **this link**. A useful review of sponge spicules in general, but not so convenient for issues of terminology, is Uriz (2006).

Actually, there ought to be some way of discussing sponges without getting enmeshed in the terminology of spicules. We actually tried to do this, but ultimately failed. The subject can't be ignored, won't fit in a glossary entry, and is simply too boring to slip into some phylogenetic discussion. We will restrict the discussion to megascleres -- the large, structural spicules. Megasclere terms are built from (a) a numerical prefix, (b) a structural suffix, and sometimes (c) some sort of language-specific grunt at the end.

Prefixes: nothing peculiar here, except the unholy mixture of Latin and Greek roots:

Mono- = 1
Di- = 2
Tri- = 3
Tetr- = 4



Hex- = 6

Suffixes: this is where it gets trickier. Many sources and some textbooks confuse these three:

-actine = rays
-axon = axes
-radiate = rays in a single plane

Grunts: ignore these

-id
-ic
-oid
-al (unnecessary sur-suffix for adjectives)

A "ray" or *actine is* supposed to refer to a growth zone. That is, a ray theoretically represents the position of one terminal *sclerocyte* (spicule-forming cell). Unfortunately, that particular theory can be difficult to put into practice. Multiple sclerocytes often cooperate on a single growth zone, split up to form branches or forks, or just wander around doing maintenance.

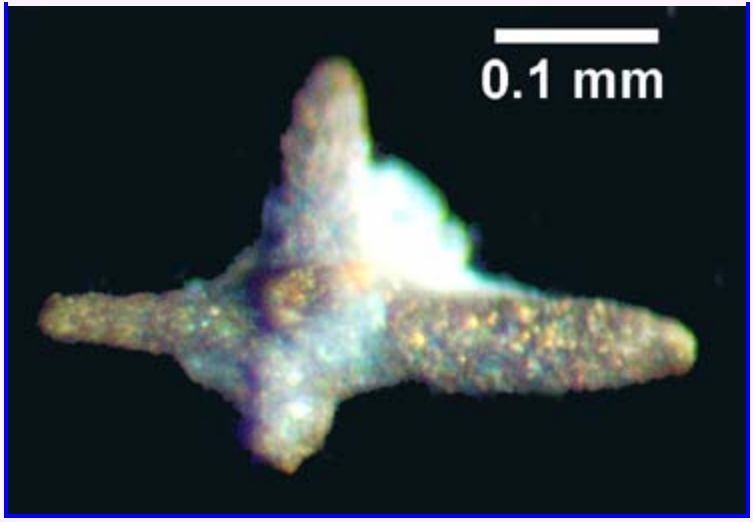
A more practical (and biologically reasonable) way to rationalize the nomenclature is to imagine each spicule element as an *axis* emanating from the center of the spicule. If the axis grows in only one direction out from the center, it is monactine. If the axis grows also grows *in the opposite direction*, it is diactine. So far as we know, these are the only two possibilities for sponge spicules.

Perhaps there are sponges out there which build boomerang-shaped axes which curve sharply at the center, so that the two ends do not grow in opposite directions. Too bad. It will probably be described as diaxonic, not diactine. That is, it will be conceived as having two separate axes, rather than a single, curved axis with two growing ends.

Further, it makes no difference whether the axis curves, branches, or forks beyond the center. Suchornamentation, however Baroque, does not alter the count of either rays or axes. **[1]**.

The system becomes a bit ambiguous in a number of cases. For example, some spicules look like a trident, with one long ray and three short, curved rays at one end. Is this a tetraxon, or perhaps an ornamented diactinic monaxon? The tendency is to treat such cases as tetraxons.

Finally, We have found one special case, with no obvious explanation. If we ever find the explanation, we will add it here. This case deals with an apparently simple tetraradiate diaxon: a '+' sign configuration. This is frequently classified as a triaxon. One possible reason is that spicules are small and fragile. Particularly with fossil materials, it can be impossible to tell whether the spicule is actually a tetraradiate diaxon, or the broken remains of a (much more common) hexactine triaxon (see image for an example). Unfortunately, the latter are diagnostic of Hexactinellida, so this practice can lead to problems.



[1] If we were able to write our own spicule nomenclature, we would include the terminology of Baroque ornamentation. This would allow for curved axes (*appoggiaturi*), terminal splitting (*mordents*), irregular turns (*turns*), and little sprays of spikelets (*trills*), all of which are as common in sponges as in Scarlatti.

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Notes & References

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LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Lophotrochozoa
```

Notes

[1] We know of two exceptions, both highly aberrant cases: in sea urchins (Echinoidea) and in vertebrates. Both are discussed later.

[2] But see the discussion by Bengston & Budd (2004), Chen et al. (2004a).

[3] Actually we still do -- but not bilaterian segmentation. However, the idea is too incomplete and too speculative to take up here.

[4] Much of this section of the paper simply confirms earlier work by others. However, since we knew very little about either anthozoans or hox genes before starting on this piece, it was very useful to have everything in one place.

[5] Main *Nematostella* hox cluster, adapted from Ryan *et al*. (2007):

[6] The Barcelona Group apparantly uses "Bilateria" to mean some kind of stem group – possibly Nebuchadnezzar > *Nematostella*. Consequently, they still refer to the Acoelomorpha as bilaterians. We will stick to the usual, crown-group definition of Bilateria.

[7] Like the echinoid hox genes, the order of the authors seems to have been altered in the course of this paper's evolution. The "suggested citation" is followed here. However, on the actual paper, the authors appear in the order:

Cameron, Rowen, Nesbitt, Bloom, Rast, Berney, Arenas-Mena, Martinez, Lucas, Richardson, Davidson, Peterson & Hood.

[8] Note that the phylogenetic position of the Vetulicolia is much more debatable than our treatment might suggest. Aldridge *et al*. (2007) suspect that that they are basal protostomes of some kind. We have some methodological uncertainties with Aldridge *et al*., but they include a very useful discussion of all the possible affinities of this group. For a contrasting view, *see* Shu (2005).

[9] "There is no work that affects me; nor do I aspire for the fruits of action. Who knows me acting thus unchained by action, is not tied down by actions." **Bhagavad Ghita** 4:14. Actually, this is a mixed translation. It has absolutely nothing to do with hox systems. However, we can't help comparing this portion of the *Ghita* to the Taoist principle (or, if you're a *real* Taoist, non-principle) of *wu-wei*.

[10] To be fair, lots of respectable people believe that rhombomeres are merely an extension of the somites, and no one doubts that the gill arch ("branchiomere") system is very closely coordinated with the rhombomeric system. Thus Liem *et al*. (2001), for example, treat the whole thing as one system of segmentation. We strongly disagree. More importantly, so do a lot of respectable scientists, *e.g*. Janvier (1996).

[11] That isn't quite right, but a more precise definition requires a lot more explanation than we can give until we've covered a lot more ground. A completely unambiguous definition is still not possible, but a *better* definition might be: the last common ancestor of *Drosophila lab* and *Branchistoma hox14* and all of its descendants which (a) encode a homeodomain-containing protein and (b) whose closest homologue in *Branchiostoma* lies within the *Branchiostoma* hox cluster. The exceptions are needed to exclude pseudogenes and other non-functional riff-raff, as well as the parahox genes discussed later. It is still ambiguous because we don't define *gene* (introns? promoters? miRNA sequences?) and we don't say exactly what *closest homologue* means.

[12] Update 070712: According to a report, two recent papers in **Cell** by Gregor et al. emphasize how very preceise the maternal *bicoid* gradient is and how carefully it is maintained in early embryogenesis. Again, if so, why do flies need hox genes? We have not read the papers, but the citations are T. Gregor et al., "Stability and nuclear dynamics of the Bicoid morphogen gradient," **Cell** July 13, 2007 and T. Gregor et al., "Probing the limits to positional information," **Cell**, July 13, 2007.

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Invertebrate Taxa

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LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```

Editor's note

This page is in the process of being revised, but is posted as is for now as a holding page and to provide links to other pages. Because Palaeos com is still under construction and major revision, not all links given here work. MAK120115

A

Acaenoplax: (Mollusca: Solenogastres) *see* Solenogastres.
Acantherpestes: X (Arthropoda: Myriapoda). *See* Myriapoda.
Acanthocephala: (Ecdysozoa?). *See* Bilateria.
Acanthochaetetes: (Porifera: Demospongiae), *see* Stromatoporoidea.*
Acaroceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Acfinosfromaria: X (Porifera: Stromatoporoidea?), *see* Stromatoporoidea.
Acila: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Acleistoceratidae: X? (Mollusca: Cyrtosoma: Nautiloidea). *See also*, Nautilida.
Acmacoidea: (Mollusca: Gastropoda: Patellogastropoda).
Acmaea: (Mollusca: Gastropoda: Patellogastropoda), *see* Patellogastropoda.
Acmaeidae: (Mollusca: Gastropoda: Patellogastropoda).
Acoela: (Acoelomorpha) *See* Bilateria.

Acoelomorpha: *See* Bilateria, Hox Genes.
Acrotheloidea: X (Lophotrochozoa: Brachiopoda: Linguliformea), *see* Discinida.
Acrotreta: X (Lophotrochozoa: Brachiopoda: Linguliformea) *see* Acrotretida.
Acrotretida: (Lophotrochozoa: Brachiopoda: Linguliformea).
Acrotretoidea: X (Lophotrochozoa: Brachiopoda: Linguliformea) *see* Acrotretida.
Actinoiceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Actinocerida: X (Mollusca: Cyrtosoma: Cephalopoda).
Actophila: (Mollusca: Pulmonata)
Agathylla: (Mollusca: Pulmonata), *see* Stylommatophora.
Aglaspida: X (Arthropoda: Chelicerata?) *see* Xiphosura.
Ajacicyathida: X (Porifera: Archaeocyatha) *see* Archaeocyatha, Irregulares.
Ajacicyathina: X (Porifera: Archaeocyatha) *see* Archaeocyatha.
Aldanella: X (?), *see* Gastropoda.
Aldanellidae: X (?), *see* Paragastropoda.
Allonia: X (Porifera: Chancelloriidae), *see* Porifera*.
Ambulacraria: *see also* Deuterostomia.
Ammonoidea: (Mollusca: Cyrtosoma: Neocephalopoda)
Amphibolida: (Mollusca: Pulmonata), *see* Basommatophora.
Amphidiscophora: (Porifera: Hexactinellida), *see* Hexactinellida.
Amphimedon: (Porifera: Demospongiae) see Porifera*
"Amphineura": (Mollusca), *see* Polyplacophora.
Amphipora: X (Porifera: Stromatoporoidea.
Amynilyspes: X (Arthropoda: Myriapoda). *See* Myriapoda.
Angulospira: X (Mollusca: Gastropoda: Paragastropoda), *see* Atracurinae.
Anatina: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Anodonta: (Mollusca), *see* Bivalvia.
Anomalocystis: *X* (Homalozoa: ?) *see* Homalozoa
Anomalodesmata: (Mollusca), *see* Bivalvia. *See also*, Bivalvia Dendrogram.
Anomia: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Anthozoa: (Cnidaria). See also Hox Genes.
Antigyra: X (Mollusca: Gastropoda: Paragastropoda), *see* Atracurinae.
Antispira: X (Mollusca: Gastropoda: Paragastropoda), *see* Onychochilidae.
Antizyga: X (Mollusca: Gastropoda: Paragastropoda), *see* Atracurinae.
Aphetoceras: X (Mollusca: Cyrtosoma: Nautiloidea), *see* Tarphycerina.
Aphrocallistes: (Porifera: Hexactinellida), *see* Hexactinellida*.
Apoptopegma: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Arca: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Arceodomus: X (Mollusca: Rostroconchia), *see* Conocardioida.
Archaeocyatha: X (Porifera). *See also*, Stromatoporoidea
Archaeocyathida: X (Porifera: Archaeocyatha) *see* Archaeocyatha.
Archaeocyathus: X (Porifera: Archaeocyatha) *see* Irregulares*.
"Archaeogastropoda": (Mollusca: Gastropoda) paraphyletic grade of basal crown gastropods. *See* Macluritoidea.
Archaeolynthus: X (Porifera: Archaeocyatha) *see* Irregulares*.
Archiacoceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Archiscudderia: X (Arthropoda: Myriapoda). *See* Myriapoda.
Arcoida: (Mollusca), *see* Bivalvia.
Arionoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda).
Arkarua: *X* (Metazoa, *incertae sedis*)
Armenoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Artemia: (Crustacea: Branchiopoda) see Crustacea*.
ARTHROPODA: (Protostomia) See also Hox Genes.
Ascoceras: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Ascocerida.
Ascoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda)
Ascocerida: X (Mollusca: Cyrtosoma: Neocephalopoda)
Aspinoceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Astrosclera: (Porifera: ?!Stromatoporoidea) *see* Archaeocyatha.*
Atelocerata: Hexapoda + Myriapoda. Identical to Euarthropoda here. *See also*, Myriapoda.
Athyridida: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.

Atracura: X (Mollusca: Gastropoda: Paragastropoda), *see* Atracurinae.
Atracurinae: X (Mollusca: Gastropoda: Paragastropoda).
Atrina: (Mollusca), *see* Bivalvia.
Atrypida: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.
Atta: (Insecta) *see* Bilateria.
Augustoceras: X (Mollusca: Cyrtosoma: Nautiloidea), *see* Oncocerida.
Aulacera: X (Porifera: Stromatoporoidea) *see* Stromatoporoidea.*
Austrolimulidae: X? (Arthropoda: Chelicerata: Merostoma).
Autobranchia: (Mollusca), *see* Bivalvia.
Autolamellibranchia: (Mollusca), *see* Bivalvia. = Autobranchia.
Aviculopecten: (Mollusca: Bivalvia), *see* Bivalvia Shell.

B

Bactrites: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Bactritida.
Bactritida: (Mollusca: Cyrtosoma: Neocephalopoda)
Balkoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Plectronocerida.
Balkoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Baltoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Baltoeurypterus: X (Arthropoda: Chelicerata: Eurypterida), *see* Eurypterida.
Banffia: *X* (Deuterostomia?) *see* Vetulicolia.
Barrandeoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Barrandeocerina: X (Mollusca: Cyrtosoma: Nautiloidea).
Barroisella: X (Lophotrochozoa: Brachiopoda: Linguliformea) *see* Lingulida.
Basommatophora: (Mollusca: Pulmonata)
Bassleroceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Ellesmerocerida.
Basslerocerati dae: X (Mollusca: Cyrtosoma: Cephalopoda).
Bathmoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Bellerophon: X (Mollusca: Gastropoda: Tergomya). *See* Bellerophontida. *See also*, "Bellerophontiforms".
Bellerophontida: X? (Mollusca: Gastropoda: Tergomya). *See also* Coreospiridae.
Bellerophontidae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Bellerophontidea: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Bellerophontina: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Bellerophontoidea: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Bellinuridae: X (Arthropoda: Chelicerata: Merostoma).
Bellinurina: X (Arthropoda: Chelicerata: Merostoma).
Bellinuroopsis: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Bellinurus: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Bigalea: X (Mollusca: Rostroconchia), *see* Conocardioida.
Bilateria: starfish + silverfish, ***not*** Deuterostomia + Protostomia. *See also*, Deuterostomia.
Billingsites: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Ascocerida.
BIVALVIA: (Mollusca).
Bodospira: X (Mollusca: Gastropoda: Paragastropoda), *see* Atracurinae.
Botsfordioidea: X (Lophotrochozoa: Brachiopoda: Linguliformea), *see* Discinida.
BRACHIOPODA: (Lophotrochozoa), *see also* Stromatoporoidea.
Brachiospongia: X (Porifera: Hexactinellida), *see* Hexactinellida*.
Brachiozoa: *see* Deuterostomia.
Branchiopoda: (Crustacea) see Crustacea.
Bransonia: X (Mollusca: Rostroconchia), *see* Conocardioida.
Brevicoceratidae: X? (Mollusca: Cyrtosoma: Nautiloidea). *See also*, Nautilida.
Bryozoa: *see also* Stromatoporoidea.
Bucanella: X (Mollusca: Gastropoda: Tergomya). *See* Bellerophontida.
Bucanellidae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Bucaniidae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Buddenbrockia: (Myxozoa) *See* Bilateria.
Bunodes: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.

Bunodidae: X (Arthropoda: Chelicerata: Merostoma)
Bunodinae: X (Arthropoda: Chelicerata: Merostoma)
Burgundia: X (Porifera: Stromatoporoidea?), *see* Stromatoporoidea.

C

Caenorhabditis: (Nematoda). See Hox Genes*.
Calcarea: (Porifera). *See also* Archaeocyatha, Demospongiae, Stromatoporoidea.
"Calcichordata": *see* Homalozoa
Cambretina: X (Mollusca: Gastropoda: Paragastropoda), *see* Pelagiellida.
Cambropodus: X (Arthropoda: ?Myriapoda)
Canpbelloceras: X (Mollusca: Cyrtosoma: Nautiloidea), *see* Tarphycerina.
Capitella: (Annelida, Polychaeta) *See* Bilateria.
Carbactinoceratidae: X (Mollusca: Gastropoda: Paragastropoda)
Carcinoscorpius: (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Cardiomya: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Carnicoelus: *see also* Solenogastres
Carinaropsidae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Cassinoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Endocerida.
Castericystis: *X* (Deuterostomia: Homalozoa)
Cellana: (Mollusca: Gastropoda: Patellogastropoda), *see* Eogastropoda, Patellogastropoda.
Cenoceras: (Mollusca: Cyrtosoma: Nautiloidea), *see* Nautilida.
Centroonoceras: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Ascocerida.
Cepaea: (Mollusca: Pulmonata), *see* Stylommatophora.
Cephalocarida: (Crustacea) see Crustacea.
Cephalochordata: *see also* Deuterostomia.
CEPHALOPODA: (Mollusca: Cyrtosoma). *See also* Helcionelloida Dendrogram, Hox Genes, Rostroconchia.
Chaetognatha: *See* Bilateria.
Chaetopterus: (Annelida, Polychaeta) *See* Bilateria, Hox Genes.
Chancelloria: X (Porifera: Chancelloriidae), *see* Porifera*.
Chancelloriidae: X (Porifera?), see Archaeocyatha, Porifera, Porifera Dendrogram.
Chaetoderma: (Mollusca: Aplacophora) *see* Caudofoveata.
Chama: (Mollusca), *see* Bivalvia.
Cheilostomata: (Lophotrochozoa: Bryozoa)
CHELICERATA: (Arthropoda), *see also* Eurypterida.
Chihlioceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Chione: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Chippewaella: X (Mollusca: Gastropoda: Tergomya), *see* Tropidodiscidae.
Choanoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda)
Choanoflagellata: *see* Bilateria, Demospongiae.
Cincta: X (Deuterostomia: Homalozoa).
Clathryodictya: X (Porifera; Stromatoporoidea), see Stromatoporoidea.
Clinoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda).
Cliospira: X (Mollusca: Gastropoda: Paragastropoda), *see* Cliospirinae.
Cliospiridae: X (Mollusca: Gastropoda: Paragastropoda). *See also*, Macluritoidea.
Cliospirinae: X (Mollusca: Gastropoda: Paragastropoda).
Cloudia: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Cloudina: X (Metazoa *i.s.*) *see* Irregulares.
Cnidaria: (Metazoa: Radiata). *See also* Protostomia, Hox Genes.
Coleicarpus: *X* (Deuterostomia: Homalozoa).
COLEOIDEA: (Mollusca: Cyrtosoma)
CONCHIFERA: (Mollusca)
Conocardia: X (Mollusca: Rostroconchia) *see*, Rostroconchia.
Conocardioida: X (Mollusca: Rostroconchia). *See also*, Rostroconchia.
Conocardia: X (Mollusca: Rostroconchia), *see* Conocardioida.
Conoctisa: X (Mollusca: Gastropoda: Paragastropoda), *see* Trochoclisinae.

Consinocodium: X (Porifera: Stromatoporoidea), *see* Stromatoporoidea.*
Coreospira: X (Mollusca: Conchifera), *see* Coreospiridae.
Coreospiridae: X? (Mollusca: Conchifera).
Cornuta: X (Deuterostomia: Homalozoa), *see* Stylophora.
Corticium: (Porifera: Homoscleromorpha), *see* Homoscleromorpha.
Costipelagiella: X (Mollusca: Gastropoda: Paragastropoda), *see* Pelagiellida.
Cothurnocystis: *X* (Deuterostoma: Homalozoa) *see* Stylophora.
Crambe: (Porifera: Demospongiae: Ceractinomorpha: Poecilosclerida), *see* Homoscleromorpha.
Craniacea: X (Lophotrochozoa: Brachiopoda), *see* Craniiformea.
Craniida: (Lophotrochozoa: Brachiopoda)
Craniidae: X (Lophotrochozoa: Brachiopoda), *see* Craniiformea.
Craniiformea: (Lophotrochozoa: Brachiopoda).
Cranioposida: X (Lophotrochozoa: Brachiopoda)
Crassostrea: (Mollusca), *see* Bivalvia.
Crinoidea: (Echinodermata), *see also*, Stromatoporoidea.
CRUSTACEA: (Protostomia)
Crustaceomorpha: *see* Euarthropoda.
Cryptodonta: (Mollusca), *see* Bivalvia. *See also*, Bivalvia Gills.
Cryptostomida: (Lophotrochozoa: Bryozoa)
Crytolites: X (Mollusca: Helcionelloidea?) *see* Gastropoda.
Ctenocystis: X (Deuterostomia: Homalozoa) *see* Ctenocystoidea.
Ctenocystoidea: X (Deuterostomia: Homalozoa)
Ctenostomata: (Lophotrochozoa: Bryozoa)
Cuspidaria: (Mollusca), *see* Bivalvia.
Cyamocephalus: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Cycloidea: X (Deuterostomia *incertae sedis*), *see* Homalozoa: Haplozoa
Cyamoidea: X (Deuterostomia *incertae sedis*), *see* Homalozoa: Haplozoa
Cyclestheria: (Crustacea: Branchiopoda) See Crustacea*.
Cycloholcus: X (Mollusca: Conchifera), *see* Coreospiridae.
Cyclomedusa: X (Ediacaran) *See* Bilateria.
Cyclopectoceras: X (Mollusca: Cyrtosoma: Nautiloidea), *see* Tarphycerina.
Cyclostomata: (Lophotrochozoa: Bryozoa)
Cyclostomiceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Ellesmerocerida.
Cyclostomiceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Cymatopegma: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Cymbionites: *X* (Deuterostomia *incertae sedis*), *see* Homalozoa: Haplozoa
Cymbulariidae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Cyrtendoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Endocerida.
Cyrtendoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Cyrtobactrites: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Bactritida.
Cyrtocerinidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Cyrtocertinina: X (Mollusca: Cyrtosoma: Cephalopoda).
Cyrtogomphoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Cyrtolites: X (Mollusca), *see* Monoplacophora.
Cyrtonella: X (Mollusca: Gastropoda: Tergomya: Bellerophontida), *see* "Bellerophontiforms".
Cystosporida: (Lophotrochozoa: Bryozoa)
Cyrena: (Mollusca: Bivalvia), *see* Bivalvia Shell.
CYRTOSOMA: (Mollusca). *See also* Helcionelloida Dendrogram.

D

Dakeoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Ellesmerocerida.
Dehornella: X (Porifera: Stromatoporoidea?), *see* Stromatoporoidea.
Demospongiae: (Porifera). See also, Homoscleromorpha, Stromatoporoidea.
Dendrocystoides: *X* (Deuterostomia: Homalozoa) *see* Soluta
Dentaliida: (Mollusca: Scaphopoda) Scaphopoda

Dentalium: (Mollusca: Scaphopoda) Scaphopoda
DEUTEROSTOMIA: sea stars + movie stars. This is the crown group, *not* the stem group.
"Dexiothetica": *see* Deuterostomia.
Diamphidiocystis: *X* (Deuterostomia: Homalozoa) *see* Stylophora.
Dianchicystis: *X see* Vetulocystidae
Dictyonina: X (Brachiopoda: Lingululiformia) *see* Paterinida.
Dicyemida: (Mesozoa) *See* Bilateria.
Didazoon: *X* (Deuterostomia: Vetulicolia) *see* Vetulicolia.
Diestoceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Dirhachopea: X (Mollusca: Gastropoda: Orthogastropoda: Sinuopeidae). *See* Sinuopeidae.
Discinida: (Lophotrochozoa: Brachiopoda: Linguliformea)
Discinoidea: (Lophotrochozoa: Brachiopoda: Linguliformea), *see* Discinida.
Discoceras: X (Mollusca: Cyrtosoma: Nautiloidea), *see* Tarphycerida.
Discosorida: X (Mollusca: Cyrtosoma: Cephalopoda).
Discosoridae: X (Mollusca: Cyrtosoma: Cephalopoda)
Dokidocyathina: X (Porifera: Archaeocyatha) *see* Archaeocyatha.
Dokidocyathus: X (Porifera: Archaeocyathida), *see* Irregulares.
Dolichopterus: X (Arthropoda: Chelicerata: Eurypterida), *see* Eurypterida.
Drosophila: (Arthropoda, Insecta) *See* Bilateria, Hox Genes.

E

Eburoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Ellesmerocerida.
Ecdysozoa: bugs > slugs, the arthropod half of Protostomia. *See also*, Bilateria.
ECHINODERMATA: We use the crown group crinoids + sea urchins. *See also* Ambulacraria, Deuterostomia, Hox Genes.
Echinoidea: (Echinodermata). See Hox Genes.
Eifellia: X (Porifera). *See* Demospongiae, Hexactinellida, Porifera*, Porifera Dendrogram.
Elleriidae: X (Arthropoda: Chelicerata: Merostoma).
Ellesmeroceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Ellesmerocerida: X? (Mollusca: Cyrtosoma: Cephalopoda).
Endoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Endocerida: X (Mollusca: Cyrtosoma: Cephalopoda)
Endoplectoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Discosorida
Eoarthrolpeura: X (Arthropoda: Myriapoda).
EOGASTROPODA: (Mollusca: Gastropoda)
Eolimulidae: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Eopteria: X (Mollusca: Rostroconchia), *see* Conocardioida.
Eothinoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Ephydatia: (Porifera: Demospongiae). *See* Demospongiae.
Erismacoscinina: X (Porifera: Archaeocyatha) *see* Archaeocyatha.
Ethmophyllum: X (Porifera: Archaeocyatha), *see* Archaeocyatha.*
Euarthropoda: (Chelicerata + Crustacea + Myriapoda + Hexapoda)
Euchasma: X (Mollusca: Rostroconchia), *see* Ribeirioida, Conocardioida (!?).
Euconia: X (Mollusca: Gastropoda: Orthogastropoda: Sinuopeidae). *See* Sinuopeidae.
"Euconiidae": X (Mollusca: Gastropoda: ?Orthogastropoda: Sinuopeidae).
Euomphalida: X (Mollusca: Gastropoda: Eogastropoda).
Euomphalus: (Mollusca: Gastropoda: Eogastropoda), *see* Eogastropoda.
Euphausia: (Crustacea: Malacostraca) *see* Crustacea
Euphemetidae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Euphoberia: X (Arthropoda: Myriapoda). *See* Myriapoda.
Euproopidae: X (Arthropoda: Chelicerata: Merostoma)
Euproops: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Euprymna: (Mollusca: Cephalopoda). See Hox Genes*.
EURYPTERIDA: X (Arthropoda: Chelicerata)
Eurypterus: X (Arthropoda: Chelicerata: Eurypterida), *see* Eurypterida.

Exogyra: (Mollusca: Bivalvia), *see* Bivalvia Shell.

F

Fenestrida: (Lophotrochozoa: Bryozoa)
Ferrogyra: X (Mollusca: Gastropoda: Paragastropoda), *see* Cliospirinae.
Flabellicarpus: *X* (Deuterostomia: Homalozoa) *see* Stylophora.
Flagellophora: (Nemertodermatida) *See* Bilateria.
Fordilla: X (Mollusca), *see* Bivalvia.

G

Gadilida: (Mollusca: Scaphopoda) Scaphopoda
Gastraea: X hypothetical organism, probably equivalent to *Urbilateria*. *See* Bilateria.
Gastropoda: (crown group) (Mollusca).
GASTROPODA: (stem group) (Mollusca). *See also*, Tropidodiscidae.
Geisonoceras: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Orthocerida.
Geisonoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda).
Gervillia: (Mollusca: Bivalvia), *see* Bivalvia Shell.
"Gigantoceras": X (Mollusca: Cyrtosoma: Cephalopoda), *see* Barrandeocerina.
Glomeropsis: X (Arthropoda: Myriapoda). *See* Myriapoda.
Glossoceras: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Ascocerida.
Glycomeris: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Gnathostomulida: *See* Bilateria.
Gonioceras: X (Mollusca: Gastropoda: Paragastropoda), *see* Actinocerida
Goniceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Goniophora: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Graciloceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Grandostomatinae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida). *See* Bellerophontida.
Gymnolaemata: (Lophotrochozoa: Bryozoa)
Gyrocystis: X (Deuterostomia: Homalozoa).

H

Haikouella: *X* (Chordata) *see also* Vetulicolia.
Halkieria: *see* Monoplacophora, Solenogastres
Haliclona: (Porifera: Demospongiae), *see* Demospongiae*
Haliotis: (Mollusca: Gastropoda) see Hox Genes.
Halisarca: (Porifera: Demospongiae), *see* Demospongiae*
Halisarcida: (Porifera: Demospongiae), *see* Demospongiae.
Haplogonaria: (Acoela) *See* Bilateria.
Haplosclerida: (Porifera: Demospongiae) *See* Demospongiae, Homoscleromorpha,
Haplozoa: X (Deuterostomia, *incertae sedis*)
Hebetoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda)
Hederellida: (Lophotrochozoa: Bryozoa)
Helcionella: X (Mollusca: Conchifera), *see* Helcionellidae. *See also*, Helcionelloida, Helcionelloida Dendrogram.
Helcionellidae: X? (Mollusca: Conchifera).
HELCIONELLOIDA: X? (paraphyletic) (Mollusca). *See also* Rostroconchia, "Bellerophontiforms".
Helicotis: X (Mollusca: Gastropoda: Paragastropoda), *see* Onychochilidae.
Helix: (Mollusca: Pulmonata), *see* Stylommatophora.
Hemichordata: (Deuterostomata) *See* Bilateria.
Hemiphragmoceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Henneguya: (Myxozoa) *See* Bilateria.

Helicoplacoidea: X
Hemichordata: *see* Deuterostomia.
Helminthochiton: X (Mollusca), *see* Polyplacophora.
Heracloceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Barrandeocerina.
Heraultipegma: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Heteractinida: X (Porifera, rejected paraphyletic grade). *See* Porifera.
Heterodonta: (Mollusca), *see* Bivalvia.
Heterolimulidae: X? (Arthropoda: Chelicerata: Merostoma).
Hexactinellida: (Porifera). *See also* Demospongiae.
Hexapoda: see also Crustacea.
Hexasterophora: (Porifera: Hexactinellida), *see* Hexactinellida.
Hiatella: (Mollusca), *see* Bivalvia.
Hippocardia: X (Mollusca: Rostroconchia), *see* Conocardioida.
Hippurotoida: X (Mollusca), *see* Bivalvia. ("Rudists")
HOMALOZOA:
Homoiostelia: alternate name for **Soluta**.
Homoscleromorpha: (Porifera), *see* Demospongiae, Porifera, Porifera Dendrogram.
Homosclerophorida: (Porifera) = Homoscleromorpha, *q.v*.
Huaiheceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Huroniidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Hydnoceras: X (Porifera: Hexactinellida), *see* Hexactinellida*.
Hydroides: (Annelida, Polychaeta) *See* Bilateria.
Hyperstrophema: X (Mollusca: Gastropoda: Paragastropoda), *see* Onychochilidae.
Hypseloconida: X (Mollusca), *see* Monoplacophora.
Hypseloconus: X (Mollusca: ?Gastropoda), *see* Tergomya.

I

Illex: (Mollusca: Cyrtosoma: Decapodiformes), *see* Cephalopod Brain.
INSECTA: *see also* Crustacea.
Invertospira: X (Mollusca: Gastropoda: Paragastropoda), *see* Onychochilidae.
Irregulares: X (Porifera: Archaeocyatha), *see also* Archaeocyatha.*
Ischyrinia: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Isodiametra: (Acoela). See Hox Genes*.
Isodictya: (Porifera: Demospongiae), *see* Porifera*.

J

Jaekelocarpus: *X* (Deuterostomia: Homalozoa). A mitrate with ?gills
Jolietoceras: X (Mollusca: Cyrtosoma: Nautiloidea), *see* Barrandeocerina.
Jovellaniidae: X (Mollusca: Cyrtosoma: Nautiloidea).

K

Kakoeca: (Choanoflagellata), *see*, Demospongiae.*
Karoceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Kasibelinuridae: X? (Arthropoda: Chelicerata: Merostoma)
Kasibelinurus: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Kazachstanicyathida: X (Porifera: Archaeocyatha) *see* Archaeocyatha, Irregulares.
Kimberella: X (Ediacaran). *See* Bilateria.
Kimopegma: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Kionoceras: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Orthocerida.
Kiringella: X (Mollusca), *see* Monoplacophora. *See also*, Helcionelloida Dendrogram.

Knightites: X (Mollusca: Gastropoda: Tergomya: Bellerophontida), *see* "Bellerophontiforms".
Knightitidae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Kobayashiella: X (Mollusca: Gastropoda: Paragastropoda), *see* Mimospirida.

L

Labechiida: X (Porifera: Stromatoporoidea), *see* Stromatoporoidea.
Laeogyra: X (Mollusca: Gastropoda: Paragastropoda), *see* Onychochilidae.
Lamellipedia: *see* Euarthropoda.
Lamellorthoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda).
Latouchella: (Mollusca: Conchifera), *see* Helcionellidae. *See also* Helcionelloida, Helcionelloida Dendrogram.
Lechitrochoceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Legrandella: (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Leiopteria: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Lemoneites: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Lepetidae: (Mollusca: Gastropoda: Patellogastropoda).
Lepetopsina: (Mollusca: Gastropoda: Patellogastropoda).
Lepetopsis: (Mollusca: Gastropoda: Patellogastropoda), *see* Patellogastropoda.
Leptorhynchoides: (Acanthocephala). *See* Bilateria.
Leucosolenia: (Porifera: Calcarea). *See* Demospongiae.
Lima: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Limulidae: (Arthropoda: Chelicerata: Merostoma).
Limulina: (Arthropoda: Chelicerata: Merostoma).
Limulinae: (Arthropoda: Chelicerata: Merostoma).
Limulini: (Arthropoda: Chelicerata: Merostoma).
Limulitella: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Limuloides: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Limuloidinae: X (Arthropoda: Chelicerata: Merostoma)
Limulus: (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura. *See also* Eurypterida.
Lindstroemoceras: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Ascocerida.
Lineus: (Nemertini) *See* Hox Genes.
Lingula: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda, Hox Genes.
Lingulella: X ((Lophotrochozoa: Brachiopoda: Linguliformea) *see* Lingulida.
Lingulida: (Lophotrochozoa: Brachiopoda: Linguliformea), *see also* Stromatoporoidea.
Liomesaspis: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura, Euproopidae.
Lituitidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Lituites: X (Mollusca: Cyrtosoma: Nautiloidea), *see* Barrandeocerina.
Lobobactrites: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Bactritida.
Loligo: (Mollusca: Cyrtosoma: Decapodiformes), *see* Cephalopod Brain.
Lorieroceras: X (Mollusca: Cyrtosoma: Nautiloidea), *see* Oncocerida.
LOPHOTROCHOZOA: slugs > bugs, the molluscan half of Protostomia. *See also*, Bilateria, Hox Genes.
Lottia: (Mollusca: Gastropoda: Patellogastropoda), *see* Patellogastropoda.
Lottidae: (Mollusca: Gastropoda: Patellogastropoda).
Lowoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Lymnaea: (Mollusca: Pulmonata), *see* Basommatophora.
Lymnaeoidea: (Mollusca: Pulmonata), *see* Basommatophora.
Lyropecten: (Mollusca: Bivalvia), *see* Bivalvia Shell.

M

Maclurites: X (Mollusca: Gastropoda: Eogastropoda or Paragastropoda), *see* Macluritoidea.
Macluritidae: X (Mollusca: Gastropoda: Paragastropoda?). *See also*, Mimospirida.
Macluritoidea: X (Mollusca: Gastropoda: Eogastropoda or Paragastropoda). *See also*, Mimospirida.
Malacostraca: (Crustacea) see Crustacea.
Manchuroceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)

Mandaloceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Discosoridae.
Mandaloceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Mandibulata: Crustacea + Atelocerata. Redundant with Euarthropoda here. *See also* Myriapoda.
Matherella: X (Mollusca: Gastropoda: Paragastropoda), *see* Mimospirida. *See also,* Paragastropoda.
Matherellina: X (Mollusca: Gastropoda: Paragastropoda), *see* Mimospirida.
Maxillopoda: (Crustacea) see Crustacea.
Mercenaria: (Mollusca), *see* Bivalvia.
Merostomata: (Arthropoda: Chelicerata), *see* Chelicerata.
Mesolimulinae: X (Arthropoda: Chelicerata: Merostoma).
Mesolimulus: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Mesozoa: *See* Bilateria.
METAZOA: toads > toadstools
Metoptomatidae: X (Mollusca: Gastropoda: Patellogastropoda).
Michelinoceras: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Orthocerida.
Michelinoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda).
Micromitra: X (Brachiopoda: Linguliformea) *see* Paterinida.
Middendorffia: (Mollusca: Solenogastres) *see* Solenogastres.
Mimospira: X (Mollusca: Gastropoda: Paragastropoda), *see* Cliospiridae, Atracurinae.
Mimospirida: X (Mollusca: Gastropoda: Paragastropoda).
Mitrata: X (Deuterostomia: Homalozoa) *see* Stylophora.
Mixopterus: X (Arthropoda: Chelicerata: Eurypterida), *see* Eurypterida.
Monocyathida: X (Porifera: Archaeocyatha), *see* Archaeocyatha, Irregulares.
Modiomorphoida: X (Mollusca), *see* Bivalvia.
Monoplacophora: (Mollusca).
Monopleura: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Monorhaphis: (Porifera: Hexactinellida) *see* Hexactinellida.
Montenegrina: (Mollusca: Pulmonata: Stylommatophora), *see* Pulmonata.
Montyoceras: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Ascocerida.
Moravuridae: X (Arthropoda: Chelicerata: Merostoma).
Mulceodens: X (Mollusca: Rostroconchia), *see* Conocardioida.
Mya: (Mollusca: Bivalvia), *see* Bivalvia., Bivalvia Shell.
Myocaris: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Myoida: (Mollusca), *see* Bivalvia. *See also*, Bivalvia Dendrogram.
Myriapoda: centipedes & millipedes.
Mytiloida: (Mollusca), *see* Bivalvia.
Mytilus: (Mollusca), *see* Bivalvia, Bivalvia Shell.

N

Nacellina: (Mollusca: Gastropoda: Patellogastropoda).
Nacelloidea: (Mollusca: Gastropoda: Patellogastropoda).
Namacalathus: X (Metazoa, *i.s.*), *see* Irregulares.
Nautilida: (Mollusca: Cyrtosoma: Nautiloidea).
NAUTILOIDEA: (Mollusca: Cyrtosoma).
Nautilus: (Mollusca: Cyrtosoma: Nautiloidea), *see* Nautilida.
Nectocaris: *X* (?) *see* Vetulicolia.
Nematoda: (Ecdysozoa) *See* Bilateria, Hox Genes.
Nematomenia: (Mollusca: Solenogastres) *see* Solenogastres.
Nematostella: (Cnidaria: Anthozoa) *See* Hox Genes*.
Nemertini: (Protostomia) See Hox Genes*.
Nemertoderma: (Nertodermatida): See Hox Genes.
Nemertodermatida: (Acoelomorpha) *See* Bilateria.
Neomenia: (Mollusca: Solenogastres) *see* Solenogastres.
Neopilina: (Mollusca), *see* Monoplacophora.
Neotrigonia: (Mollusca), *see* Bivalvia.
Nephriticeratidae: X (Mollusca: Cyrtosoma: Nautiloidea).

Nerineidae: X (Mollusca: Gastropoda) *see* Gastropoda.
Nochoroicyathus: X (Porifera: Archaeocyatha) *see* Archaeocyatha.*
Nothoceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Nucula: (Mollusca: Bivalvia) *see* Bivalvia. *See also*, Ambulacraria.
Nuculana: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Nuculoidea: (Mollusca), *see* Bivalvia.
Nyuelia: X (Mollusca: Conchifera), *see* Helcionellidae.

O

Octopus: (Mollusca: Cyrtosoma: Vampyropoda), *see* Cephalopod Brain.
Oepikila: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Omphalocirridae: X (Mollusca: Gastropoda: Paragastropoda).
Omphalocirrus: X (Mollusca: Gastropoda: Paragastropoda), *see* Omphalocirridae.
Oncocertidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Oncocerida: X? (Mollusca: Cyrtosoma: Nautiloidea). *See also*, Nautilida.
Onychochilidae: X (Mollusca: Gastropoda: Paragastropoda)
Onychochilius: X (Mollusca: Gastropoda: Paragastropoda), *see* Mimospirida. *See also*, Paragastropoda.
Oopsacas: (Porifera: Hexactinellida), *see* Hexactinellida.
Ophidioceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Orbiculoidea: (Lophotrochozoa: Brachiopoda: Linguliformea) *See*, Discinida.
Ormoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Orthida: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.
Orthoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda).
Orthocerida: X (Mollusca: Cyrtosoma: Neocephalopoda).
ORTHOGASTROPODA: (Mollusca: Gastropoda)
Oscarella: (Porifera: Homoscleromorpha), see Homoscleromorpha*, Porifera*, Porifera Dendrogram.
Orthomyelina: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Orthonectida: (Mesozoa) *See* Bilateria.
Ostracoda: (Crustacea) see Crustacea.

P

Palaeoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Plectronocerida.
Palaeoheterodonta: (Mollusca), *see* Bivalvia. *See also*, Bivalvia Dendrogram.
Palaeotoxodonta: (Mollusca), *see* Bivalvia. *See also*, Bivalvia Gills.
Paleolimulidae: X (Arthropoda: Chelicerata: Merostoma).
Paleolimulus: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Paleomerus: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Pancrustacea: see also Crustacea.
PARAGASTROPODA: X (Mollusca: Gastropoda).
Paraphragmitidae: X (Mollusca: Cyrtosoma: Neocephalopoda).
Parastylonurus: X (Arthropoda: Chelicerata: Eurypterida), *see* Eurypterida.
Pasternakevia: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Patella: (Mollusca: Gastropoda: Patellogastropoda), *see* Patellogastropoda, Bilateria, Hox Genes.
Patellina: (Mollusca: Gastropoda: Patellogastropoda).
Patellogastropoda: (Mollusca: Gastropoda).
Paterinida: X (Lophotrochozoa: Brachiopoda: Linguliformea).
Pauropegma: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Pecten: (Mollusca), *see* Bivalvia.
Paleophragmodictya: X (Porifera: ?Hexactinellida) *see* Hexactinellida*.
Pelagiella: X (Mollusca: Gastropoda: Paragastropoda), *see* Pelagiellida.
Pelagiellida: X (Mollusca: Gastropoda: Paragastropoda).
Pelagiellidae: X (Mollusca: Gastropoda: Paragastropoda), *see* Pelagiellida.
Pentamerida: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.

Peridionites: *X* (Deuterostomia *incertae sedis*), *see* Homalozoa: Haplozoa
Pervertina: X (Mollusca: Gastropoda: Paragastropoda), *see* Onychochilidae.
Petrocrania: X (Lophotrochozoa: Brachiopoda), *see* Craniiformea.
Philhedra: X (Lophotrochozoa: Brachiopoda), *see* Craniiformea.
Pholadomyoida: (Mollusca), *see* Bivalvia. *See also*, Bivalvia Gills.
Pholas: (Mollusca), *see* Bivalvia.
Phragmoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Discosorida.
Phragmoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Phylactolaemata: (Lophotrochozoa: Bryozoa)
Piloceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Endocerida.
Piloceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Pinctada: (Mollusca), *see* Bivalvia.
Pinnocaris: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Pinnotheres: (Crustacea: Malacostraca). See Crustacea*.
Pipiscius: *X* (Chordata?) *see* Vetulicolia.
Plakina: (Porifera: Homoscleromorpha). *See* Demospongiae, Homoscleromorpha*.
Plakinidae: (Porifera) = Homoscleromorpha.
Plakortis: (Porifera: Homoscleromorpha). *See* Homoscleromorpha*.
Planorbis: (Mollusca: Pulmonata), *see* Pulmonata, Basommatophora.
Platyhelminthes: (Ecdysozoa). *See* Bilateria.
Plectoceratidae: (Mollusca: Cyrtosoma: Cephalopoda).
Plectronoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Plectronocerida.
Plectronoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Plectronocerida: X (Mollusca: Cyrtosoma: Cephalopoda)
Pleurojulus: X (Arthropoda: Myriapoda). *See* Myriapoda.
Plicatula (Mollusca: Bivalvia), *see* Bivalvia Shell.
Pojetaia: X (Mollusca), *see* Bivalvia.
Polychaeta: (Annelida) *See* Bilateria.
Polydesmiidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Polyplacophora: (Mollusca)
Polypodium: (Cnidaria, *i.s.*) *See* Bilateria.
Pomatrum: *X* (Deuterostomia: Vetulicolia) *see* Vetulicolia.
PORIFERA: the sponges. Probably a paraphyletic grade. See also Hox Genes.
Poromyacea: (Mollusca), *see* Bivalvia Gills.
Poterioceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Praecardioida: X (Mollusca), *see* Bivalvia.
Problognathia: (Gnathostomulida) *See* Bilateria.
Productida: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.
Proeccyliopterus: X (Mollusca: Gastropoda: Paragastropoda), *see* Pelagiellida.
Proschizoramia: X. *See* Euarthropoda.
Protactinoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Plectronocerida.
Protactinoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Protactinocerida: X (Mollusca: Cyrtosoma: Cephalopoda)
Proteoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda).
Proterocameroceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Protocycloceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Ellesmerocerida.
Protocycloceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Proterospongia: (Choanoflagellata), *see* Porifera*
Protolimulus: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Protopharetra: X (Porifera: Archaeocyatha), *see* Irregulares*.
Protoscaevogyra: X (Mollusca: Gastropoda: Paragastropoda), *see* Onychochilidae.
Protospongia: X (Porifera: Hexactinellida), *see* Hexactinellida*.
Protostomia: slugs + bugs. This is the crown group, *not* the stem group. *See also* Bilateria.
Psammonlimulus: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Pseudoconocardium: X (Mollusca: Rostroconchia), *see* Conocardioida.
Pseudocorticum: (Porifera: Homoscleromorpha), *see* Homoscleromorpha.
Pseudoniscidae: X? (Arthropoda: Chelicerata: Merostoma)
Pseudoniscus: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.

Pseudorthoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Pseudorthoceratidae.
Pseudorthoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Pseudorthocerida: X (Mollusca: Cyrtosoma: Cephalopoda)
Pseudotechnophorus: X (Mollusca: Rostroconchia), *see* Conocardioida.
Ptenoceras: X (Mollusca: Cyrtosoma: Nautiloidea), *see* Nautilida.
Pterioida: (Mollusca), *see* Bivalvia.
Pteriomorpha: (Mollusca), *see* Bivalvia. *See also*, Bivalvia Gills.
Pterothecinae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida). *See* Bellerophontida.
Pterygotus: X (Arthropoda: Chelicerata: Eurypterida), *see* Eurypterida.
Ptilosarcus: (Metazoa: Cnidaria) *see* Cnidaria.
Ptychopegma: X (Mollusca: Rostroconchia), *see* Ribeirioida.
PULMONATA: (Mollusca).
Pycnogonida: (Arthropoda: Chelicerata), *see* Chelicerata.

R

Radiata: no precise definition at the moment. Generally, the jellyfish, corals, comb-jellies, and related forms.
Rasetticyathus: X (Porifera: Archaeocyatha) *see* Irregulares*.
Receptaculitidae: X (Metazoa *i.s.*) *see* Archaeocyatha.
Regulares: X (Porifera: Archaeocyatha, rejected clade), *see* Archaeocyatha.*
Rehbachiella: X (Crustacea: Branchiopoda). See Crustacea*.
Remipedia: (Crustacea) see Crustacea.
Reticulosa: X (Porifera: ?Hexactinellida), *see* Hexactinellida.
Rhabdopleura: (Hemichordata: Pterobranchia?) *see* Deuterostomia.
Rhenocystis: *X* (Deuterostomia: Homalozoa) *see* Stylophora.
Rhipidiorhynchus: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.
Rhombozoa: (Mesozoa) *See* Bilateria.
Rhynchonellata: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.
Ribeiria: X (Mollusca: Rostroconchia), *see* Ribeirioida. *See also*, Rostroconchia.
Ribeirioida: X (Mollusca: Rostroconchia). *See also*, Rostroconchia.
Rolfeia: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Rolfeiidae: X? (Arthropoda: Chelicerata: Merostoma).
ROSTROCONCHIA: X (Mollusca)
Ruedemannoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Rugosa: X (Cnidaria), *see also* Stromatoporoidea.

S

Salpingostomatinae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida). *See* Bellerophontida.
Sandineria: X (Arthropoda: Myriapoda). *See* Myriapoda.
Scaevogyra: X (Mollusca: Gastropoda: Paragastropoda), *see* Mimospirida.
Scaphopoda: (Mollusca: Cyrtosoma). *See also*, Helcionelloida Dendrogram, Rostroconchia.
Scenella: X (Mollusca: Conchifera), *see* Scenellidae. *See also*, Helcionelloida Dendrogram.
Scenellidae: X (Mollusca: Conchifera).
Schizopea: X (Mollusca: Gastropoda: Orthogastropoda: Sinuopeidae).
Schizoramia: *see* Euarthropoda.
Schuchertoceras: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Ascocerida.
Scurriopsis: (Mollusca: Gastropoda: Patellogastropoda), *see* Patellogastropoda.
Sellithyris: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.
Sempteochitonida: X (Mollusca: Polyplacophora), *see* Polyplacophora.
Sepia: (Mollusca: Cyrtosoma: Decapodiformes), *see* Cephalopod Brain.
Silicispongia: (Porifera, rejected clade), *see* Porifera Dendrogram.
Shamattawaceras: X (Mollusca: Cyrtosoma: Neocephalopoda), *see* Ascocerida.
Sinistracirsa: X (Mollusca: Gastropoda: Paragastropoda), *see* Mimospirida.
Sinuella: X (Mollusca: Conchifera), *see* Coreospiridae.

Sinuites: X (Mollusca: Gastropoda: Tergomya). *See* Bellerophontida, "Bellerophontiforms".
Sinuitidae: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Sinuitina: (Mollusca: Gastropoda: Tergomya) (parphyletic).
Sinuitopsis: X (Mollusca: Gastropoda: Tergomya), *see* "Bellerophontiforms".
Sinuopeidae: (Mollusca: Gastropoda: ?Orthogastropoda).
Siphonariida: (Mollusca: Pulmonata), *see* Basommatophora.
Siphonodentalioida: (Mollusca: Scaphopoda) Scaphopoda
Skeemella: X (Deuterostomia?) *see* Vetulicolia.
Solactiniella: X (Porifera: Hexactinellida), see Porifera*.
Solemyoidea: (Mollusca), *see* Bivalvia.
Solenogastres: (Mollusca)
Soluta: X (Deuterostomia: Homalozoa)
Spadella: (Chaetognatha): See Hox Genes.
Spiriferida: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.
Stapicyathus: X (Porifera: Archaeocyatha) *see* Archaeocyatha.*
Stenolaemata: (Lophotrochozoa: Bryozoa)
Stenothecidae: X? (Mollusca: Conchifera).
Stenothecoida: X? (Mollusca), *see* Stenothecidae.
Stenothecoides: X (Mollusca: Conchifera) , *see* Stenothecidae.
Stereoplasmoceratidae: X (Mollusca: Cyrtosoma: Neocephalopoda).
Stichopus: (Echinodermata: Holothuroidea) *see* Ambulacraria.
Streblochondria: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Strepsodiscus: X (Mollusca: Gastropoda: Tergomya), *see* Tropidodiscidae.
Stromatocerium: X (Porifera: Stromatoporoidea), *see* Stromatoporoidea.*
Stromatocystites: X (Deuterostomia: Homalozoa) *see* Ctenocystoidea.
Stromatoporoidea: X? (Porifera). *See also*, Archaeocyatha, Irregulares.
Strongylocentrotus: (Echinodermata: Echinoidea) see Hox Genes.
Strophomenata: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.
Stylommatophora: (Mollusca: Pulmonata).
Stylophora: **X** *see also*, Vetulocystidae.
Suberites: (Porifera: Demospongiae), *see* Demospongiae.
Suecoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Endocerida.
Symsagittifera: (Acoela) see Hox Genes.
Synziphosurida: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Syringocnemidina: X (Porifera: Archaeocyatha) *see* Archaeocyatha.
Syringocrinus: *X* (Deuterostomia: Homalozoa) *see* Soluta.
Systellommatophora: (Mollusca: Pulmonata).

T

Tabulata: X (Cnidaria: Hexacorallia), *see also* Stromatoporoidea.
Tachypleini: (Arthropoda: Chelicerata: Merostoma).
Tachypleus: (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Tapinogyra: X (Mollusca: Gastropoda: Paragastropoda), *see* Atracurinae.
Tarphyceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Tarphycerida: X (Mollusca: Cyrtosoma: Nautiloidea)
Tarphycerina: X (Mollusca: Cyrtosoma: Nautiloidea)
Technophorus: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Tellina: (Mollusca), *see* Bivalvia.
Terebratulida: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.
TERGOMYA: X (Mollusca: Gastropoda). *See also*, Helcionelloida, Helcionelloida Dendrogram, Monoplacophora.

Testacella: (Mollusca: Pulmonata: Stylommatophora), *see* Pulmonata.
Tetracapsula: (Myxozoa) *See* Bilateria.
Tetraconata: see Crustacea.
Tetractinomorpha: (Demospongiae).

Tetranota: X (Mollusca: Gastropoda: Tergomya: Bellerophontida).
Thalamocyatha: X (Porifera: Archaeocyatha), *see* Archaeocyatha.*
Thecideida: (Lophotrochozoa: Brachiopoda) *see* Brachiopoda.
Thescaloceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Plectronocerida.
Titusvillea: X (Porifera: Hexactineelida), *see* Hexactinellida*.
Todarodes: (Mollusca: Cyrtosoma: Decapodiformes), *see* Cephalopod Brain.
Tolmachovia: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Tonicella: (Mollusca), *see* Polyplacophora.
Tragoceras: X (Mollusca: Cyrtosoma: Nautiloidea), *see* Tarphycerina.
Tremadictyon: X (Porifera: Hexactinellida), *See* Hexactinellida*.
Tremanotus: X (Mollusca: Gastropoda: Tergomya: Bellerophontida), *see* "Bellerophontiforms".
Trematis: X (Lophotrochozoa: Brachiopoda: Linguliformea), *see* Discinida.
Trigonia: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Trigonioida: (Mollusca), *see* Bivalvia.
TRILOBITA: X (Arthropoda), *see also* Stromatoporoidea.
Trimerellida: X (Lophotrochozoa: Brachiopoda).
Trimeroceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Tripleuroceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Trepostomatida: (Lophotrochozoa: Bryozoa).
Tripteroceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Trochoclisa: X (Mollusca: Gastropoda: Paragastropoda), *see* Trochoclisinae.
Trochoclisinae: X (Mollusca: Gastropoda: Paragastropoda).
Trochocystites: X (Deuterostomia: Homalozoa) *see* Cincta.
Trocholitidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Tropidodiscidae: X? (Mollusca: Gastropoda). *See also,* Monoplacophora.
Tropidodiscus: X (Mollusca: Gastropoda: Tergomya), *see* Tropidodiscidae.
Tryblidiida: (Mollusca) = Monoplacophora. , *see* Polyplacophora. *See also*, Helcionellidae, Helcionelloida.
Tryblidium: X (Mollusca), *see* Monoplacophora. *See also*, Polyplacophora.

U

Undospira: X (Mollusca: Gastropoda: Paragastropoda), *see* Atracurinae.
Unionoida: (Mollusca), *see* Bivalvia.
Unionoidea: (Mollusca), *see* Bivalvia.
Uranoceratidae: (Mollusca: Cyrtosoma: Cephalopoda).
Urbilateria: *see* Bilateria, Protostomia
Urochordata: *see also* Deuterostomia.

V

Valoisella: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Valcouroceratidae: X (Mollusca: Cyrtosoma: Nautiloidea).
Valloisellidae: X? (Arthropoda: Chelicerata: Merostoma).
Veneroida: (Mollusca), *see* Bivalvia. *See also*, Bivalvia Dendrogram.
Venus: (Mollusca: Bivalvia), *see* Bivalvia Shell.
Vernanimalcula: X (Metazoa *i.s.*) *see* Hox Genes.
Versispira: X (Mollusca: Gastropoda: Paragastropoda), *see* Onychochilidae.
Vetulicola: *X* (Deuterostomia: Vetulicolia) *see* Vetulicolia.
Vetulicolia: X the mostbasal deuterostomes currently known. *See also*, Deuterostomia, Hox Genes.
Vetulocystidae: X *see also,* Deuterostomia, Hox Genes.
Vetulocystis: X see Vetulocystidae
Volsella: (Mollusca: Bivalvia), *see* Bivalvia Shell.

W

Wanwanella: X (Mollusca: Rostroconchia), *see* Ribeirioida.
Warthia: X (Mollusca: Gastropoda: Tergomya). *See* Bellerophontida.
Weinbergina: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Weinberginidae: X (Arthropoda: Chelicerata: Merostoma)
Westonoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Willwerathia: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Wiwaxia: *see also* Monoplacophora, Solenogastres
Wutinoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)

X

Xaniopyramus: X (Arthropoda: Chelicerata: Merostoma) *see* Xiphosura.
Xenoturbella: (Deuterostomia: Ambulacraria) *see also* Deuterostomia, Bilateria.
Xiashanoceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Ellesmerocerida.
Xiashanoceratidae: X (Mollusca: Cyrtosoma: Cephalopoda).
Xidazoon: *X see* Vetulicolia.
Xiphosura: (Arthropoda: Chelicerata: Merostoma), *see also* Eurypterida.
Xiphosurida: (Arthropoda: Chelicerata: Merostoma).

Y

Yangtzespiriidae: X (Mollusca: Gastropoda: Paragastropoda).
Yanheceras: X (Mollusca: Cyrtosoma: Cephalopoda), *see* Plectronocerida.
Yanheceratidae: X (Mollusca: Cyrtosoma: Cephalopoda)
Yanhecerida: X (Mollusca: Cyrtosoma: Cephalopoda)
Yochelcionella: X (Mollusca: Conchifera), *see* Helcionelloida.
Yochelcionellidae: X? (Mollusca: Conchifera). *See also*, Helcionelloida Dendrogram, "Bellerophontiforms".
Yoldia: (Mollusca), *see* Bivalvia.
Yunnanozoa: X *see* Vetulicolia.
Yunnanozoon: *X* (Deuterostomia: Vetulicolia) *see* Vetulicolia. See also Hox Genes*.

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Metazoa Glossary

```
LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```

This is the index page for the metazoa glossary. The eventual aim is to combine all the glossaries distributed throughout the metazoan section. This will takes many years.

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Metazoa Glossary A-B

```
LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```

The eventual aim is to combine all the glossaries distributed throughout the metazoan section. This will takes many years.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

A

abd-A: abbreviation for *abdominal-A*, a middle class hox gene of arthropods. See Hox Genes.

abd-B: abbreviation for *abdominal-B*, the posterior class hox gene of arthropods. See Hox Genes.

abdominal-A: a gene, abbreviated *abdA*, a middle class hox gene of arthropods. See Hox Genes.

abdominal-B: a gene, abbreviated *abdB*, the posterior class hox gene of arthropods. See Hox Genes.

Numerical	*Drosophila*	Abbreviation	Notes
Hox1	*labial*	*lab*	**Beginning of anterior class** (and ANTP complex in *Drosophila*)
Hox2	*proboscipedia*	*pb*	
Hox3	*(Zerknüllt, Bicoid)*	*(zen, bcd)*	**Hox3 class**. Hox3 is probably its own "upper middle class" homology group. *Drosophila* has two hox3 homologues, but neither is homeotic.
Hox4	*Deformed*	*Dfd*	**Beginning of middle class**
Hox5	*Sex combs reduced*	*Scr*	Insects have a "hox 5½," *fushi tarazu (ftz)*, which is not homeotic
Hox6	*Antennapedia*	*Antp*	Hox6-8 are homologues of *Antp*,*Ubx* and *AbdA* as a group. That is, all 6 (and *ftz*) derive from a single "lower middle class" gene in *Urbilateria*.

Hox7	*Ultrabithorax*	*Ubx*	Beginning of UBX complex in *Drosophila*
Hox8	*Abdominal A*	*AbdA*	
Hox9	*Abdominal B*	*AbdB*	**Beginning of posterior class**
Hox10, 11 ...			No arthropod homologues -- or (more exactly) *AbdB* is homologous to all posterior hox.

acron: (arthropod anatomy) the most anterior region of the body. The acron may or may not be a segment. It contains the *protocerebrum* and the eyes (ocelli and compound eyes). The jury is still out on the existence, identity, and homologies of any appendages.

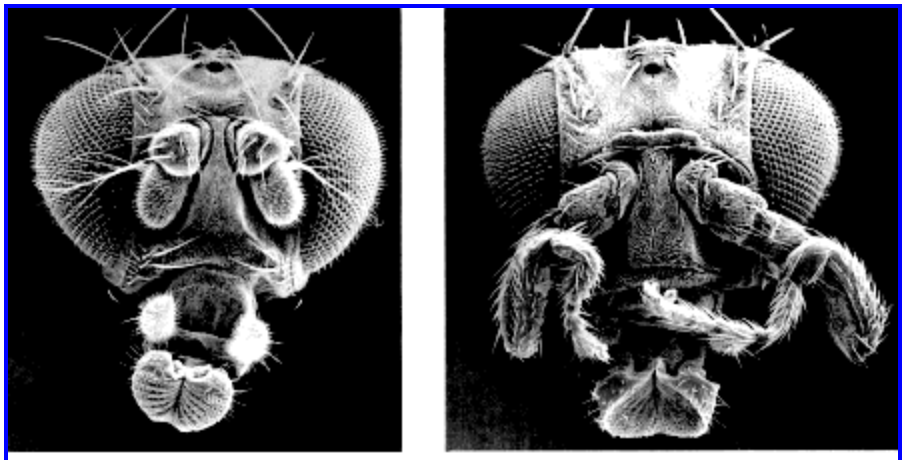
acrosome: an anterior structure of animal spermatozoa. The acrosome is functionally similar to the warhead of an armor-piercing artillery shell and assists in fertilization. The **acrosome reaction** actually seems to involve three related steps: (1) it assists the spermatozoon to cut a channel through the layer of glycoprotein surrounding the egg; (2) the membrane surrounding the acrosome fuses with the egg's plasma membrane; and (3) since the acrosome membrane is continuous with the nuclear membrane, presumably promotes insertion of the sperm's nucleus. The acrosome is a modified Golgi apparatus. See Acrosome Reaction for more details and link to an animation.

amoebocyte: (general cell biology), any of various types of amoeboid, generally undifferentiated cells which frequently function as a stem cell lineage for several different types of differentiated tissues.

anamorphic: crustacean embryology. Developmental program in which a nauplius larva develops to adult state through a series of incremental changes involving the addition of posterior segments and appendages.

ANT-C: see *antennapedia*.

antenna: in Crustacea, this can either refer to any of the four anterior head appendages, or just to the second pair. The second antennae tend to be flattened and more laterally placed. Modifications of the antennae are relatively common in crustaceans. For example, the second antennae are also frequently modified to act as chemosensory organs or copulatory claspers.



Drosophila: wildtype on left. Right is antennapedia mutant with fully developed legs in place of antennae. Photo by FR Turner, Indiana Univ.

Antennapedia: genetics. (1) ***Antennapedia* gene**: a *homeobox gene* (abbreviated *Antp* or *Atpa*) the middle class (hox6-8) of vertebrates (2) The **Antennapedia Complex**: (*Deformed* (*Def* or *Dfd*), *Sex combs reduced* (*Scr*), *fushi tarazu* (*ftz*), and *Antennapedia*, in that order (although, naturally, not all of these elements are present in all metazoans). The other major complex of hox genes is the Bithorax Complex (BX-C), the component genes of which are expressed in the more posterior parts of the developing organism. (3a) **Antennapedia class**: Finally, just to make things more complicated, note that the genes which are most closely related to *Atpa* by sequence (and the structure of the proteins they ultimately encode) are not all located in the Antennapedia complex. Thus the Antennapedia class (not "complex") includes genes of all major Bithorax Complex genes, including *ultrabithorax (ubx)*, for which the complex is named. (3b) Other authors apparently use "antennapedia class" to mean something much broader. We have not yet been able to determine the contours of this usage.

antennule: first antenna of a crustacean. These tend to be longer then the second antennae and to function as tactile organs, like the whiskers of a cat, but more so.

anthox: a general prefix for the *hox genes* of Anthozoa.

antp: see *antennapedia*.

aragonite: One of the two common polymorphs (chanically identical, alternate crystal forms) of calcium carbonate, $CaCO_3$. The other common polymorph is calcite. Aragonite tends to form in environments with higher magnesium concentration although, unlike calcite, it cannot incorporate megnesium into the crystal. Aragonite is less stable than calcite and tends to recrystalize as calcite within a few million years. Aragonite crystals are also typically smaller than calcite crystals and often have a needle-like form.

armature: crustacean anatomy, a collective term for the entire battery of spines, setae, and other projections from an appendage which don't rate a special name as limb elements or gills.

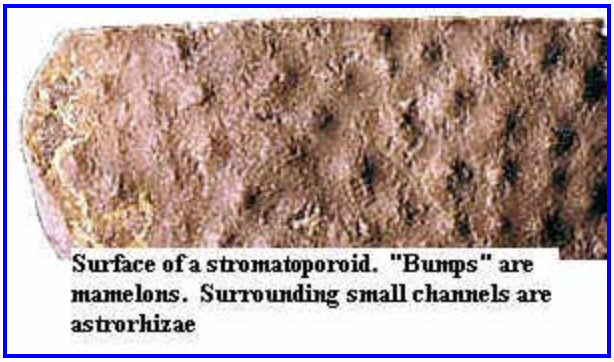
arthro-: in anatomy, a prefix suggesting that a structure is related to a joint.

article: an element of a crustacean *antenna* or *antennule*.

astrorhizae: a pattern of channels on the surface of a sponge (stromatoporoid), believed to contain the exhalent pores.

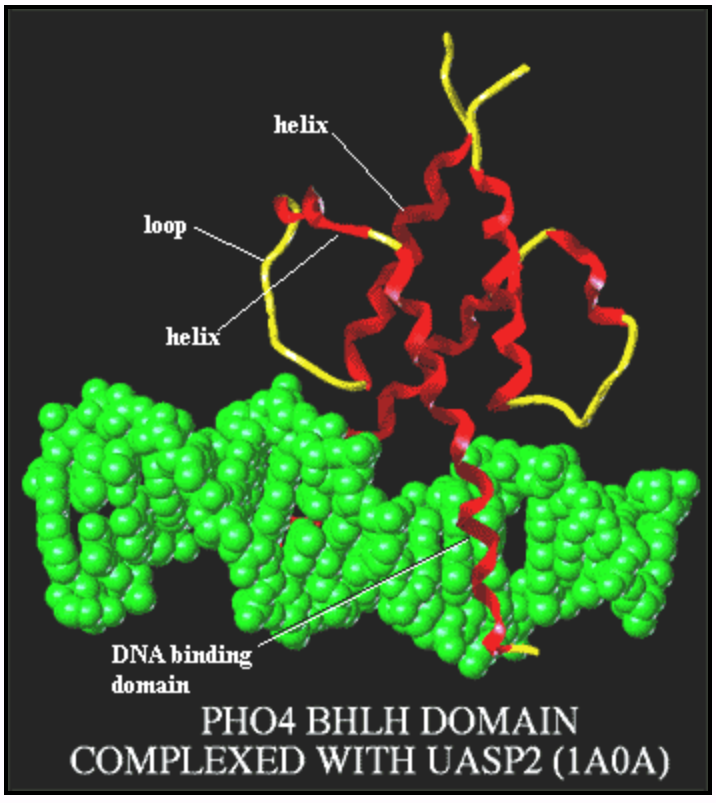
atrium: (general anatomy) a common term referring to any of hundreds of types of large, internal anatomical spaces.

axoneme: the fundamental 9+2 doublet microtubule structure at the core of the eukaryotic *flagellum*. The axoneme arises from the *basal body* and inserts into the *axosome*.


Surface of a stromatoporoid. "Bumps" are mamelons. Surrounding small channels are astrorhizae

B

basement membrane: "Basement membranes are sheet-like complexes of extracellular matrix proteins, highly structured and containing specifically *type IV collagen* as scaffold. They underlie epithelial, endothelial tissues, most glial cells and they surround several mesenchymal cells and especially all the muscle cell types. Basement membranes exert not only a mechanical function as supporting structures, but they also play a major biological role as molecular sieves and in the control of cell differentiation and stability." Boute *et al*. (1996).



basic helix-loop-helix: (*bHLH*) another diverse and important DNA-binding protein motif, including many transcription factors, not to be confused with helix-**turn**-helix. They have been described as follows: "The bHLH transcription factors are named after their highly conserved domain (about 60 amino acids long) that consists of a DNA-binding basic region (b) followed by two a-helices separated by a variable loop region. Interaction between the helix regions of two different proteins leads to the formation of homodimeric or heterodimeric complexes, and the basic region of each partner recognizes and binds to a core hexanucleotide DNA sequence. Many bHLH proteins also include additional domains that are important for their activity as transcriptional regulators, such as 'leucine zipper', 'PAS' or 'orange' domains, which are mainly involved in protein-protein interactions." Simonionato *et al*. (2007).

basis: the second segment of a crustacean appendage. See image at *protopod*. See Dr. Joel Martin's **Crustacea Glossary** for details and exceptions.

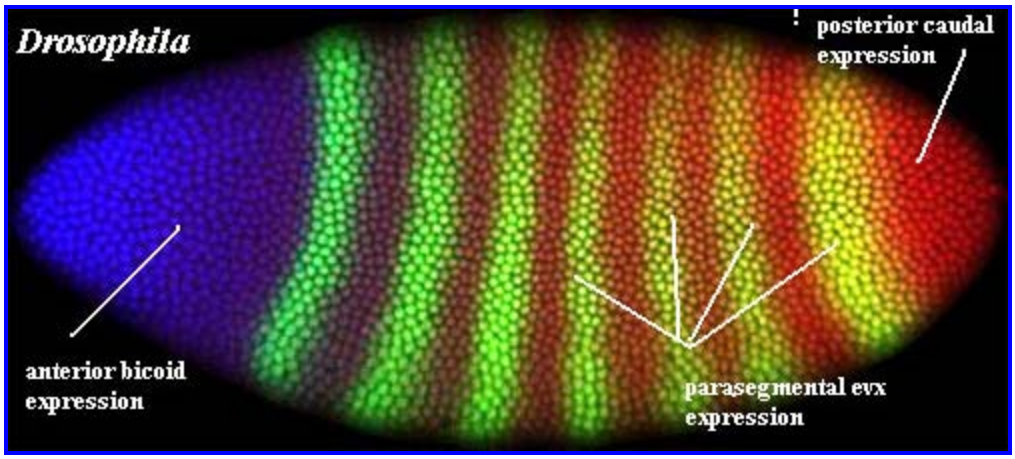
bauplän: pl. *baupläne*. See *body plan*.

bcd: abbreviation for *bicoid*, a hox3 homologue of arthropods. See Hox Genes.

benthic: bottom-living, i.e. living on the sea floor.

bHLH: See *basic helix-loop-helix*.

bicoid: a gene, abbreviated *bcd*, a hox3 homologue of arthropods. See Hox Genes.



biramous: having two "stems" or long axes. Tends to be used for any long structure which bifurcates. The biramous limb has special significance in the Crustacea. See *endopod* for explanation and complaints.

body plan: The concept of a body plan, *Bauplän* (pl. *Baupläne*), is critical to understanding the most fundamental evolutionary radiations. What is a body plan? This is a difficult question to define, and it is usually answered with examples: the insect body plan, the jellyfish body plan, or whale body plan. Loosely defined, a body plan is primarily morphological, involving the shared structural homologies of upper taxa. For example, the vertebrate bauplän might be described as comprising a "cephalised, sensate, bilaterally symmetrical, motile, ceolomate gnathostome having a segmented endoskeleton, a dorsal hollow nerve chord, and a ventral gut." Ostrom (1992: 119). Body plans reflect development at its most basic level, thus developmental constraints strongly influence the range of body plans possible. Even in simple animals, axes of symmetry are so fundamental that significant internal co-adaptation is required for viable body plan mutations to occur. This raises the question of why a number of different body plans arose at the cusp of the Cambrian Period – the so-called Cambrian Explosion. Some paleobiologists believe the answer lies in the Ediacaran fossil remains dating back before the Cambrian, in the Ediacaran Period (630-542 million years ago).

branch- or **-branch**: a prefix, suffix, or particle intended to suggest that an organism or structure has or is a gill. MAK010510.

Burgess Shale: Middle Cambrian of British Columbia, Canada. The Burgess Shale fauna is preserved in the deep water Stephens Formation. However it probably represents organisms swept off a shallower carbonate escarpment formed by the adjacent Cathedral Formation and rapidly buried by some catastrophic event, *i.e.* storm, marine landslide, loss of grant funding, etc.

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Invertebrate Glossary C

```
LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```

The eventual aim is to combine all the glossaries distributed throughout the metazoan section. This will takes many years.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

C

calcareous: containing calcium. Unless the context dictates otherwise, it implies calcium carbonate (calcite).

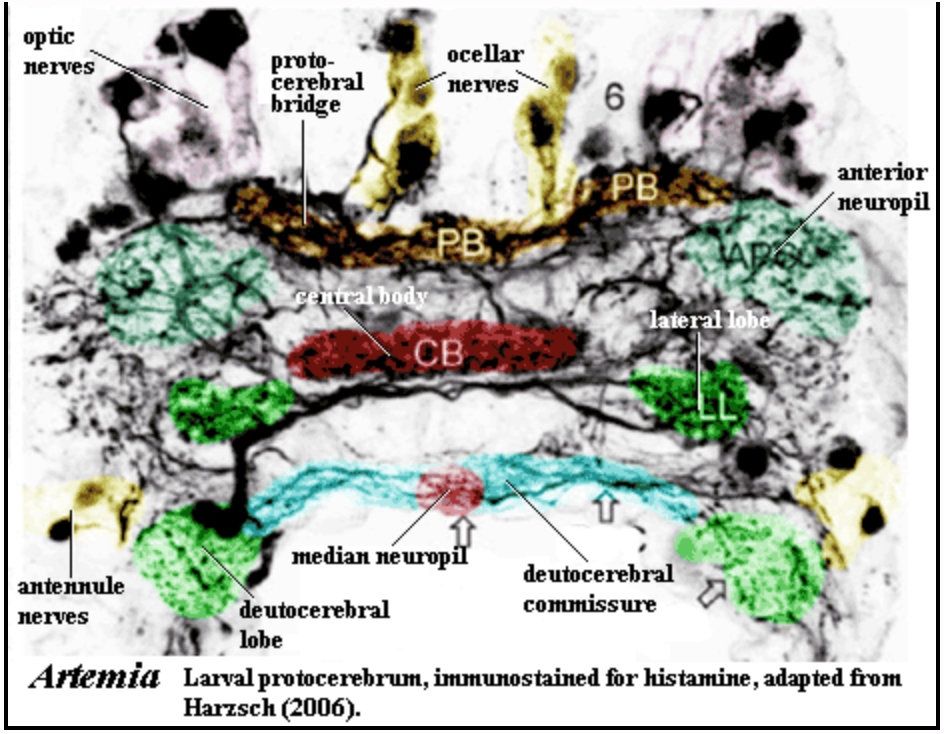
calcite: (geochemistry, biochemistry) one of the two crystal forms of calcium carbonate commonly found in nature. See *aragonite* for more information. The image (from the **Colorado Gem & Mineral Co.**) shows needles of aragonite emerging from a calcite matrix.

calthrop: (sponge anatomy) a four-pointed spicule (*tetractine*) with all four branches of roughly equal size.

carbonic anhydrase: (general biochemistry) an enzyme which catalyzes the formation of carbonate from carbon dioxide and water.

carcinology: the study of crustaceans.

central body: In arthropod neuroanatomy, a median neuropil in the *protocerebrum*, associated with optic



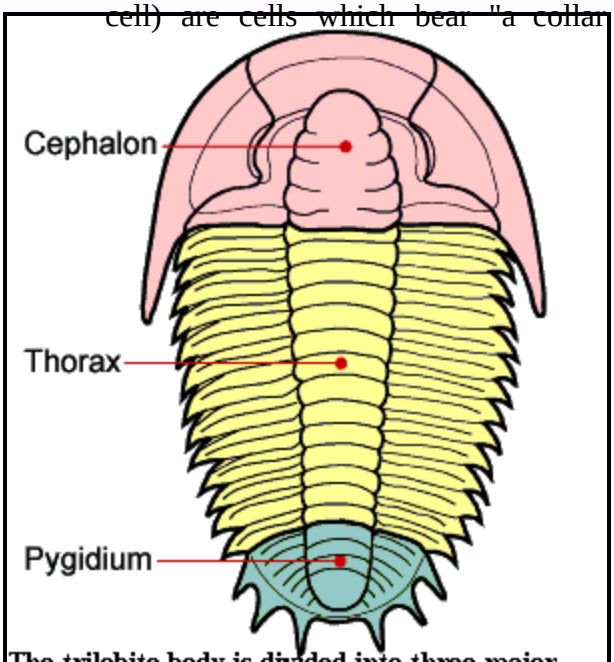
Artemia Larval protocerebrum, immunostained for histamine, adapted from Harzsch (2006).

and/or olfactory processing. The central body is quite large in crustaceans and insects and is associated with other neural structures unique to insects and non-branchiopod crustaceans.

cephalon: (arthropod anatomy) The head. Anterior region of the body bearing the antennules (in Crustacea), antennae, eyes, and mandibles.

-cerite: (crustacean anatomy) a suffix applied to limb elements, suggesting that the element is part of an antenna or antennule.

choanocyte: (sponge anatomy) choanocytes (choano = collar; cyte = cell) are cells which bear "a collar of tentacles surrounding a single anterior flagellum. Undulation of the flagella of thousands of choanocytes creates a current of water that is drawn in from outside the animal, passes through the internal chambers and is expelled through an exhalant opening. Choanocytes are responsible for transporting oxygen-rich water to the internal cavity of the sponge and for bringing food particles, particularly bacteria, to the surface of the collars where they can be ingested." Leadbeater (2001).



The trilobite body is divided into three major sections, a cephalon with eyes, mouthparts and sensory organs such as antennae, a thorax of multiple similar segments, and a pygidium, or tail section

choanoderm: (sponge anatomy) sponge endoderm analogue. The choanoderm is lined with *choanocytes*.

Chuar Group: Neoproterozoic of northern Arizona (USA), with exposures along the Grand Canyon. Composed of the Galeros and Kwagunt Formations (older to younger). The upper limit is constrained to be about 742 My old. Porter & Knoll (2000).

cinctoblastula: sponge embryology. The characteristic larva of Homoscleromorpha, cells with paracrystalline intranuclear inclusions that form a belt around the posterior pole. Leys & Erevskosky (2006).

clade: a natural group, i.e., a group consisting of a particular organism and *all* of its descendants, i.e. a *monophyletic* group. Example: Dinosauria, defined as the last common ancestor of *Triceratops* and *Corvus* (the crow) and all of its descendants.

coenosteum: in stromatoporoid (sponge) anatomy, the calcitic skeleton.

collagen: the major insoluble fibrous protein in the extracellular matrix and in connective tissue. It is the single most abundant protein in Metazoa. There are at least 16 types of collagen, but types I, II, and III predominate. These collagen molecules pack together to form long thin fibrils. Type IV, in contrast, forms a two-dimensional reticulum. The various collagens and the structures they form all serve the same purpose, to help tissues withstand stretching. The basic structural unit of collagen is a triple helix. The triple-helical structure of collagen is produced by the characteristic repeating motif Gly-Pro-X, where X can be any amino acid. Each amino acid has a precise function. The side chain of glycine, an H atom, is the only one that can fit into the crowded center of a three-stranded helix. Hydrogen bonds linking the peptide bond NH of a glycine residue with a peptide carbonyl (C-O) group in an adjacent polypeptide help hold the three chains together. (quoted, with slight modifications, from **Lodish *et al.*, 2000**).

collagen, type IV: The characteristic collagen of the *basement membrane*. "The type IV collagen molecule is a long triple helix containing several interruptions, which is characterized by a specific carboxyl-terminal, non-collagenous NC1 domain. Among the six different a chains (numbered 1 to 6) of type IV collagen it is generally assumed (although not definitely demonstrated) that the more frequent molecular stoichiotry is of two a1, a3 or a5 chains for one a2, a4 or a6 chain, respectively." Boute *et al*. (1996).

collencyte: (sponge biology) a cell which is specialized to produce collagen.

coxa: the most proximal segment of a crustacean appendage. See image at *protopod*. See Dr. Joel Martin's **Crustacea Glossary** for details and exceptions.

cruciform: in the shape of a cross.

cruciform cells: (sponge development) four specialized, possibly photosensitive cells, one in each quadrant, near the equatorial plane of certain calcareous sponge embryos. Amano & Hori (2001); Leys & Degnan (2001).

cryptic habitat: in ecology, a class habitat in which the organism is largely enclosed, including underground burrows, caves, under rocks, within the shells of other dead or living organisms, etc.

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Invertebrate Glossary D-G

```
LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```

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A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

D

decapentaplegic: a gene (*dpp*), a transcriptional regulator associated with formation of viscera. See Hox Genes.

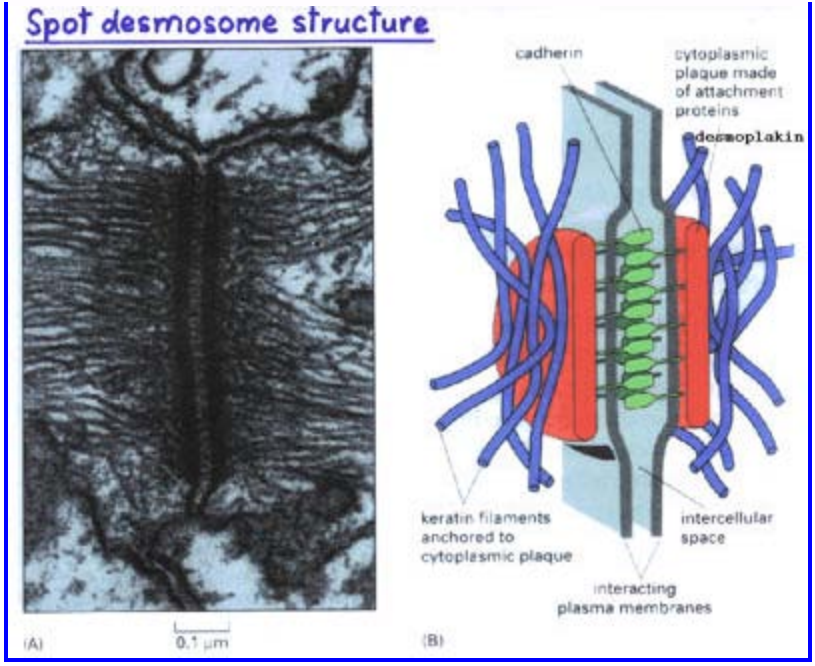
Deformed: a gene, abbreviated *dfd*, a hox4 homologue of arthropods. See Hox Genes.

desmosome: a portion of a cell membrane specialized for contact with other cells. This is an important structure shared by all Eumetazoa. Wikipedia has an excellent short discussion. More information ans electron micrographs of vertebrate desmosomes may be found here.

deuterocerebrum: same as *deutocerebrum*.

deutocerebrum: (arthropod anatomy; also called deuterocerebrum) the portion of the arthropod brain in the segment 1 (acron = #0). In Crustacea, it is associated with chemosensation and olfaction through the *antennules*.

dfd: abbreviation for *Deformed*, a hox4 homologue



of arthropods. See Hox Genes.

diactine: (sponge anatomy) a spicule or spicule axis with two rays. *See* Spicule Terms.

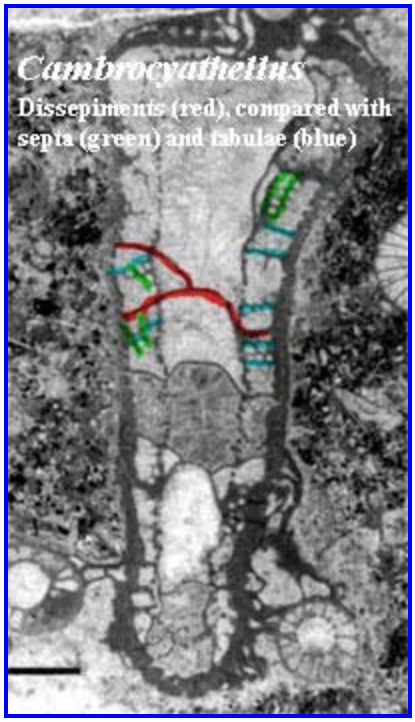
diagenetic: in paleontology, used to describe a change in chemical composition or crystalline structure which occurs during fossilization.

diaxon: (sponge anatomy) a spicule with two axes. *See* Spicule Terms.

diploblast: an animal having only two fundamental embryonic layers, i.e., lacking mesoderm.

dispherula: (sponge embryology) the characteristic larva of the Halisarcida, consisting of two balls of cells, one inside the other. Both are lined with ciliated cells. The cilia of the outer layer face outward. Those of the inner ball, outward. The dispherula arises from a process which looks very much like classical eumetazoan gastrulation, i.e. by invagiation of ectodermal cells at one point (*emboly*).

dissepiment: "dissepiment: 'partition'; a horizontal, or nearly horizontal, plate of tissue supporting a tabula in an archaeocyathan or coral skeleton; a connecting structure in the rhabdosome of a dendroid graptolite." Benton & Harper (1997).



distalless: a gene (*dll*), a transcriptional regulator associated with formation of appendages. See Hox Genes.

dll: see *distalless*.

dmbx: a class of homeobox transcription factor genes found only in cnidarians and deuterostomes. During development, it is expressed at the anterior limit of hox expression. See Hox Genes.

dolomite: (geology) calcium magnesium carbonate, $CaMg(CO_3)_2$. In practice, calcium carbonates fall in a continuum from pure calcite, with no magnesium, through high-magnesium calcite, to dolomite (50% magnesium), and even to magnesite (magnesium carbonate). The substitution of magnesium for calcium ions in calcite skeletons can occur diagenetically (after death). This process is called **dolomitization.**

dorsal: (bivalve anatomy) on the edge, or in the direction of the edge, bearing the hinge ligament and (usually) the curved peaks of the *umbos*. If the

Doushantuo Fm: (geology) "The ... Doushantuo Formation is of early [Ediacaran] age, ~590 Ma at its base to ~565 Ma at its top. It is represented by a phosphate-dolostone sequence in Wengan, where it is 33 to 55 m thick and consists mainly of dark phosphate, cherty phosphate, chert, and gray dolomite. ... About 15 km west of the county town of Wengan on Beidaoshan, the Doushantuo Formation consists of three units: the Lower Phosphate unit (20 m

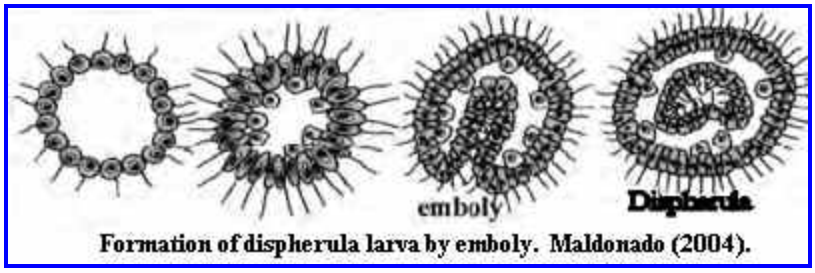
thick), the Middle Dolostone unit (3.7 m) and the Upper phosphate unit (15 m)." Li *et al*. (1998).

dpp: see *decapentaplegic*.

E

element: a segment of a segmented appendage.

emboly: (embryology) gastrulation by invagination of cells at a particular point.



Formation of dispherula larva by emboly. Maldonado (2004).

en: abbreviation for *engrailed*.

endite: In Crustacean anatomy, usually an appendage element projecting downwards or inwards from the *protopodium*. See image at *protopod*. See Dr. Joel Martin's **Crustacea Glossary** for details and exceptions.

endo-: **1)** In anatomy, a prefix suggesting that the structure lies, grows, or points below or within the root structure (e.g. *endoderm*). **2)** In crustacean appendages, it suggests that a limb element grows ventrally or ventrolaterally, generally as an outgrowth of the protopod (e.g. *endite*, *endopod*).

endopod: See image at *protopod*. The crustacean appendage is often described as "biramous." The idea is that the crustacean appendage splits, distal to the protopod, into two axes, the exopod and the endopod. The endopod is usually conceived to be a continuation of the main axis. The assumed evolutionary scenario is that the endopod was a swimming appendage, while the exopod was a gill. Many crustacean appendages don't actually look like this, and the actual evolution of their structure may have been quite different and various. However, this is the ground-plan which carcinologists almost always have had in mind when they describe the details of an appendage. We must learn this frame of reference or remain befuddled by terminology which makes sense (if at all) only as an expression of this particular "anatomical philosophy," to borrow Janvier's (1996) useful phrase. On the other hand, we must also be careful to understand that the "biramous appendage" is, at most, only a conceptual tool among other tools. The problem with having a good hammer is that we may come to approach all problems as nails. The problem with the "biramous appendage" is that we may go beyond using it as morphological shorthand and begin to accept its unstated assumptions about evolution, development, and homology as proven fact. See Dr. Joel Martin's **Crustacea Glossary** for details and exceptions.

engrailed: a homeobox gene associated with segment formation in crustaceans and some insects, abbreviated *en*.

epi-: **1)** In anatomy, a prefix suggesting that the structure lies, grows, or points above or out from the root structure (e.g. *epidermis*). **2)** In crustacean appendages, it suggests that a limb element grows dorsally or dorsolaterally, generally as an outgrowth of the protopod (e.g. *epipod*). **3)** In development or evolution, a prefix suggesting that a structure, form, or process is a later addition to, or elaboration of, the root structure, form, or process (e.g. *epigenetic*, *epimere*).

epifauna: the animal community living on the sea bottom -- *not* in, under, or above the bottom. Epifauna walk on, or are attached to, the bottom, but with the bulk of their bodies in the water column.

euryhaline: tolerating a broad range of salinities

even-skipped: a *Drosophila* homeobox gene of the evx class associated with segment formation.

evo-devo: evolutionary developmental biology. For an explanation, see Why we care.

evx: a class of homeobox genes. Evx genes are associated with segment formation in some arthropods.

exo- or **exi-**: **1)** In anatomy, a prefix suggesting that the structure lies, grows, or points out from the root structure. **2)** In crustacean appendages, it suggests that a limb element grows laterally, generally as an outgrowth of the protopod.

exopod: In crustacean anatomy, the structure conceived of as the dorsal branch (from the *protopod*) of the original biramous limb. See *endopod* for explanation and complaints. The exopod typically consists of several elements (segments). See image at *protopod*. See Dr. Joel Martin's **Crustacea Glossary** for details and exceptions.

F

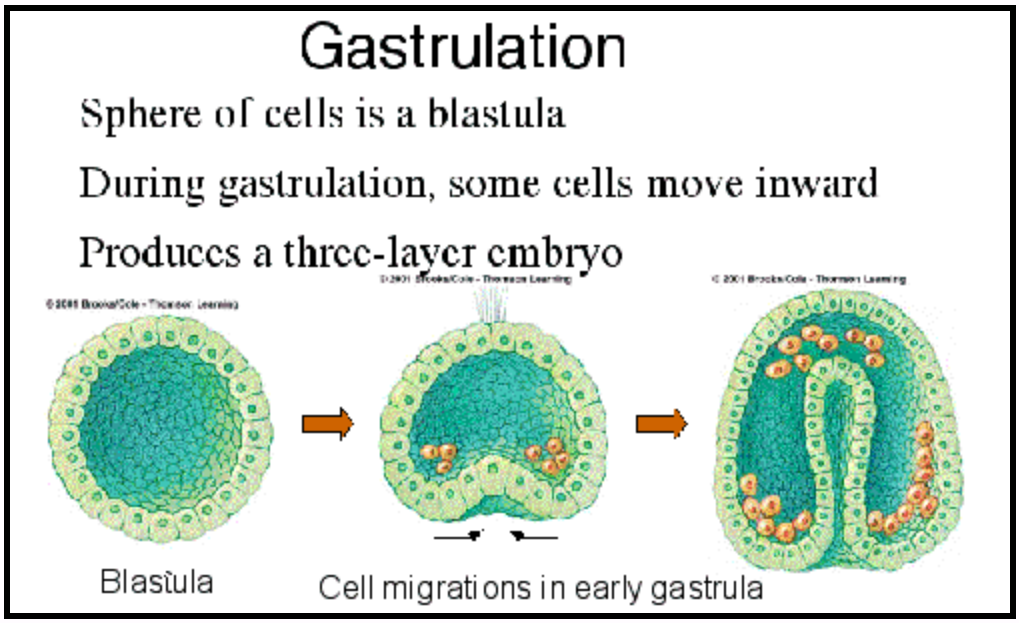
flagellum: (pl. *flagella*) A eukaryotic flagellum is a bundle of nine fused pairs of *microtubules* called "doublets" surrounding two central single microtubules (the so-called 9+1 structure of paired microtubules; also called the "axoneme"). At the base of a eukaryotic flagellum is a microtubule organizing center about 500 nm long, called the *basal body* or kinetosome. The flagellum is encased within the cell's plasma membrane, so that the interior of the flagellum is accessible to the cell's cytoplasm. This is necessary because the flagellum's flexing is driven by the protein dynein bridging the microtubules all along its length and forcing them to slide relative to each other, and ATP must be transported to them for them to function. This extension of the cytoplasm is called the *axosome*. **Important note:** The eukaryotic flagellum is completely different from the prokaryote flagella in structure and in evolutionary origin. The only thing that the bacterial, archaeal, and eukaryotic flagella have in common is that they stick outside of the cell and wiggle to produce propulsion. From **Flagellum - Wikipedia**. Image: O'Kelly *et al*. (1999).

G

galectin: a lectin which binds galactose. See excellent short discussion at **Galectin**.

gamete: haploid sex cell, *i.e*. egg or sperm cell.

gastrulation: (embryology) Actually, there is no iron-clad definition of gastrulation. Classically, it is the series of moves an embryo makes to form a gut.



glyconectin: a family of glycoproteins, each member of which is capable of tight, specific adhesion to other copies of the same protein. Glyconectins are the basis for cell-cell adhesion in at least some sponges.

gonochoric: having two distinct sexes, dioecious.

guild: in ecology, a group of organisms having a similar morphology, and exploiting the same food resources, living the same life-style and in the same environment, but which are not necessary related. Because no two types of organisms can occupy the same ecological niche (one will inevitably outcompete the other, and push it aside), comparable guilds have to be separated by geographical or chronological distance. A good example of the same guild is the Crocodilian today, and the phytosaurian thecodont (parasuchia) of the late Triassic. Both are astonishingly similar in size, appearance, and life-style, and indeed modern crocodiles only appeared after the phytosaurs had become extinct. But they are only distantly related (both are archosaurian reptiles, but their common ancestor lived millions of years before the first phytosaur appeared). MAK010510.

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Invertebrate Glossary H-N

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LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```

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A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

H

helix-turn-helix: another diverse and important DNA-binding protein motif, including many transcription factors, not to be confused with helix-**loop**-helix. For figure and brief discussion see Helix-Turn-Helix.

hexactine: (sponge anatomy) a spicule with six rays. *See* Spicule Terms.

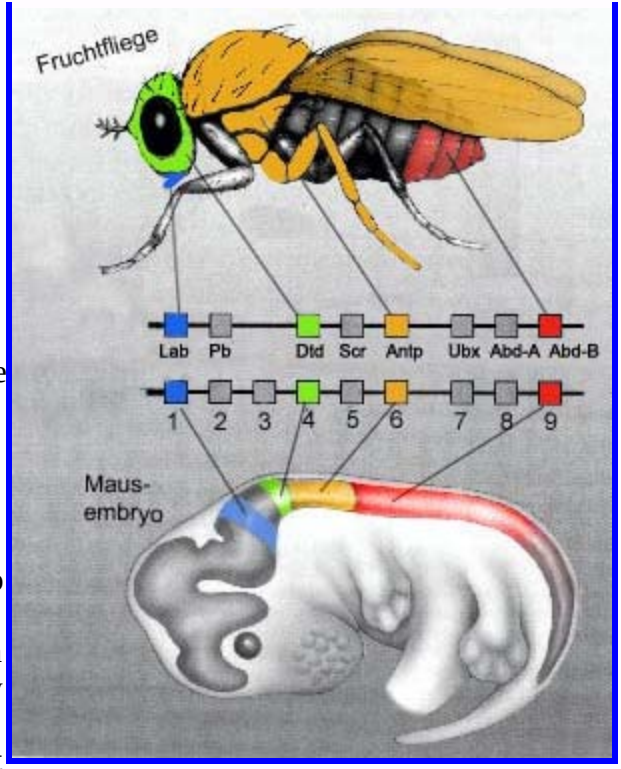
histogenesis: (embryology) formation of tissues.

holoblastic: (embryology) type of cleavage of the very early embryo in which the planes of cleavage divide the entire embryo.

homeobox: (molecular biology) The DNA sequences corresponding to the *homeodomain*.

homeodomain: a particular DNA-binding protein motif containing about 60 amino acids. Proteins with a homeodomain are encoded by *homeobox* genes. The homeodomain proteins are important transcriptional regulators, particularly in embryonic development. They include the hox genes.

homeotic mutation: a mutation in which anterior structures are



shifted to, or (more often) repeated in, more posterior parts of the body.

hom gene: alternative name for hox genes.

homology: two genes are homologous if they derive from a single ancestral gene. This isn't a precise term, because genes can pick up bits and pieces of other DNA through various types of transposition or errors during mitotic recombination. At some point -- a point which has no objective definition -- it is no longer homologous. Homology between structures is a concept in flux. The theoretical definition has always been essentially the same as homology applied to genes. That is, homologous structures are the phenotype resulting from homologous genes. However, for both historical and practical reasons, the definition is often confused with the operational *tests* of homology; "similarity," "congruence," and (sometimes) "conjunction." See, e.g. Witmer (1995); Hutchinson (2001). However the ultimate issue in homology is always ancestry. See also *paralogy*, *orthology*.

homonomous: anatomy. Having repeated, identical structures (usually said of body segments).

homoplasy: "convergent evolution" Similar structures/genes which are not homologous are homoplastic.

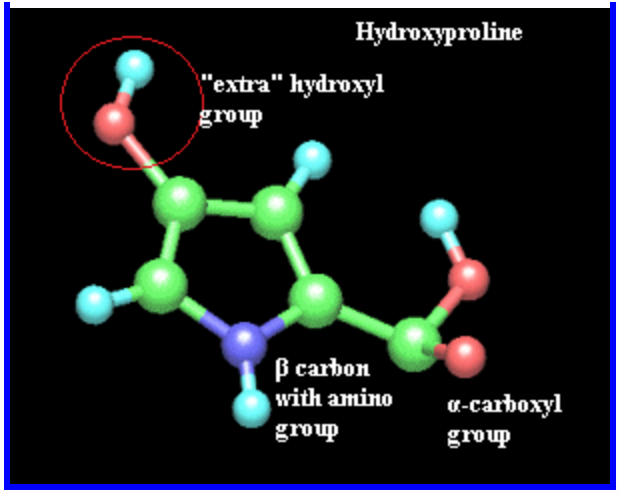
hox: see Hox genes for an extended discussion. Hox genes are homeobox genes with a special role in development. Homeobox genes are frequently found in clustered groups in the organism's DNA, always (almost) in the same order. The jaw-dropping and eyebrow-raising feature of hox genes is that their order along the organism's DNA corresponds to the physical order in which these genes are first expressed along the anteroposterior axis of the body during development. For example, the first member of the series is expressed in the anterior part of the head, and the last is expressed in the most posterior part (typically, the telson, or "tail"). The metazoans include animals with almost every imaginable variation on this theme, but arthropods, and vertebrates, and various other phyla all have essentially identical homeobox genes, in the same order, all expressed in (almost) the same order along the anteroposterior axis. It is almost universally believed that these homeobox genes specify the type of segment which will develop and the type of appendages (if any) that the segment will produce. The term *hox* is sometimes used to refer to all homeobox genes. However, *hox* is not the only class of homeobox genes. There are many others. In addition, some of the *hox* series are recycled later in development for other purposes, such as helping to specify the proximal to distal axis of the appendages.

hsp70, (biochemistry) a class of "chaperone" proteins which assist in the folding of other newly synthesized proteins. Hsp70 proteins have a particular target preference for hydrophobic amino acid sequences.

hydroxyproline: (biochemistry) an atypical amino acid. Hydroxyproline is not found in the genetic code. Instead it is made from proline enzymatically, after this amino acid has already been incorporated into a protein. Hydroxyproline is common in collagens.

hypomorph: a mutant phenotype which is characterized by quantitative changes.

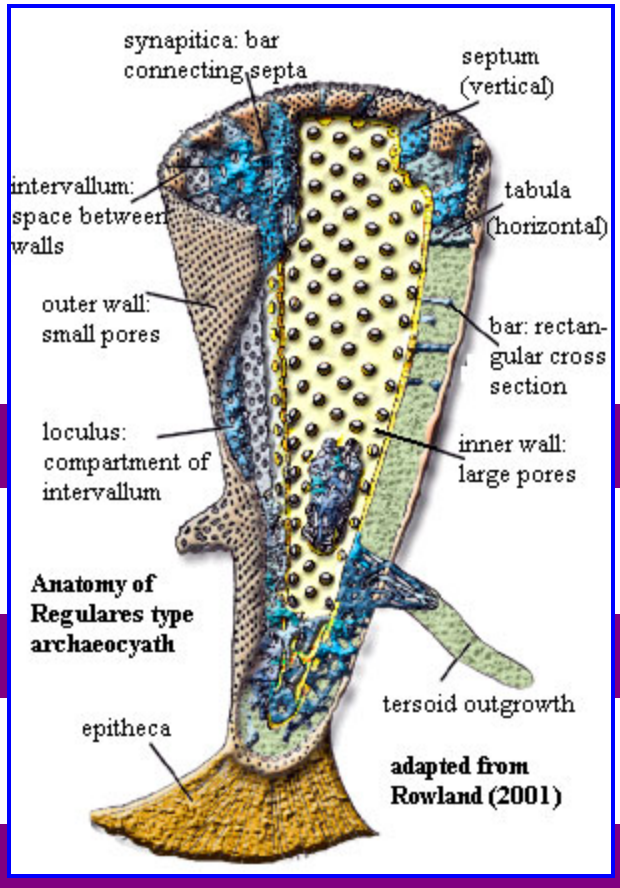
hypostome: "The hypostome is a ventral sclerotic plate between the antennulae and the antennae (with sclerotic extensions, named



wings, which serve as holdfast for limb musculature), while the labrum is a soft, bulged outgrowth at the posterior end of the hypostome, only present in labrophoran Crustacea (most likely originating from the distal part of the mouth membrane, well developed in *Agnostus pisiformis* [a trilobite] ... . Accordingly, both structures are not the same and cannot be synonymized, thus." Stein *et al*. (2005).

I

instar: any discreet stage in a developmental series separated by successive molts, metamorphoses, etc.



intervallum: in archaeocyath anatomy, the space between the inner and outer walls.

intron: part of a gene which is flanked on both sides by sequences coding for the corresponding protein, but which is not itself part of the coding sequence.

-ite: (Crustacea) a suffix applied to appendage elements, perhaps originally meant to suggest that the element was a secondary outgrowth from the main axis, but now essentially meaningless.

J

K

L

lab: abbreviation for *labial*, the hox1 homologue of arthropods. See Hox Genes.

labial: (a) towards the periphery of the mouth (b) of or related to lips (c) a gene, abbreviated *lb*, the hox1 homologue of arthropods. See Hox Genes.

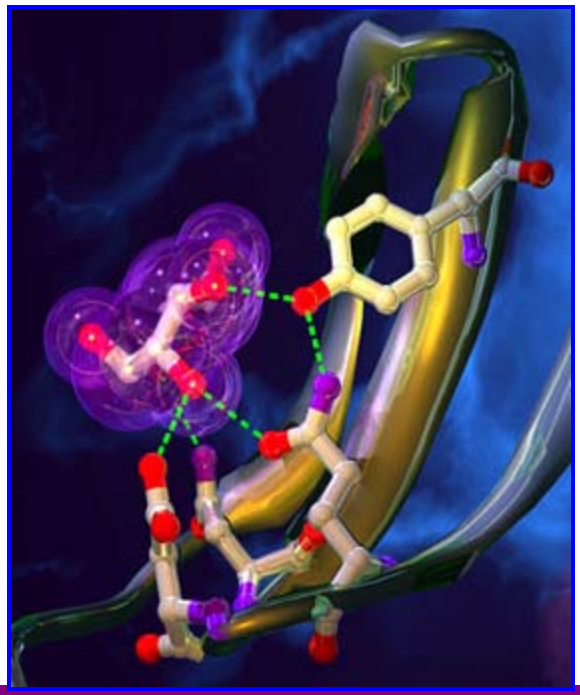
lamina, lamination: originally a flat metal plate (for example, the red-hot *laminae ardentes* used as torture device by the Romans). In biology or geology, a layer. Anything with numerous layers is thus *laminated*.

latilamina: in stromatoporoid anatomy, a region where the horizontal elements are closely spaced, and vertical

elements may terminate, conceived as a temporary region of slow or halted growth.

lecithotrophic: (embryology) larval development in which the embryo is largely or completely non-feeding, living on stored yolk.

lectin: a large and important superfamily of animal proteins which bind tightly, and very specifically, to particular sugar residues of glycoproteins.



lithistid: formerly, a taxonomic group of sponges, now generally regarded as polyphyletic. The lithistids have massive, silicate skeletons created by fusion of spicules. However, this appears to be a body plan which evolved several times within both the demosponges and hexactinellids. The term is sometimes used in a quasi-phylogenetic way to refer only to the demosponge lithistids.

loculus: generic anatomical term for any small compartment or recess, e.g. the spaces in the *intervallum* of an archaeocyath.

lophose: (sponge anatomy) of spicules, branched.

lorica: (anatomy) a hard shell, coating or crust around an organism. Maggenti *et al*. (2005).

M

MADS-box: protein structure, evo-devo. A DNA-binding protein motif present in almost all Eukarya, but particularly important in plants. See MADS box gene home page.

magnetic resonance imaging: *see MRI*.

mamelon: in sponge anatomy, a low, rounded protruberance, conceived of as being centered on a primary water inhalant (or, possibly, exhalant) pore.

manca: a type of isopod larva which is morphologically similar to the adult but lacks a seventh pair of pereonic appendages.

mandible: in crustacean anatomy, the most anterior pair of mouth parts, derived from the appendages of the third cephalic segment.

maxilliped: Crustacea. Anterior thoracic limb exapted to act as mouth part, with its body segment usually fused to the head (*cephalon*).

megasclere: (sponge anatomy), a large, typically elongate, sponge spicule.

mesohyl: (sponge anatomy) acellular layer between *pinacoderm* and *choanoderm*. The mesohyl contains spicules and amoebocytes.

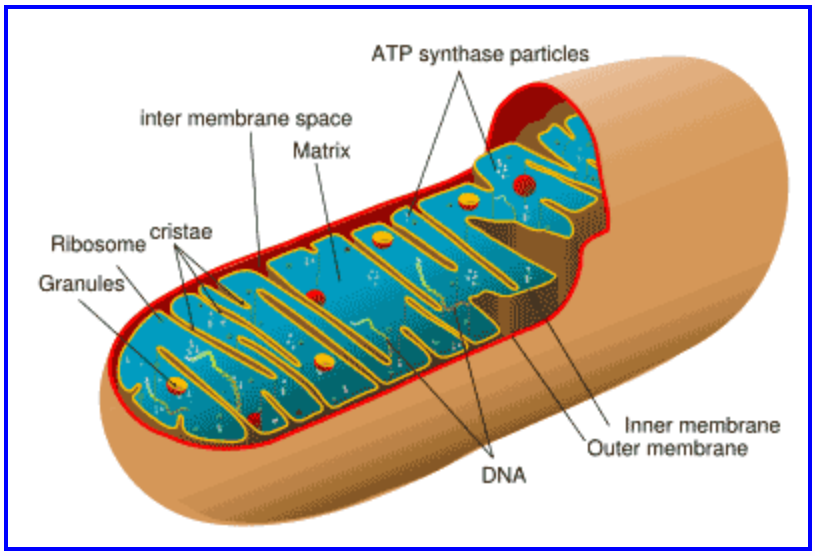
metamere: in anatomy or development, a segment, usually a body segment.

metamerization: segment formation.

microbialite: ""Burne and Moore (1987) introduced the term *microbialite* as [meaning] organosedimentary deposits of benthic microbial communities and, following this definition, stromatolite can be seen as a type of microbialite showing lamination as a specific feature." Dupraz *et al*. (2006), *citing* Burne RV & LS Moore (1987), *Microbialites: organosedimentary deposits of benthic microbial communities*. **Palaios** 2: 241– 254 (which we have not personally read).

micromere: in embryology, the smaller of the two daughter cells from an unequal division. More generally, any small cell.

microsclere: (sponge anatomy), a small spicule.



mitochondrion: an organelle responsible for most of the oxidative metabolism in the cell. There is far too much to cover in a glossary definition. See Mitochondrion - Wikipedia for a relatively brief introduction.

monactine: (sponge anatomy) a spicule or spicule axis with only one ray. *See* Spicule Terms.

monaxon: (sponge anatomy) a spicule with only one axis. *See* Spicule Terms.

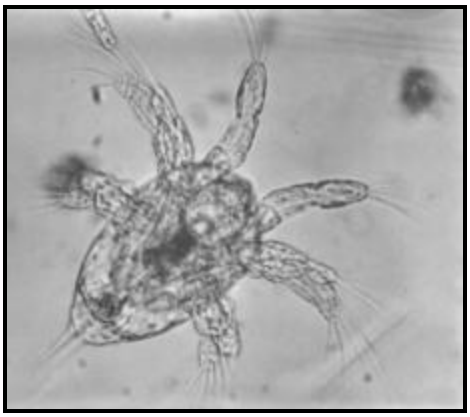
mox: a class of homeobox genes, one of which is frequently located just upstream of the hox cluster (if one exists). See Hox Genes.

MRI: magnentic resonance imaging. The protons in the nucleus have a quantum mechanical property called "spin." It has nothing much to do with rotation, but it is harmless to think of it that way for our purposes. Protons normally pair up, so that net spin is zero if the nucleus has an even number of protons. However, if the element has an odd atomic number, one proton is unpaired, most significantly in hydrogen, with just one proton. exposing these atoms to an intense magnetic field forces the spins to line up (again, the analogy to an axis of rotation is false, but harmless). The target is then pulsed with electromagnetic radiation which causes some of the protons to flip. Between pulses, the protons flip back, causing a slight disturbance in the magnetic field. The wave form of this disturbance is what is actually measured. It is exquisitely sensitive to the chemical environment of the proton in hydrogen, and yeilds a detailed three-dimensional map. Unfortunately, this requires the use of Fourier transforms, which cause our eyes to cross, followed rapidly by tremors, catatonia, and eventual death. Thus we will quit now.

mu (µ): the Greek lower case mu alone, or as as "µm" signifies a micron or micrometer = 10^{-6} meters = 0.001 mm = 1000 nm, about the diameter of a small bacterium.

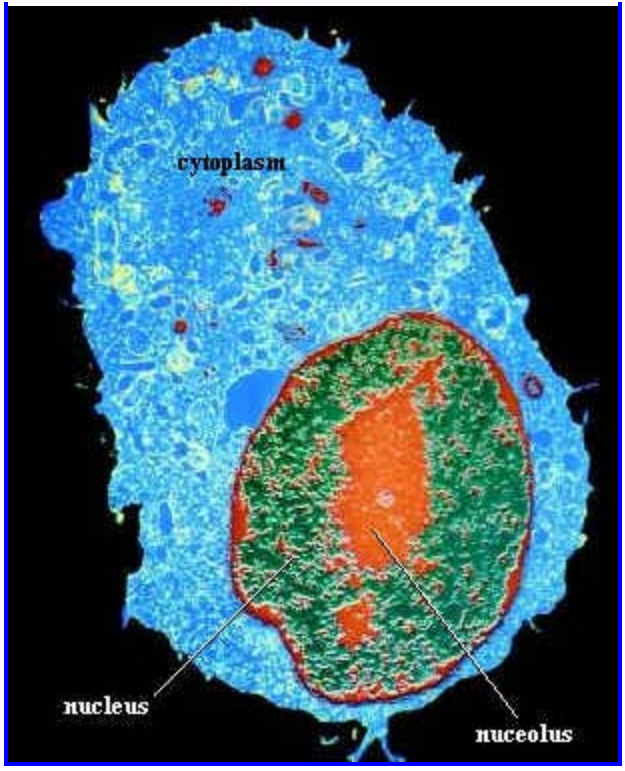
N

nauplius: (crustacean embryology) first larval stage of crustaceans, in which the larva has three pairs of appendages. These will later become antennae and a pair of anterior mouth parts.



neuropil: (neuroanatomy) a brain, or any large collection of neurons (ganglion), consists of cell bodies with a nucleus and all the usual machinery of metabolism, plus long cell processes which actually do the work of transmitting signals. A neuropil is a dense tangle of these processes. The cell bodies normally sit outside the neuropil, where they won't get in the way, and where they will have easier access to the glial (non-neuronal) support cells.

nucleolus: (cell biology)
a dark staining body in the nucleus of many eukaryotes which is associated with the production of ribosomal RNA.



S T U V W X Y Z

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Last Revised: ATW070825
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Metazoa Glossary O-Z

```
LIFE
|--Eubacteria
`--+--Archaea
   `--Eukarya
      |--Chlorobionta
      `--+--Fungi
         `--METAZOA
            |--Choanoflagellata
            `--Porifera
               |--Radiata
               `--+--Cnidaria
                  `--Bilateria
                     |--Deuterostomia
                     `--Protostomia
                        |--Ecdysozoa
                        `--Spiralia
```

The eventual aim is to combine all the glossaries distributed throughout the metazoan section. This will takes many years.

A B C D E F G H I J K L M N O P Q R S T U V W X Y Z

O

obrution: in paleontology, sudden burial, as by a storm, turbidite flow, etc.

ocellus: a simple (*i.e.*, not compound) eye.

orthology: two genes are said to be *orthologous* if they are *homologous* and are found in the same organism. This is generally pointless word, for the same reasons discussed under *paralogous*.

orthogonal: having each axis at right angles to all other axes, like a Cartesian coordinate system.

osculum: (sponge anatomy), a large excurrent opening. Sometimes called **oscule**.

oviparous: egg-laying, as opposed to having live young.

P

paracrystalline: in some areas of chemistry and physics, this word has a fairly precise meaning referring to short-range order, without a fixed long range structure. In biology, it tends to be used in a relatively sloppy manner to mean "sort of crystalline." We understand that it used to describe the characteristic "sparkle" of small crystalline regions

embedded in an amorphous substance when viewed with traditional light microscopes. Thus, it is essentially a word with an operational meaning, rather than describing a particular physical chemistry.

parahox: a class of homeobox genes. There are typically three paralogues in eumetazoans. Phylogenetically, they are hox genes, but don't seem to function in the same manner. They are sometimes clustered. See discussion at Hox Genes.

paralogous: two genes are said to be *paralogous* if they are *homologous* and are found in the same organism. That is, the two genes derived from duplication of a single gene in some ancestor of the organism. For most genes, that covers a great deal of territory, and the definition is also fuzzy for the reasons described in the *homology* definition. The word is generally useless unless coupled with the name of the gene from which the paralogues are derived. For example, human *hoxa2* is paralogous with any of the hundreds of other DNA-binding proteins in the human genome, so the term *paralogous* isn't very useful. However, if I say that human *hoxa2* belongs to the anterior [hox] paralogy group, I am asserting that this gene is one of several derived from a specific gene, even if I don't know what ancestor owned that gene. Even used in this fashion, the word is rarely all that necessary, and frequently carries a fuzzy implication of analogous function, making it even less clear. Consequently, we will typically avoid using it.

paraphyletic: cladistics. Technically, a paraphyletic group is one which contains an ancestral organism and some, but not all, of its descendants. A paraphyletic group is therefore not a clade, since a clade must include *all* the descendants of a chosen organism. In ordinary use, "paraphyletic" is a term is used to indicate that a clade is simply bigger than we thought it was, because it is found to include groups which were thought to be unrelated. The classic example is Dinosauria (*Tyrannosaurus* + *Stegosaurus*). It was commonly said that Dinosauria was "paraphyletic," after we learned that birds are also descendants of the last common ancestor of these two dinosaurs. Butthis discovery means only that birds are dinosaurs. Dinosauria is still a clade, because we defined it cladistically. Think of it this way: we may define your family cladistically as consisting of your parents and all of their children. One day, you learn that you actually have an Evil Twin, a psychotic megalomaniac who has been confined to a secret underground bunker since he used his mutant telepathic powers to enslave a baby-sitter at age 4. You still have a family. It's just a little bigger and more diverse than you had been led to expect.

parenchymella: (sponge embryology) "The parenchymella type is the larva of many demosponges, a group comprising the largest taxonomic class in the phylum Porifera. Parenchymellae are 150 to 5,000 µm in length, 30 to 500 µm in width, externally ciliated, solid, and have just a few cell types. They are lecithotrophic" (*i.e.* don't feed and derive energy from maternal yolk). Maldonado et al. (2003). *See* images at Demospongiae.

parthenogenesis: process of producing, or ability to produce, offspring without fertilization of the egg.

pax-6: a homeodomain transcription regulator associated with eye development in many bilaterians. See Hox Genes.

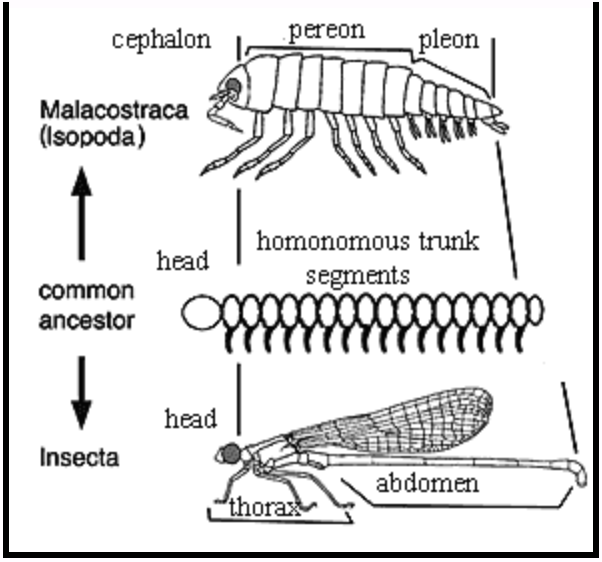
pb: abbreviation for *proboscipedia*, the hox2 homologue of arthropods. See Hox Genes.

pedipalp: Arachnid anatomy. "Pedipalps, the second pair of appendages of the cephalothorax in Arachnida, is homologous with mandibles in Crustacea, and corresponding to the mandibles of insects. The pedipalps are appendages of six segments: the coxae, a single trochanter, the femur, a short patella, the tibia, and the tarsus." Wikipedia 070617.

pereon: crustacean anatomy. Generally, the thorax; the anterior portion of the trunk, posterior to the maxilliped-bearing segments. If part of the thorax is fused to the head (a *cephalothorax*), the term refers to the unfused portion. The pereon typically includes 6-7 segments (*pereonites* or *thoracomeres*) and bears uniramous appendages which are used for locomotion. The region posterior to the pereon is the pleon (abdomen). Image adapted from Abzhanov & Kaufman (2000).

phenotype: the observable characteristics corresponding to a particular DNA complement, or genotype. For example, humans whose genotype includes an extra copy of chromosome 21 show the phenotype known as Down's Syndrome.

phylogenetic: used to describe a system, tool, technique or grouping



which attempts to follow or demonstrate the actual evolutionary sequence of events.

photic zone: in ecology, that part of the water column and sea bottom within which sunlight penetrates in sufficient amounts to permit photosynthesis.

phototaxis: movement in response to light.

pinacocyte: flat cells which form the pinacoderm. The pinacocytes may form a closely-packed layer, but may also be loosely arranged, with the intervening space occupied by collagen bundles. Bavestrello et al. (1998).

pinacoderm: (sponge anatomy) sponge ectoderm analogue, containing incurrent pores.

pleon: crustacean anatomy. The abdomen; the body region posterior to the pereon, typically with 3-5 segments. The term does not include the post-genital segments and telson, where these elements are present.

plesiomorphic: "primitive." A plesiomorphic character is one retained, essentially unmodified, from the common ancestor of a group.

pleuro-: in anatomy, a prefix or particle meant to suggest that a structure is associated with the side of the root structure.

plicate: folded or, more accurately, pleated or wrinkled.

plugged junction: protein (or at least non-membranous) partition between the *syncytium* and a cell in hexactinellid sponges. The plugged junction is probably permeable to ions and contains pores which seem to allow vessicles to pass through. See image, citations, and additional discussion at Hexactinellida.

-pod: (Crustacea) a suffix applied to appendage elements, perhaps originally meant to suggest that the element was part of the main axis of a leg, but now essentially meaningless.

-podite: (Crustacea) a suffix applied to appendage elements, perhaps originally meant to suggest that the element was a secondary outgrowth from the main axis of a leg, but now essentially meaningless.

-podium: = -*pod*.

podomere: crustacean anatomy. Leg segment.

polyphyletic: a term used to describe a taxon which does not include the last common ancestor of its members. This usually occurs when two separate groups converge on the same form by "convergent evolution" or homoplasy.

porocyte: (sponge anatomy) toroidal cell which forms an incurrent pore. See image at Porifera.

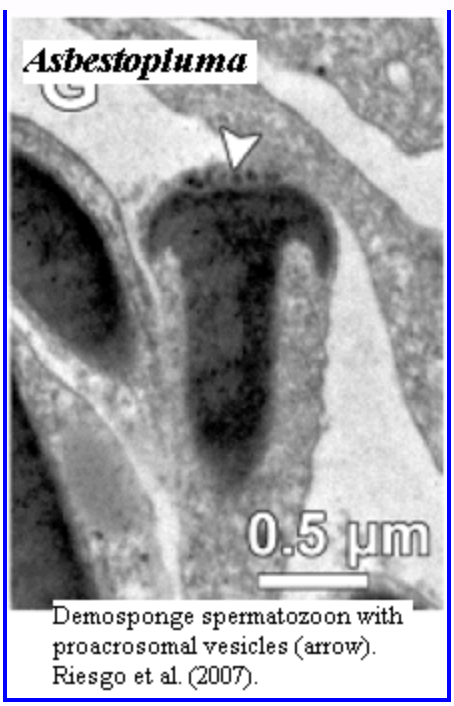
primorph: cultured, "long-term aggregates of ... sponge tissue that were developed as a model system for understanding gene expression during the construction of the adult sponge body plan." Leys & Erevskosky (2006).

proacrosomal vesicle: vesicles formed from the Golgi apparatus in developing spermatozoa. "The round Golgi apparatus of spermatocytes becomes hemispherical in Step 1 spermatids. At this step, the TGR [trans Golgi reticulum, a region of the Golgi apparatus] shows a few dense-cored vesicles (proacrosomal vesicles) and many coated vesicles of different sizes. Proacrosomal vesicles are considered the first intermediates in the formation of the *acrosome*." Martínez-Menarguez et al. (1996). Since the quoted paper deals with rat biology, don't assume that it necessarily applies to all invertebrates.

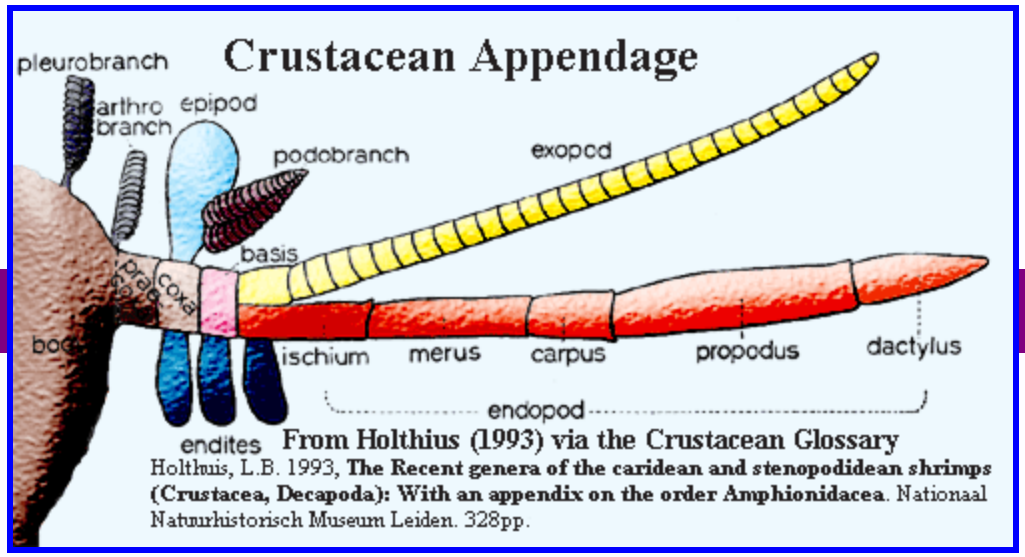
proboscipedia: a gene, abbreviated for *pb*, the hox2 homologue of arthropods. See Hox Genes.

prospyle: (sponge anatomy), "the entry hole/channel/pore leading into the area of choanocytes. It is formed by one donut-shaped cell, the porocyte." Midterm Review.

protocerebrum: (arthropod anatomy) the neural apparatus of the acron, generally the largest part of the brain, associated with vision and chemosensation. See image at *central body*.



Demosponge spermatozoon with proacrosomal vesicles (arrow). Riesgo et al. (2007).



From Holthius (1993) via the Crustacean Glossary

Holthuis, L.B. 1993, **The Recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda): With an appendix on the order Amphionidacea**. Nationaal Naturhistorisch Museum Leiden. 328pp.

protopod: The proximal part of the crustacean appendage, consisting of the proximal *coxa* and more distal *basis*. See Dr. Joel Martin's **Crustacea Glossary** for details and exceptions.

R

receptor tyrosine kinase: "Protein-tyrosine kinases (PTKs) play important roles in the response of cells to different extracellular stimuli. They are divided into two major groups, the receptor tyrosine kinases (RTKs), which are membrane-spanning molecules with similar overall structural topologies, and the non-receptor TKs, also composed of structurally similar molecules." Müller (2001). RTKs are important signal transduction molecules which mediate the effects of various develomental signals.

reticulum, reticular: a network, net- or web-like, or (conceptually) complex and interconnected.

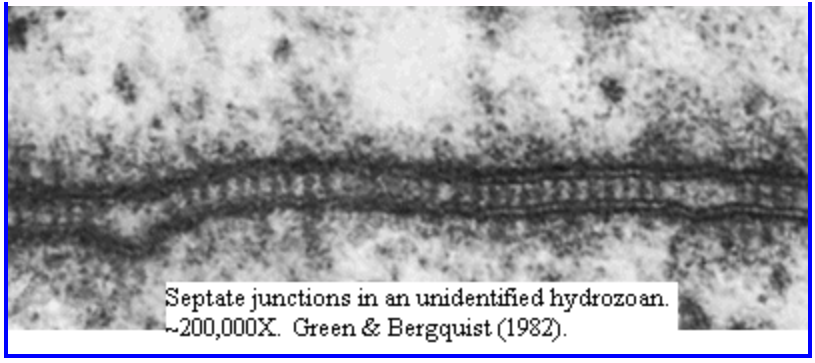
rhizoid: generic anatomical term referring to any outgrowth that looks or acts like a root.

S

sclerocyte: (sponge biology) a spicule-forming cell in sponges. Sclerocytes often work in pairs.

scr: abbreviation for *Sex combs reduced*, a hox5 homologue of arthropods. See Hox Genes.

septate junction: (ultrastructure) "An intercellular junction found in invertebrate epithelia that is characterized by a ladder like appearance in electron micrographs. Thought to provide structural strength and to provide a barrier to


Septate junctions in an unidentified hydrozoan. ~200,000X. Green & Bergquist (1982).

diffusion of solutes through the intercellular space. Occur widely in transporting epithelia and are controversially considered analogous [now probably *homologous* -- ATW] to tight junctions (*zonula occludens*)." Biology Online. "The best-characterized function of invertebrate pleated septate junctions, hereafter referred to simply as septate junctions, is to form a barrier that prevents free diffusion of water and solutes between adjacent epithelial cells ... [S]eptate junctions ... have regularly spaced septa bridging an ~15-nm intercellular space." Wu *et al*. (2004).

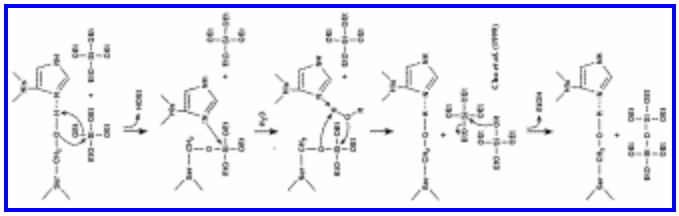
septum: (1) in anatomy, any wall-like structure which divides a space or **(2)** a flexible partition which controls movement between two anatomical spaces. **(3)** In archaeocyath anatomy, one of the vertical walls which partions the *intervallum*.

sessile: opposite of motile. A mode of life in which the organism is fixed to a substrate and does not move.

sex combs reduced: a gene, abbreviated for *scr*, a hox5 homologue of arthropods. See Hox Genes.

silicase: (sponge biochemistry), enzyme in sponges, proposed to be involved in silica restructuring and maintenance. The proposed mechanism involves bound zinc acting as a Lewis acid catalyst to break the silicate ester bond between silicon and oxygen.

silicatein: (sponge biochemistry), enzyme which catalyzes the formation of silicate polymers. Click on thumbnail for details of mechanism from Cha *et al*. (1999).



siliceous: composed of, or containing, silicates.

somite: in crustacean anatomy, a body segment. This word carries no baggage relating to a specific developmental program or germ layer, as it does in vertebrate anatomy. It tends to be used in discussions of development, but is not limited to embryology.

spicule: a mineralized skeletal element.

spongin: (sponge biology) a collagen-related protein which is found as an important structural element in demosponges. Unlike most collagens, it is a glycoprotein and apparently also contains halogen-substituted tyrosine (bromine or iodine).

spongocoel: (sponge anatomy) "the large cavity of tubular sponges through which water passes before being expelled through the osculum." Glossary.

stem: in phylogenetics, (a) a **stem group** is a clade defined in the form "all organisms who are more closely related to their last common ancestor with X than to their last common ancestor with Y." This is usually abbreviated X > Y. (b) more loosely , a "stem X" is any organism more closely related to clade X than to any other clade of equivalent size or importance.

symplesiomorphy: a shared primitive character. This awkward word is actually one of Willi Hennig's most profound contributions. He pointed out that you cannot infer anything about phylogeny from the fact that two organisms share characters inherited from a common ancestor, other than that common ancestry. Example: we suppose that Rudolph the Red-Nosed Reindeer is the founder of a clade (Erythronaria) with living members A, B, C, and D. A and B have

red noses. C and D have green and blue noses, respectively. What phylogenetic facts can we infer? ***None!*** Both C and D are derived, relative to Rudolph, but their noses are *apomorphic* (derived, but not shared). A and B have a shared character, but it is a symplesiomorphy (shared, but not derived). Since none of the reindeer have a shared, derived character (*synapomorphy*) relative to Rudolph, we can draw no phylogenetic inferences and know nothing about the branching order of their descent from Rudolph. *See* further discussion at *synapomorphy*. *See also* Dendrograms: Introduction.

synapomorphy: (cladistics) See background of example at *symplesiomorphy*. A derived character which is shared by members of a group and distinguishes them from other organisms descended from the same common ancestor. Using the same example as at *symplesiomorphy*, suppose that A and B have rednoses, as before, but C and D *both* have blue noses. Since blue nose is a synapomorphy (both shared and derived, with respect to the original red nose) we may correctly infer that C and D are more closely related to each other than either one is to Rudolph, A, or B. That is, C and D form a *clade*. Only synapomorphies may be used to infer phylogeny. We still know nothing about the relative positions of A and B. (Note also that a synapomorphy may be secondarily lost in later descendants, but still "counts" for phylogenetic inference). *See also* Dendrograms: Introduction.

syncytium: (cell biology) a tissue composed of cells without individual plasma membranes. In essence, the entire tissue/organ is a single cell with multiple nuclei. Muscle fibers are usually syncytial.

T

tabulate: having (flat) horizontal partitions, or resembling such a partition. The partitions may be referred to as **tabulae**.

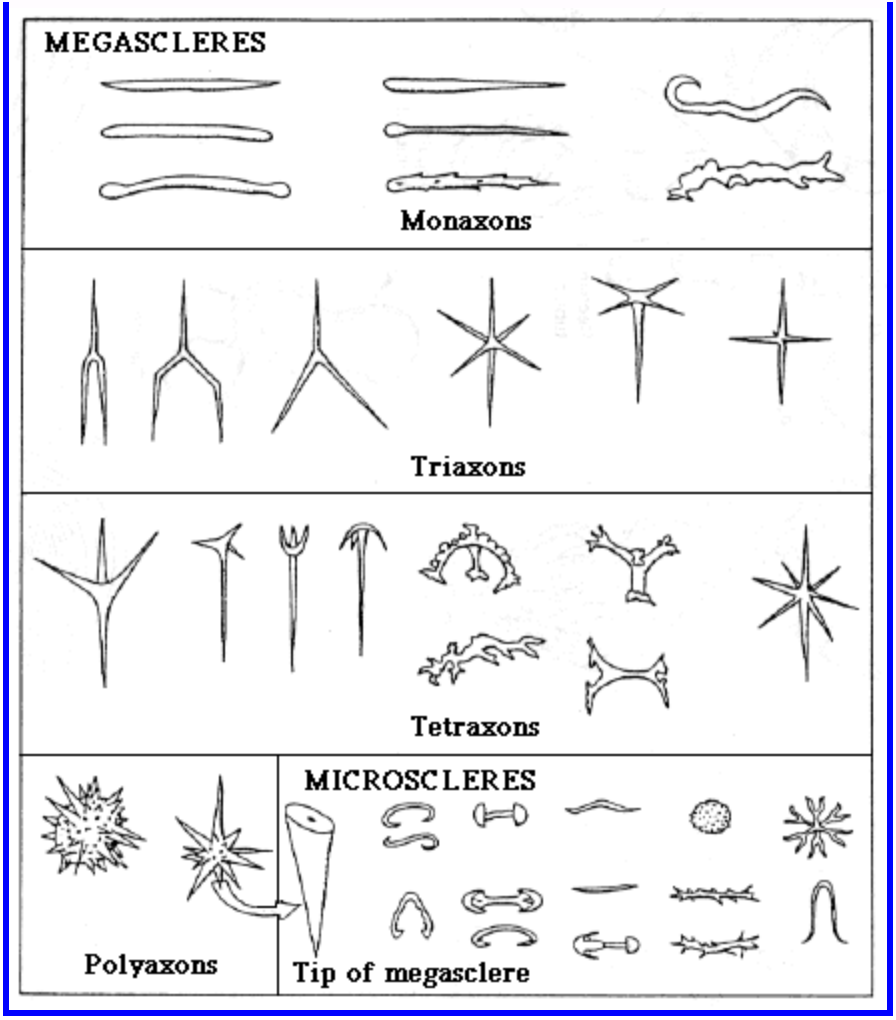
tagma: arthropod anatomy. Plural = **tagmata**. Major body division, made up of several segments with similar specializations, e.g. thorax, abdomen.

tapetum lucidum: the reflective layer of the retina that causes the eyes of, *e.g.*, cats to appear to shine in darkness. An adaptation for vision at low light intensity.

tetractine: (sponge anatomy) a spicule with four rays. *See* Spicule Terms.

tetraxon: (sponge anatomy) a spicule with four axes. Maggenti *et al*. (2005) define the term to include only "spicule[s] of 4 *equal and similar* rays meeting *at equal angles*" (emphasis aded). As far as we know, no sponge has such a spicule. Same as **teraxonid**. According to some sources, same as *quadriradiate*. We suspect this is wrong. Tetraxons may have either four or eight radii. *See* the exmple on the far right of the "Tetraxon" row in the figure. Linguistically, "tetractine" also refers to four points and so is also potentially misleading. *See* Spicule Terms.

thrombolite: a form of microbialite or bacterial "reef." "Stromatolites are microbial structures (microbialites) with internal laminations; thrombolites are microbial masses with clotted internal textures. ... Thrombolites range from the Neoproterozoic to the Recent. They were common in the Cambrian and Ordovician and the Devonian, but rarer though present in every other Phanerozoic system. Thrombolites have a



much more varied environmental distribution than stromatolites, being found in cryptic spaces such as cavity walls as well as on exposed surfaces." Taylor & Wilson (2003). See several images at Irregulares.

tinman: a homeodomain transcription regulator associated with heart development in divers bilaterians. See Hox Genes.

triactine: (sponge anatomy) a spicule with three rays. *See* Spicule Terms.

triaxon: (sponge anatomy) a spicule with three axes. *See* Spicule Terms.

tritocerebrum: (arthropod anatomy) the third and most posterior section of the brain, associated with the *antennae* in crustaceans.

toolkit genes: see Hox Genes. Genes coding for transcriptional regulators which are often adapted for use in different ways during the development of different organisms, or even in the same organism, during different stages of development.

transcription: the process by which RNA is synthesized from a DNA template.

trophic: in ecology, relating to feeding -- not the mechanics of eating, but the issues relating to who eats whom in the ecosystem, food resource allocation and partitioning within a species or guild, etc.

twist: a gene, a transcriptional regulator associated with formation of mesoderm. See Hox Genes.

U

ubx: abbreviation for *ultrabithorax*, a middle class hox gene of arthropods. See Hox Genes.

ultrabithorax: a gene, abbreviated for *ubx*, a middle class hox gene of arthropods. See Hox Genes.

V

vesicle: in archaeocyath anatomy, same as *dissepiment*.

W

Williston's Law: "Williston (1914, p. 21) stated that, 'a law in evolution [is] that the parts in an organism tend toward reduction in number, with the fewer parts greatly specialized in function.' This principle has been inferred to be prevalent feature of invertebrate evolution, for example, within arthropod limbs and body segments ... ." Sidor (2001: 1433).

X

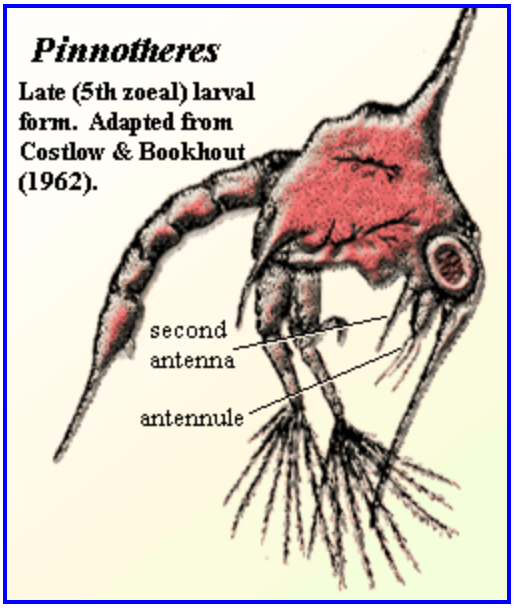
Y

Z

zen: abbreviation for *Zerknüllt*, a hox3 homologue of arthropods. See Hox Genes.

Zerknüllt: a gene, abbreviated for *zen*, a hox3 homologue of arthropods. See Hox Genes.

zoea: In crustacean development, the name sometimes applied to intermediate larval stages (after the *nauplius*). The zoea is a free-living larva with functional thoracic appendages, but appendages on the pleon (if any) are absent or rudimentary.



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Porifera - 1

```
METAZOA
|--Choanoflagellata
`--PORIFERA
   |--Archaeocyatha
   `--+--Stromatoporoidea
      `--+--Calcarea
         `--+--Hexactinellida
            `--+--Demospongiae
               |  |--Tetractinomorpha
               |  `--Ceractinomorpha
               `--+--Homoscleromorpha
                  `--EUMETAZOA
```

Cross Reference Palaeos.org

Porifera

Tube Sponge; photo from Dive Time

The simplest and perhaps the most ancient of all metazoa, sponges are little more than colonial protozoa (choanoflagellates). At one time classified as "Parazoa" and thought to represent a sterile side-branch on the line of evolutionary ascent to humans and butterflies, molecular phylogeny (e.g. Borchiellini et al 2001Sperling et al, 2006) now tends to reveal them as a paraphyletic grade of metazoa ancestors (in other words, we all evolved from sponges, or more technically a sponge-like organism, through loss of choanocytes, spicules, and internal water current system. The humble sponge is indeed more surprising than it at first appears. MAK120110

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page by MAK120110

Porifera - 1

Paraphyletic Grade: Ediacaran to Recent

```
METAZOA
|--Choanoflagellata
`--PORIFERA
   |--Archaeocyatha
   `--+--Stromatoporoidea
      `--+--Calcarea
         `--+--Hexactinellida
            `--+--Demospongiae
               |  |--Tetractinomorpha
               |  `--Ceractinomorpha
               `--+--Homoscleromorpha
                  `--EUMETAZOA
```

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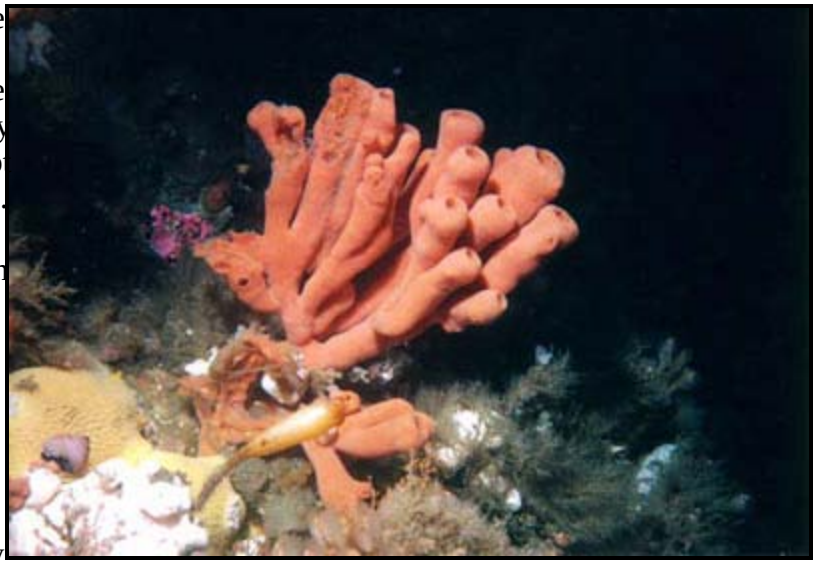
Organization of the Sponge
Sponge Evolution
Classification of the Sponges
Ecological Role
Dendrogram
References

Introduction

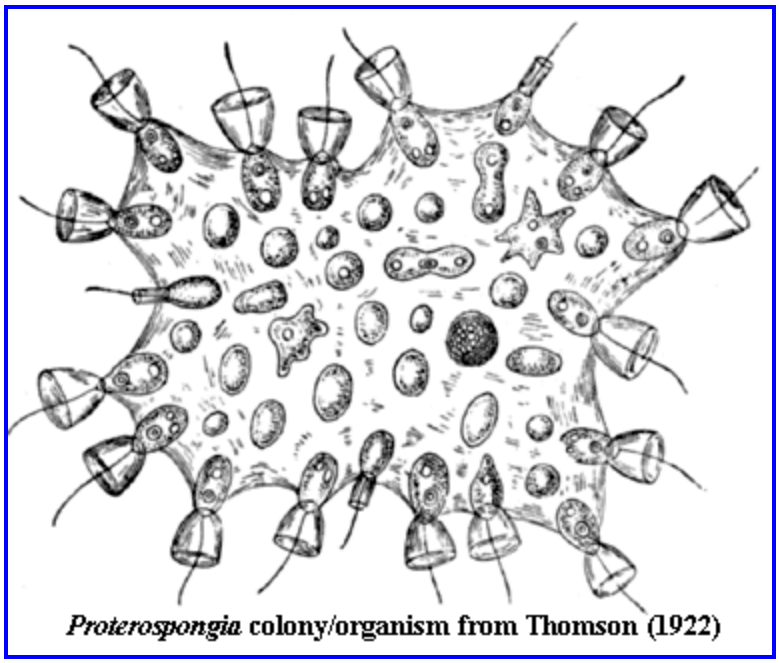


Sponges are an absorbing topic. If we were to define Porifera cladistically (*e.g.* as Porifera = Calcarea + Hexactinellida), then essentially all animals would be poriferans. That's because the Porifera, as usually conceived, are not a "natural group." They do not include all of the descendants of a single organism. Instead, they probably include only the basal members of an early radiation of the animals. This radiation included our own ancestors. Thus, any cladistic definition of Porifera which captures all of the organisms we usually think of as sponge-like, must also include all of their descendants, including ourselves.

For this reason, we tend to use the informal term "sponge" to refer to things which are morphologically sponge-like, rather than the Latinate "Porifera," which implies a *clade*. We have always detested the phrase "grade of organization," since many crimes of sloppy thinking have been committed in its name. However, it is a fitting description of the sponges. The sponges represent a series of designs for assembling animal bodies by sticking gelatinous balls of cells together. It's a bit like making a whale out of jelly doughnuts. The individual units are

squishy, fragile, and will either dissolve or make a horrible mess, unless they are supported and packed together in just the right way. Even then, we don't really recommend it.

The individual, component doughnuts are not too different from choanoflagellate colonies. As the image (below) from Thomson (1922) suggests, the individual *choanocytes* in the colonial choanoflagellate *Proterospongia* are embedded in a gelatinous matrix. Each of the cells resembles a microscopic martini glass, except that, rather than having a glass stem, it is supported by a (comparatively) immense olive with inserted toothpick. The toothpick is, of course, a *flagellum*. This flagellum is shaken (not stirred) to circulate the surrounding water from which the cells filter bacteria and more-or-less edible detritus - microscopic, but otherwise indistinguishable from the Vienna sausages and soggy canapés one usually gets with a martini glass.



***Proterospongia* colony/organism from Thomson (1922)**

This is the functional unit found in sponges **[2]**. There are over 8000 extant sponge species. If you insist on knowing *exactly* how many, you must consult the **World Porifera Database**. All sponges are benthic, sessile, suspension-feeders which inhabited a wide variety of marine and fresh water environments.

The sponges probably evolved by the Ediacaran, and fossil sponges are known from the latest Ediacaran or Terreneuvian. In fact, they have left a rather extensive fossil record, consisting largely of spicules. The spicules are secreted by *sclerocytes* and are needle-like structures composed of calcium carbonate or opalline silica. After death, these spicules are scattered across the sea floor and may be found as disarticulated microfossils. Sponges also manufacture structural organic fibers, primarily a collagen protein called *spongin*.

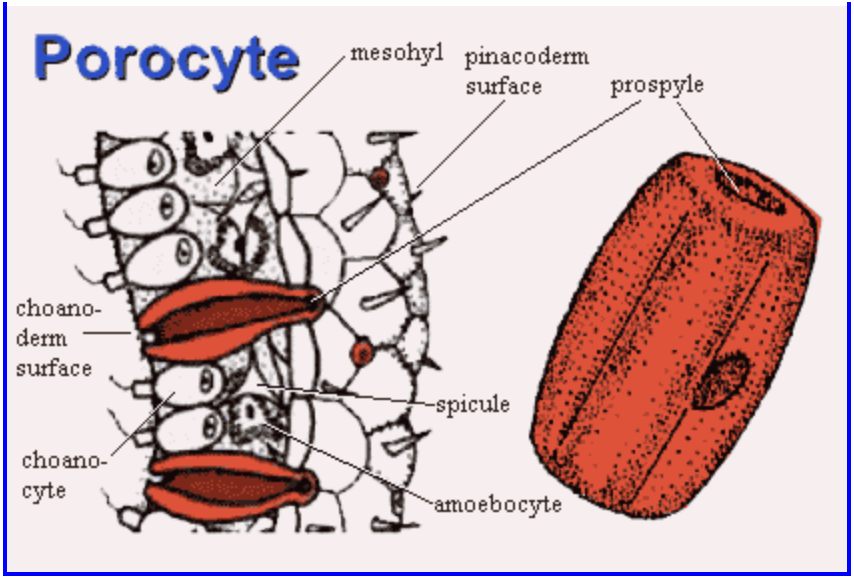
The series of essays which eventually formed this Porifera section discuss the phylogenetic arrangement of the sponges at length, if not in detail. If you want to skip directly to the bottom line, the whole business is summarized in the introduction to the sponge cladogram at the end of this unit.

Image: *Isodictya* (= *Esperiopsis*) *rigida* (Orange Finger Sponge). This specimen from Waadah Island Fingers, Strait of Juan de Fuca Size: 30 cm tall. Demospongiae: Image copyright © Keith Clements and Jon Gross **Marine Life of the Northeast Pacific**. Pedantic Note: *I. rigida* was originally described by Lawrence Lambe, who is perhaps better known for his description of the tyrannosaurid *Gorgosaurus*.

Organization of the Sponge

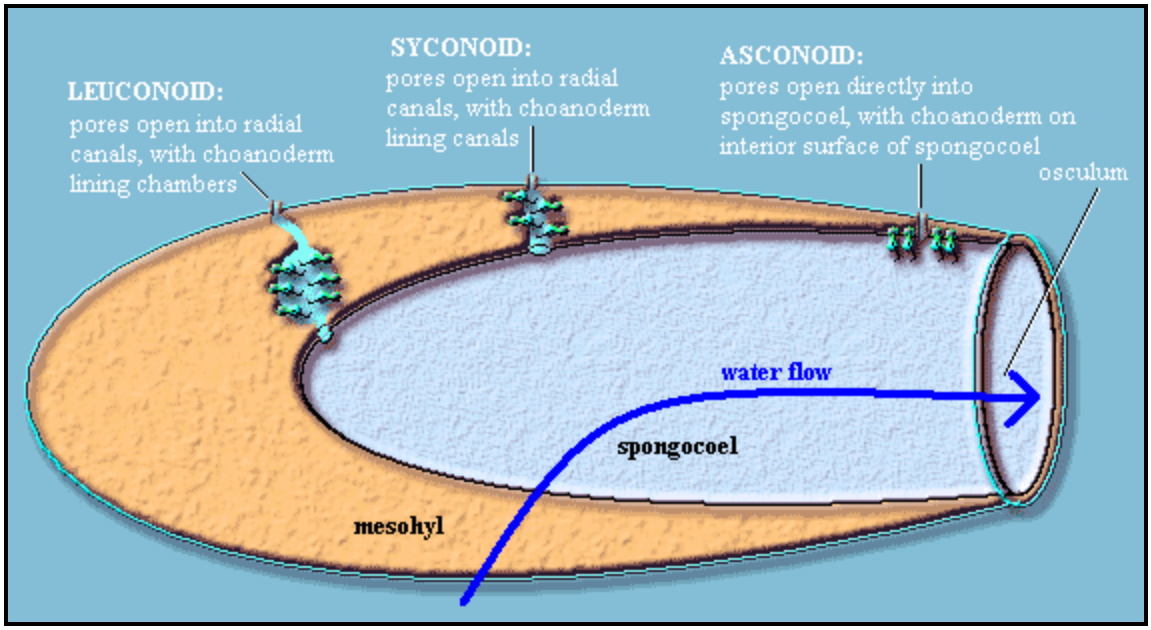
Sponges tissues are organized around a system of canals and chambers which ultimately connect to the outside world through multiple pores. Sponge have two types distinctive of tissues: *pinacoderm* and *choanoderm*. The gelatinous region between them is the *mesohyl*.

Pinacoderm. Think of the pinacoderm as an ectoderm analogue. The pinacoderm is a relatively inert wall of *pinacocytes* and *collagen* (made by the pinacocytes). However, the wall is pierced by countless small pores. Pores may be constructed in several ways. Often, they are formed by single *porocytes*, doughnut-shaped cells which enclose a channel called a *prospyle*.



Choanoderm. The pores lead to regions covered with choanoderm. As you might guess, choanoderm is an endoderm analogue which is contains the choanocytes. Choanocytes ingest food particles, as discussed above. The particles are packaged into food vacuoles and handed off to other cells.

Mesohyl. The mesohyl is not a cell layer, but a soupy liquid layer containing a few points of interest. Herein lie the spicules and the *sclerocytes* which make them. If the sponge has protein (*e.g.*, *spongin*) supporting elements, this is where you will find them. Here also are the *amoebocytes*, undifferentiated cells capable of becoming whatever other sort of cell is needed, included *gametes*.

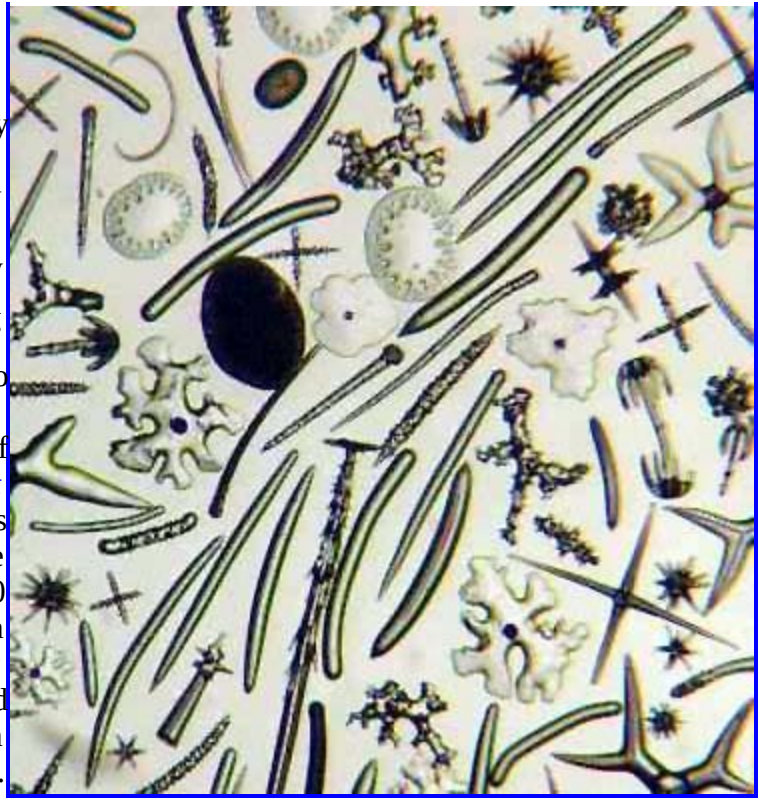


Solemn Asconoid Rite. At this point, a poriferan tradition, unbroken for almost two centuries, demands that we perform the Solemn Asconoid Rite. The purpose of this ceremony is to initiate you, the reader, into the Mystery of the Three Basic Sponge Body Plans. To our embarrassment, we have discovered that we cannot manage this with a straight face. The whole system is full of needless terminology, unjustified assumptions about phylogeny, and obsessive line-drawing. Here's the essence. Sponges generally have at least one large internal space (*spongocoel* or *atrium*), one end of which is open to the environment. This opening functions as the main water exit (*osculum*). The incurrent pores of the pinacoderm may open directly into the spongocoel, or into canals which eventually lead to the spongocoel. If canals are present, the canals may or may not include internal chambers. Clearly, choanoderm must form the lining of (a) the spongocoel, (b) the canals, (c) the chambers, or (d) some combination. That's about all there is to it.

Sponge Physics. Sponge physics holds more interest. The sponge has no way of actually pumping water. All it has is a bunch of tiny *flagella* acting like miniscule oars. Each flagellum can only exert a tiny pressure increment on the water stream. Sponges can produce a great *many* flagella, but only at the expense of adding surface area. That's a good thing for feeding, but rapidly becomes a losing proposition, since narrow or convoluted channels quickly add friction and turbulence, creating back-pressure.

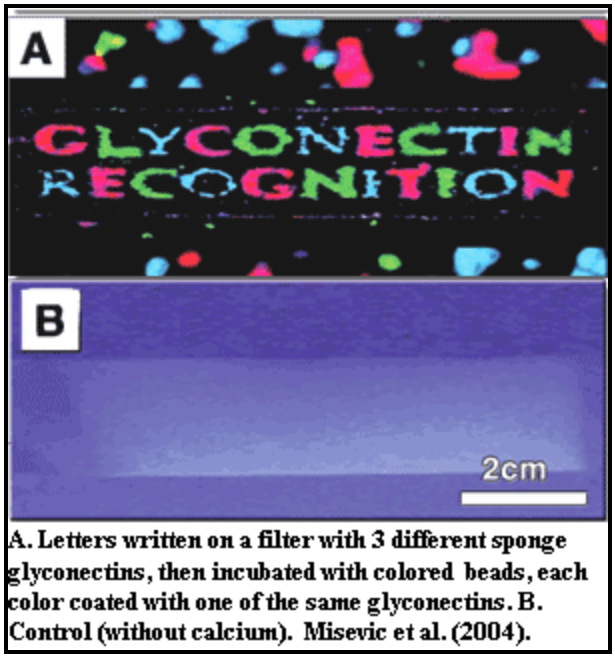
Fortunately, sponges, in addition to flagella, also have a much better handle on Bernoulli's principle than we did in

high school. One useful corollary of Bernoulli's principle is that, to a first approximation, water velocity is inversely proportional to the cross-sectional area of the flow. (1) the cross-sectional area of any given pore is considerably smaller than the channel, chamber or spongocoel it opens into. Consequently, water slows down and flows smoothly over the feeding surface. However (2) the cross-sectional area of the osculum is smaller than the *combined* areas of all of the pores, so that exit velocity is high enough to remove wastewater from the immediate vicinity of the sponge. In this way, water which has been depleted of food particles is ejected away from the sponge. Sperling *et al*. (2006) (citing Brusca & Brusca, 2002). The system is remarkably efficient. Sperling *et al*. point out that, "a large sponge can filter its own volume of water every 10 to 20 seconds (Brusca & Brusca 2002). *In situ* feeding studies on modern sponges demonstrate that some derive the majority of their food from DOC [dissolved organic carbon], and can remove an average of 10% of the DOC in the water in a single pass through the water canal system (Yahel et al. 2003)."



Internal Skeleton. As mentioned, the body of the sponge is usually reinforced with spicules made of silicate or calcium carbonate. A few basal demosponges make no spicules. Typically, a sponge makes spicules in a small variety of shapes, with characteristic hooks and processes. A common spicule repertoire includes small, stellate spicules (*microscleres*) combined with large, elongate spicules (*megascleres*). Additional structural support is provided by a collagen homologues, particularly (in demosponges) *spongin*. Most sponges make silicate spicules, but the Calcarea make spicules out of calcium carbonate. A few, both extinct and extant, appear to make both sorts, or make spicules from protein only. Bavestrello *et al*. (1998); Botting & Butterfield (2005).

Both hexactinellids and demosponges make spicules in about the same way, using the same enzymes. Müller et al. (2007). One of those enzymes is *silicase*, which is almost identical to a form of *carbonic anhydrase*. The other is *silicatein*. The spicule primordium is produced in a cell vacuole. When the spicule primordium is extruded from the cell the silicatein binds to the surface and also to another protein (a *galectin*) in the presence of calcium ions. After extrusion, the spicule undergoes further growth and "shaping" – presumably involving more silicase, as well as the attached silicatein. *Id*. The point of all this is that the carbonic anhydrase activity of silicase *will* also produce carbonate from ambient CO_2, while calcium ions *must* be present, all over the spicule surface, to bind the silicatein. Under those circumstances, it wouldn't take much to spark spontaneous growth of crystalline calcium carbonate over the scaffold of the original spicule. Thus, calcareous sponges with calcium carbonate spicules would be an almost inevitable evolutionary consequence of this mode of spicule development.



A. Letters written on a filter with 3 different sponge glyconectins, then incubated with colored beads, each color coated with one of the same glyconectins. B. Control (without calcium). Misevic et al. (2004).

Sponge Lectins. A fair amount of work has been done in the last few years on the biochemicals which hold sponges together. With the exception of homoscleromorphs (discussed later) sponges do not have a *basement membrane* to hold their outer cell layers (the pinacoderm and choanoderm) together. The space in between the cell layers (*mesohyl*) is mostly water with a few cells and some dissolved protein. Then what holds the cell layers together? How do the cells know that they are embracing another friendly sponge cell, rather than some hostile bacterium, a parasite, or a loose cell belonging to some other sponge? The answer goes to the important distinction between (1) a genetically homogeneous animal and (2) a colony of cooperating eukaryotic protists.

We will not get into the biochemistry of *lectins* and *glyconectins*, for which *see, e.g.*, Müller (2003); Misevic *et al*. (2004). In essence, these are glycoproteins. With (lectins) or without (glyconectins) help from special binding proteins, they are capable of self-recognition with a specificity rivaling that of mammalian immune systems (Müller, 2003) and extraordinary binding strength (Misevic *et al*., 2004). Thus sponges are clearly individual organisms.

Transcription Factors. From the vantage point of evo-devo, the Porifera also represent a key transitional step. Simionato *et al*. (2007) looked at essentially all of the metazoan genomes which have been completely sequenced, including the recently completed genome of the demosponge *Amphimedon*. From this data, they attempted to identify all of the genes coding for *basic helix-loop-helix* proteins. Basic helix-loop-helix (bHLH) proteins and *homeodomain* proteins are the two most important groups of *transcription factors* in bilaterians. Together, they control most of the higher level genetic switches in bilaterian development. Single-celled Eukarya have only 1-3 bHLH genes, and the proteins are used in metabolic regulation. Bilaterians and the anthozoan (sea anemone) *Nematostella* usually have about 60 (more in vertebrates) which fall into over 40 families, and are used mainly in transcriptional control of development. *Amphimedon* (and, to a lesser extent, the hydrozoan, *Hydra*) are thus far the only organisms to have an intermediate condition. In particular, the demosponge has only 16 bHLH genes, representing 10-14 families. All but a handful of *Amphimedon*'s bHLH genes fall into families also known in bilaterians. Thus, a large part of the evolution of the bHLH system seems to have taken place within or close to the poriferan grade. Simionato *et al*. (2007). Contrast this with the hox system, which seems to have evolved in the cnidarian grade.

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Porifera - 2

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METAZOA
|--Choanoflagellata
`--PORIFERA
   |--Archaeocyatha
   `--+--Stromatoporoidea
      `--+--Calcarea
         `--+--Hexactinellida
            `--+--Demospongiae
               |  |--Tetractinomorpha
               |  `--Ceractinomorpha
               `--+--Homoscleromorpha
                  `--EUMETAZOA
```
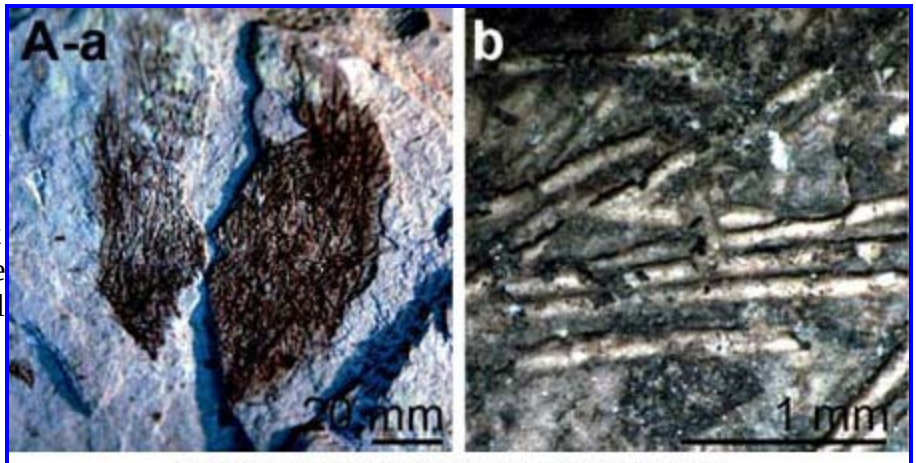


Sponge Evolution

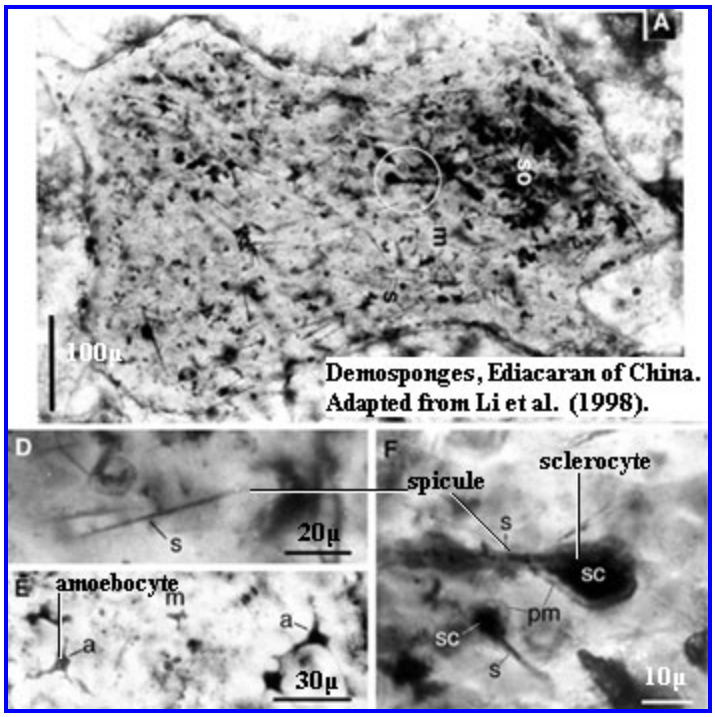
Sponges, Fungi, and Ediacarans: the Neoproterozoic "Fauna." There is now relatively general agreement that the Porifera are *paraphyletic*. That is, the last common ancestor of all sponges was also one of our own ancestors. As Sperling *et al*. (2006) have pointed out, sponge *paraphyly* implies that many of the features we thought were sponge specializations must in fact be primitive for all metazoans. In particular, the water-canal system and the poriferan *sessile*, *benthic* mode of life are probably primitive for Metazoa. Personally, we were considerably relieved to learn that our recurrent desire to sit motionless in a liquid medium, indiscriminately absorbing ambient hors-d'oeuvres, is thus not necessarily a consequence of advanced degeneracy, but merely a *plesiomorphic* desire inherited from our sponge ancestors.



Solactiniella, a hexactinellid sponge from the Early Cambrian of China. Muller et al. (2007).

Actually, this description may not fit the Porifera so much as their Ediacaran competition. The poriferan ability to circulate water actively and suck out its carbon content efficiently may well have been a key reason why we are descended from sponges, rather than from "vendobiota." Sperling *et al.* (2006). But this comparatively energetic activity may have been a later development. The Ediacaran fauna probably represent a number of different lineages which all diverged from the Eukarya at about the same time, and from very close to the same place in phylospace, as the Metazoa and Fungi. This is the most reasonable explanation for the profound observation of Peterson *et al*.

(2003) that Ediacarans are often remarkably fungal.



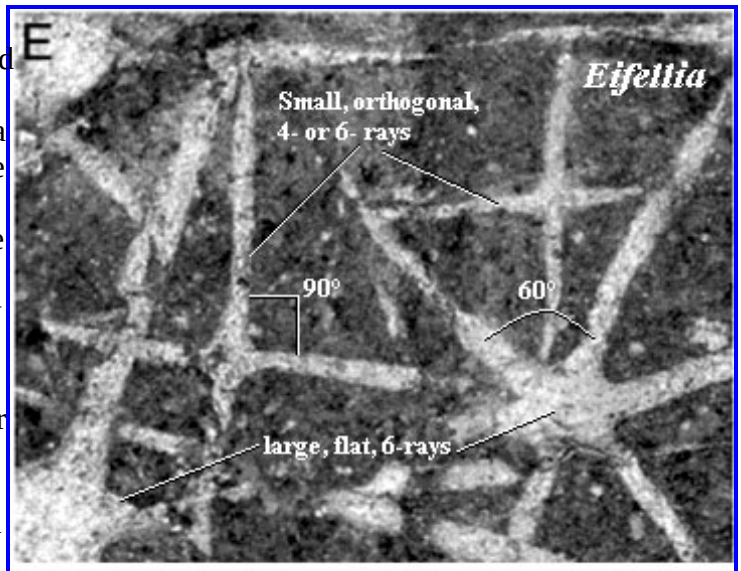
Perhaps, originally, sponges were simply another one of these lineages. Hexactinellid sponges, in particular, have at least two important characteristics which are unique among animals, but (in our view) are shared with Fungi -- secondarily syncytial tissues and "plugged pore" junctions. Leys *et al*. (2006). **[13]**.

Fossil Record. However, the sponges clearly evolved in a very different direction from Fungi. One conspicuous specialization was the ability to make a mineralized skeleton. In fact, sponge spicules are so conspicuous that their *absence* from the Ediacaran fossil record seemed peculiar. Fortunately, clear examples have of hexactinellid, demosponge and, perhaps, calcarean sponges have now been recovered from the Ediacaran of Mongolia, China and India. Li *et al*. (1998); Tiwari *et al*. (2000).

Sponges and Eumetazoa. Not so long ago, the gap between sponges and Eumetazoa (corals + cows) seemed almost unbridgeable. But the distance between Porifera and Cnidaria has shrunk considerably. One recent molecular survey demonstrated that advanced sponges (*Oscarella* again) have not only a true epithelium, but essentially 100% of the eumetazoan complement of cell adhesion proteins, including cell-surface receptors, proteins for cytoplasmic bridges, and the proteins of the extracellular matrix. Nichols *et al*. (2006). What the sponges do not appear to have is a gut or a nervous system. These still appear to be synapomorphies of the Eumetazoa.

"Heteractinida": the Stem Group of all Sponges. In a recent, influential paper, Botting & Butterfield (2005) posit that all of the major sponge groups derived from the early "heteractinid" sponges, which they describe as follows: "Heteractinids are a problematic group of Paleozoic sponges characterized by hexaradiate spicules, a pattern not seen in extant forms, but with obvious symmetry relationships with the triradial spicules of calcareans; combined with the preserved carbonate mineralogy and bilaminar bilaminar structure of late Paleozoic forms, they have been widely accepted as calcareans."

Based on a close examination of the Middle Cambrian *Eifelia*, they argue that at least some heteractinids had spicules containing both carbonate and siliceous layers. Certainly, *Eifellia* spicules had two layers, in addition to a core. What those layers were made of is less clear, but the speculation is at least reasonable. Without doubt, *Eifellia* had a peculiar mix of spicule symmetries. Its fossils include both flat, hexaradiate spicules (mostly large) and *orthogonally* symmetrical 4- or 6-armed spicules (mostly small). Thus, Botting & Butterfield assert that the heteractinellids were probably a heterogeneous group with a mosaic of characters we now think of as unique to one or another group of living sponges.



Spicules showing mixed symmetry. Botting & Butterfield (2005).

Botting & Butterfield (2005) deserves a close look, and is on our short list of Amazing Sponge Papers. It may be found at this **direct link**.

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Porifera - 3

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METAZOA
|--Choanoflagellata
`--PORIFERA
   |--Archaeocyatha
   `--+--Stromatoporoidea
      `--+--Calcarea
         `--+--Hexactinellida
            `--+--Demospongiae
               |  |--Tetractinomorpha
               |  `--Ceractinomorpha
               `--+--Homoscleromorpha
                  `--EUMETAZOA
```


Classification of Sponges

A majority of sponge people would probably agree on the following propositions:

1) The Hexactinellida are one of the most ancient group of living sponges.

2) The Calcarea are an early branch.

3) The "Scleractinellida" or "Sclerospongia" are a polyphyletic group and should be abandoned.

4) Most of the better-known extinct forms (*e.g*. Archaeocyatha, Stromatoporoidea) are probably either stem group sponges or stem group demosponges.

See, e.g., Schütze *et al*. (1998)

Thus our sponge cladogram might look something like this:

```
METAZOA
|--Choanoflagellata
`--PORIFERA
   |--Archaeocyatha
   `--+--Stromatoporoidea
      `--+--Calcarea
         `--+--Hexactinellida
            `--+--Demospongiae
               |  |--Ceractinomorpha
               |  `--Tetractinomorpha
               ???+--CNIDARIA
                  `--BILATERIA
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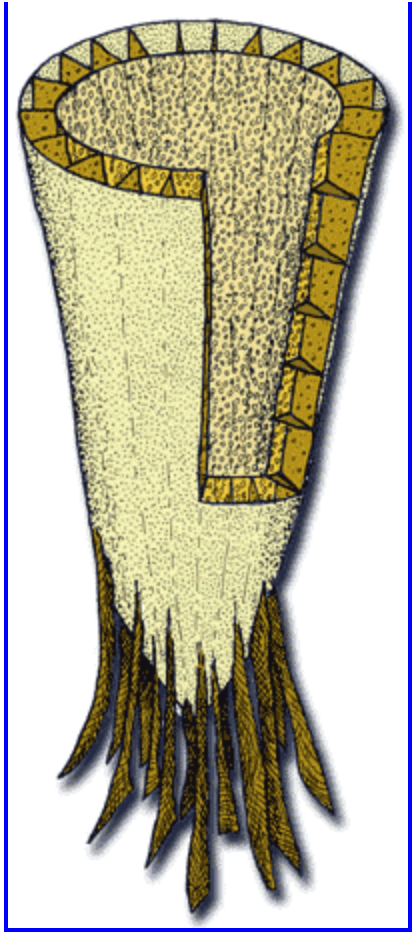


Then again, it might *not* look like that. This arrangement is something of a compromise between some of the currently respectable views and our own, pointless speculation (which is taken up later). Not that there is any lack of other opinions. For example, it is still possible, even today, to find otherwise rational people who believe they can read the far future using tea leaves and the deep past using *mitochondrial* DNA. Thus Wang & Lavrov (2007), having performed the appropriate rites, recently found that Porifera and Cnidaria form a monophyletic group to the exclusion of bilaterians. These authors unaccountably failed to include any Hexactinellida or Calcarea in the analysis. Since the Porifera are often believed to be paraphyletic, it's a bit hard to draw any conclusions about phylogeny without sampling these taxa, even supposing that one could place any confidence in this methodology **[1]**.

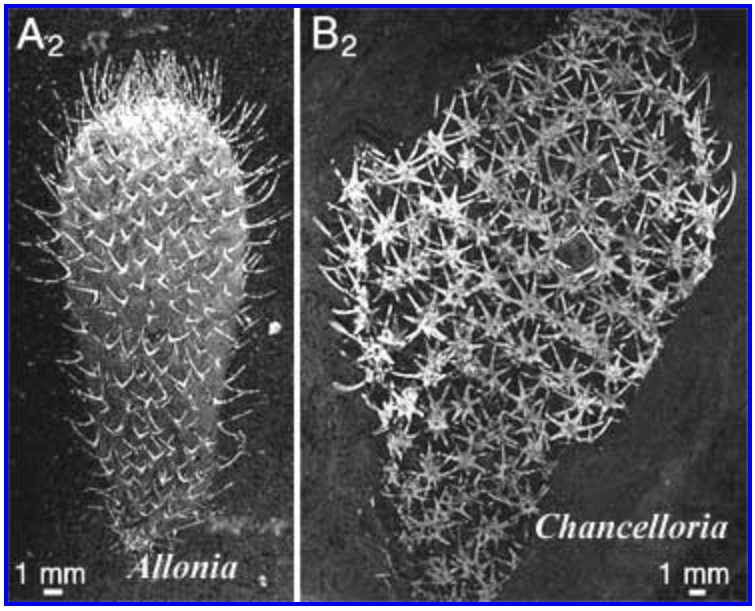
In fairness to Wang & Lavrov, their interest was not in sponge phylogeny in general, but the placement of a particular group, the Homoscleromorpha, represented in their work by *Oscarella carmela*. The homoscleromorphs were once assumed to be demosponges. However, recent morphological work has shown that they have some important characters thought to be unique to the Eumetazoa (= Cnidaria + Bilateria). Specifically, homoscleromorphs have a *basement membrane* underlying both the *pinacoderm* and the *choanoderm*. Boute *et al*. (1996). That is, they have a true epithelium. In addition, their spermatozoa have an *acrosome*. They share some unique structural features of the embryonic flagellum with Calcarea. **[14]** Finally, Wang & Lavrov show that *Oscarella* also has a distinctive organization of its mitochondrial DNA, with half the genes read in one direction and half in the opposite direction. This is unique among sponges, but similar to certain cnidarians.

This raises the distinct possibility that the Homoscleromorpha are a fourth group of sponges diverging from the main stem. While such a relationship was not recovered by Wang & Lavrov, it *was* found by Sperling *et al*. (2006), using a battery of nuclear genes coding for a number of enzymes and structural proteins involved in general metabolism. Unfortunately, Sperling *et al*. also omit hexactinellids from their study (it seems that hexactinellid DNA is very hard to come by). However, they do, indeed recover Homoscleromorpha as a fourth sponge group.

But Sperling & Co. are not yet done grafting branches onto the sponge tree. One perennial problem in poriferan taxonomy has been the inclusion (*vel non*) of the Chancelloriidae, an orphan group of sponge-like Cambrian cucumbers with spicules (image from Bengtson, 2000). Sperling *et al*. argue that they are sponges. Chancelloriid

spicules are said to be un-sponge-like. Sperling dismisses this objection, pointing out that the paraphyly of sponges requires us to accept that spicules were independently developed at least three times [3]. Thus a fourth independent invention by chancelloriids shouldn't be a cause for concern. In particular, Sperling points out that the developmental process for silicate spicules (hexactinellids, demosponges and homoscleromorphs) is different from the process for making calcareous spicules (Calcarea). Silicate spicules are made inside the cell, pre-patterned on an organic matrix. Calcareous spicules are formed outside the cell and constitute a single crystal of calcium carbonate. In addition, there are other sponges that have no spicules at all (keratose demosponges), and yet others which form a massive, interconnected "shell." *But c.f.* Botting & Butterfield (2005).

Sperling's group places Homoscleromorpha between the Calcarea and Eumetazoa. For reasons discussed in tiresome detail elsewhere, we disagree, believing that they are related more closely to demosponges. Then, accepting that homoscleromorphs are more closely related to non-sponge animals than areother sponges our cladogram might ultimately look a bit like this:

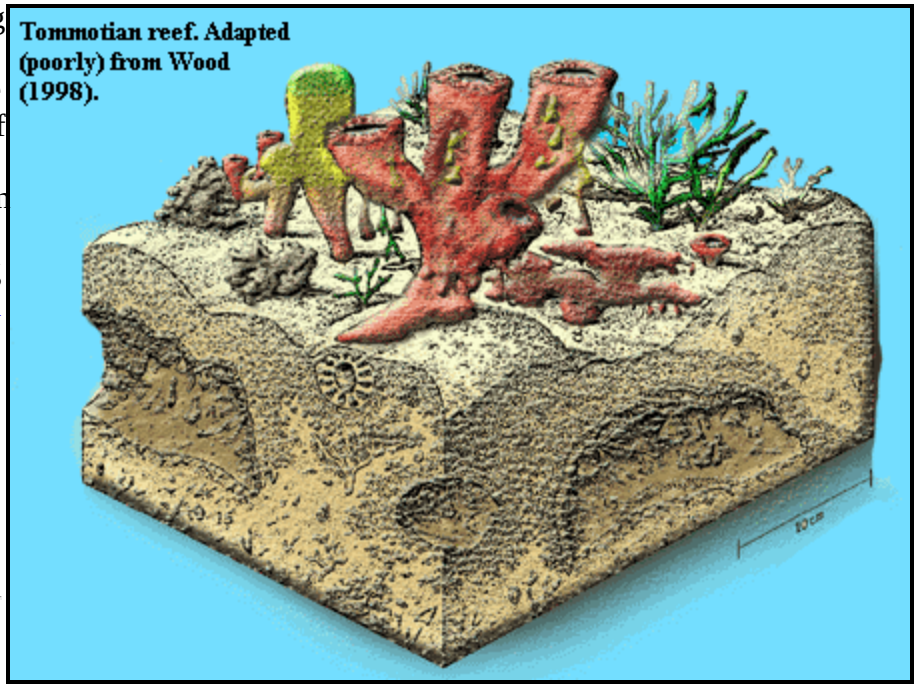



```
METAZOA
|--Choanoflagellata
`--PORIFERA (Heteractinida)
   |--Archaeocyatha
   `--+--Stromatoporoidea
      `--+--Eifellia
         `--+--+--Calcarea
            |  `--Chancelloriidae?
            `--+--Hexactinellida
               `--+--Demospongiae
                  |  |--Ceractinomorpha
                  |  `--Tetractinomorpha
                  `--+--Homoscleromorpha
                     `--+--CNIDARIA
                        `--BILATERIA
```

Additional details and discussion on the shape of sponge phylogeny may be found elsewhere. Again, this arrangement reflects a compromise between an outline which is widely accepted and probably correct, and certain aberrant ideas which we will do our best to bolster in the sections which follow. ATW080104.

Ecological Role

Sponges have played a critical role in shaping the basic form of the Phanerozoic biosphere. Archaeocyaths and perhaps even some Calcarea formed the first major biological reef systems in the middle Tommotian. Sponges seemed to have played an important role in most reef systems thereafter, and have been critical in maintaining reef systems during certain times of biological crisis (Vishnevskaya *et al*., 2002 -- Late Devonian).



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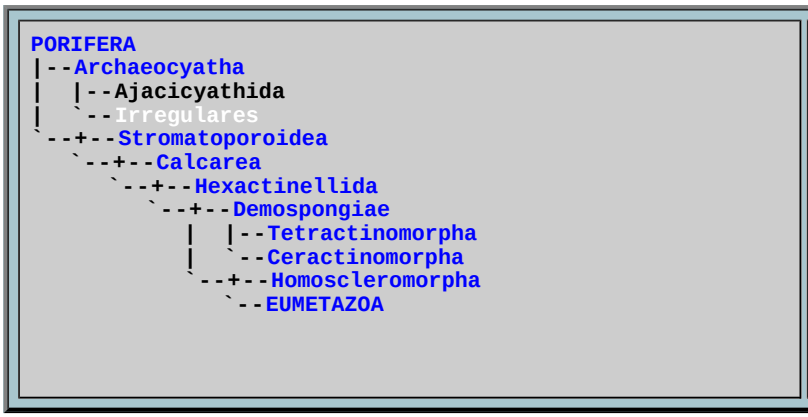
Irregulares - 1

Cambrian



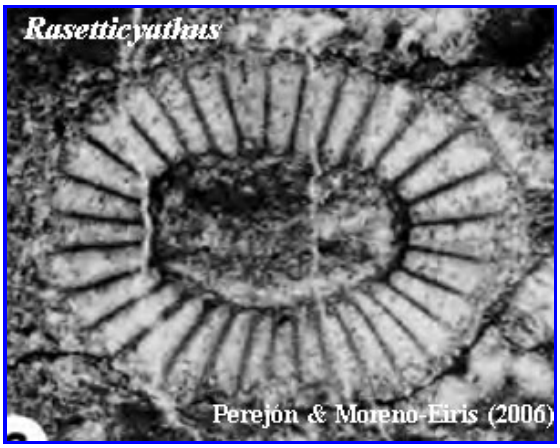
Introduction

We don't have a lot to say about the Irregulares at this point. The Archaeocyatha were traditionally divided into Regulares and Irregulares. Over the 1990's the archaeocyath people, and ultimately the sponge community in general, trashed most of their own classification schemes in a fit of melancholy. The Irregulares were thrown out along with everything else, although they may yet be monophyletic, as previously discussed. This emotional crisis was brought on by a growing suspicion that sponges are infected with chronic *homoplasy*. That is, sponges seemed to evolve in circles, with different groups continually re-inventing the same basic variations on the sponge body plan. In some areas of phylospace, paleontologists moved on to untangle these knots using cladistic methods. In others, there has been a sense of fear and trembling, existential dispair, and a belief that phylogeny is no longer their responsibility because, "the next major development in sponge phylogeny will be molecular studies that will refine the evolutionary relationships between clades." Rowland (2001).

Actually, no. But that's another story, and one we have told too often elsewhere. In any case, the DNA folks are of no use here because the archaeocyaths are all dead ... probably. So many possible lazarus taxa have shown up in the sponge world recently that it isn't safe to bet on that sort of thing. In any case, we're not going to repeat the usual rant about over-reliance on sequence data. Instead, we're essentially going to repeat a few words about morphology. Then, once we've driven off the riff-raff through sheer boredom, we will launch into one of the most outrageous, baseless, and far-fetched speculations in our long history of baseless and far-fetched speculata.

Special Credits: special thanks to Prof. Carlos M. da Silva of the Universidade de Lisboa, for posting really good material on archaeocyaths; to Lângia Colli Montresor, Universidade Federal de Minas Gerais, for help with the translation; and to Adam P. White of Trinity University for a really useful suggestion about sponge evolution. Finally, our thanks to Lin Wei-Hong for translating portions of Feng *et al*. (2002).

Morphology

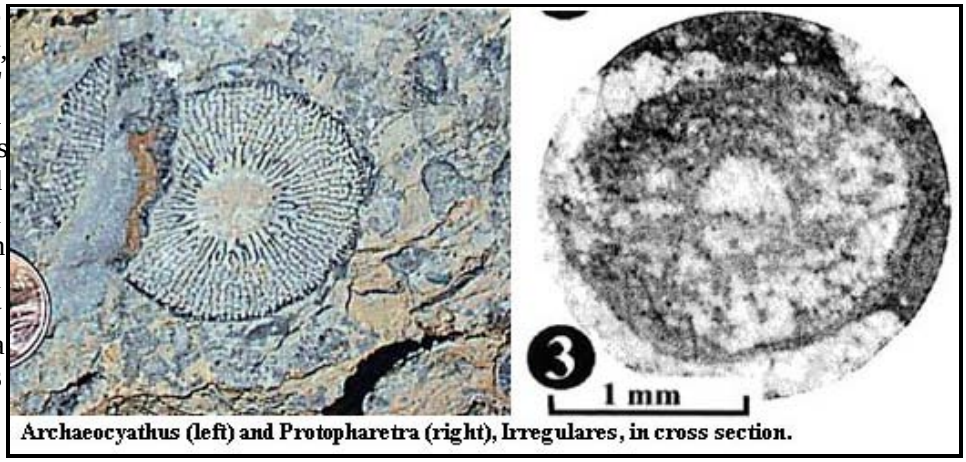


Irregulares Develomental Synapomorphies. The characteristics which are really supposed to hold the Irregulares together are, oddly enough, a suite of essentially developmental features. Otherwise, little distinguishes the typical archaeocyathid (for example) from an oddball ajacicyathid. The developmental model goes like this. All archaeocyaths start out as little cups without pores. In irregulars, the aporous stage is prolonged, and the *dissepiments* ("framing") start up right away before the organism starts builing the radial *septa* that make ajacithyacids in particular (see image of the ajacicyathid *Rasetticyathus*) look so much like a coral in cross-section. Only after this does the animal start to build more outer wall, punch out some pores, put in the *septa* and *tabulae* ("drywall"), construct the inner wall, and what have you. Archaeocyaths seem to be able to remodel and reinforce all parts throughout life. However, the Irregulares always start with a basal pore-less cup and a network of dissepiments. Benton & Harper (1997); Perejón & Moreno-Eiris (2006).

Outer Wall: The pores in the outer wall tend to be larger than in ajacicyathids. However, the irregulars have a tendency to block off some pores, later in life, with other structures which may have microporosities of their own. Perejón & Moreno-Eiris (2006).

Intervallum: Since the dissepiments are built early, everything else has to work around them. Perhaps for this reason, the partitions of the *intervallum* tend to be less ... regular. What one is usually told is that Irregulares are structurally more "complex." Rowland (2001). At least in some cases, this seems to mean "chaotic." *Compare* the neatly arranged septa of *Rasetticyathus* with the complex *Archaeocyathus*, or the simply untidy *Protopharetra*. Irregulars also tend to have other messy habits. For example, the septa get wavy and fuse into one another.

Another frequent characteristic is that the tabulae are continuous with the outer wall. Incidently, you may get tired of our use of "in most cases," "usually," etc. Recall that archaeocyath taxonomy has always been run by stratigraphers and paleoecologists. They want rapid identification tools (apomorphies) and ecomorphs, respectively. They don't care much about synapomorphies, phylogeny, or even complete circumscription. Consequently, many archaeocyaths are probably misclassified from a phylogenetic standpoint, and nothing is completely consistent.



Archaeocyathus (left) and Protopharetra (right), Irregulares, in cross section.

In addition, structures of the *intervallum* in some Irregulares seem to have a greater tendency to grow centripitally, as projections of the outer wall, and thus from the outer wall inwards. This makes good biological sense. Irregulares have to build their drywall around pre-existing framing. There are two ways to approach that problem. The first is the *Archaeocyathus* approach: start from the outside in an organized fashion and build straight inwards, in a great many places, until one hits a dissepiment. Alternatively, one may apply the *Protopharetra* technique: start wherever the hell one happens to feel like it and run the septae at any old angle around the beams. (We once lived in a house which was build in the latter fashion, during a week-long beer party. The owner fell apart after that, but the house held together for many years.) The *Archaeocyathus* approach is referred to as *centripetal* growth, while the *Protopharetra* technique is referred to as *thromboid* growth. The former is typical of Archaeocyathida, and the latter of Kazachstanicyathida. Benton & Harper (1997); Perejón & Moreno-Eiris (2006).

Inner Wall and Central Cavity: It is notable that the inner cavity may become partially, and sometimes completely blocked by all this construction activity.

Ecology: "This is Highly Irregular!"

If you have read the preceding notes with some care, you will sense that something is amiss. Let us restate a few characteristics of Irregularia: (1) prolonged developmental stage with aporous outer wall, (2) secondary blocking of pores, (3) obstruction of the central cavity, and (4) septal divisions which make no hydrodynamic sense. How can this be reconciled with the sponge model of archaeocyath physiology? Truthfully, we don't know. However, sphinctozoan sponges and stromatoporoid sponges had much the same problem and manged well enough. In fact, many archaeocyaths (not all of them Irregulares) are referred to as having

sphinctozoan or stromatoporoid growth patterns. This isn't a very satisfactory answer, but it's all we have at the moment.

Sponging Off Bacteria

Hopefully, by this point, we have no readers, and we can do a bit of unconstrained speculation without anyone asking embarassing questions. Our thesis proceeds in four steps.

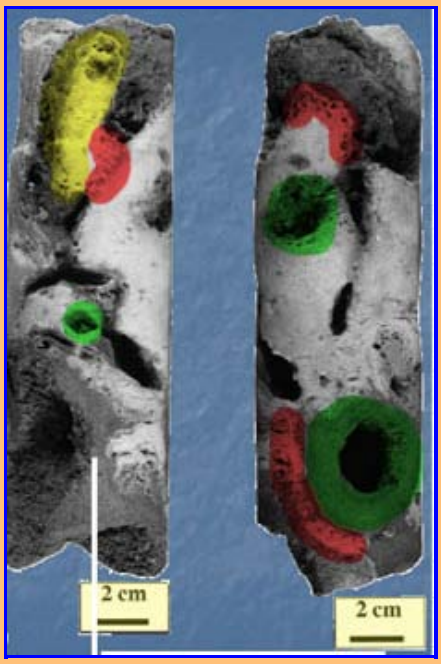
> 1) Most of the morphological features of archaeocyaths in general, and Irregulares in particular, are also found in *microbialite* structures that do not contain any archaeocyaths, or any sponges, or even any metazoans.
>
> 2) There are good reasons for (1) that have nothing to do with phylogeny.
>
> 3) It is possible to see, with existing data, the beginnings of a phylogenetic progression from microbialite "nest parasites" to archaeocyaths.
>
> 4) Irregulares in particular, and metazoans in general, didn't *evolve* a body plan so much as *adapt* to pre-existing microbial structures.

The Morphology of Mats

Today, when we think of "microbial mats" or *microbialites* -- if we think about them at all, that is -- we generally visualize stromatolites or flat, massively layered structures. But these are just the most common structures. Another important form is the *thrombolite*. In their (likewise massively layered) discussion of marine hard substrates, Taylor & Wilson (2003) discuss thrombolites in the following terms:

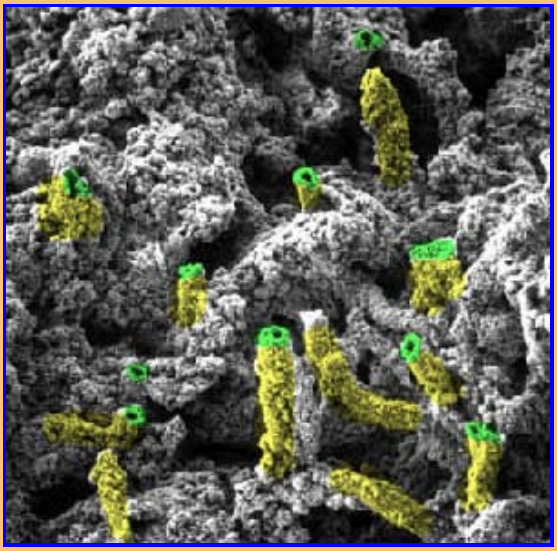
> Stromatolites are microbial structures (microbialites) with internal *laminations*; thrombolites are microbial masses with clotted internal textures. ... Thrombolites range from the Neoproterozoic to the Recent. They were common in the Cambrian and Ordovician and the Devonian, but rarer though present in every other Phanerozoic system. Thrombolites have a much more varied environmental distribution than stromatolites, being found in cryptic spaces such as cavity walls as well as on exposed surfaces.

Thrombolites come in many forms. The only way to do this properly is a walkthrough of some real thrombolites, illustrating the features we have in mind:



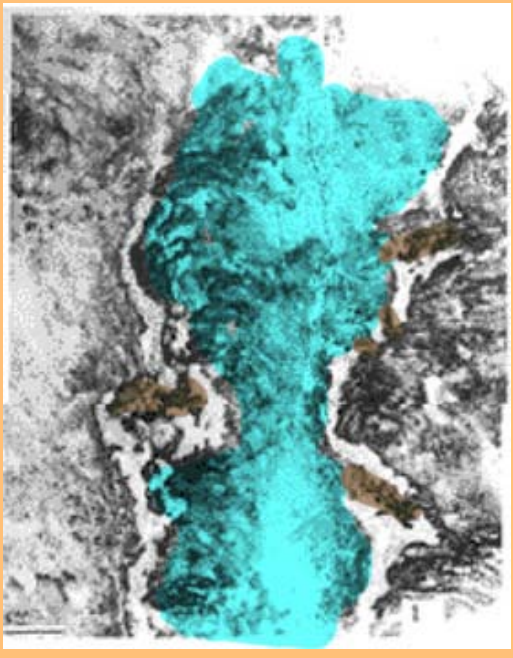
A. Note (a) tube-like, upward-widening structure (yellow), (b) "cellular" structure where outer layer has been abraded (red), and (c) round openings, some of which have well-organized rims (green).

Pleistocene of Tahiti: core of sponge reef



B. These thrombolitic structures are *aragonitic* tubes which developed around bacterial filaments. Their long, thin tubes, open core and uniform, round, terminal openings suggest how remarkably sponge-like thrombolites can be under appropriate growth conditions

Recent of the Bahamas. From the **RIBS site**.



C. A much larger (centimeter-scale) hollow (blue) tube in a thrombolitic mass from about 700 Mya. Note the openings (brown) in the outer wall, with a tendency for wall segments above and below the breaks to overlap

Cryogenian of South China. Cao (1999).

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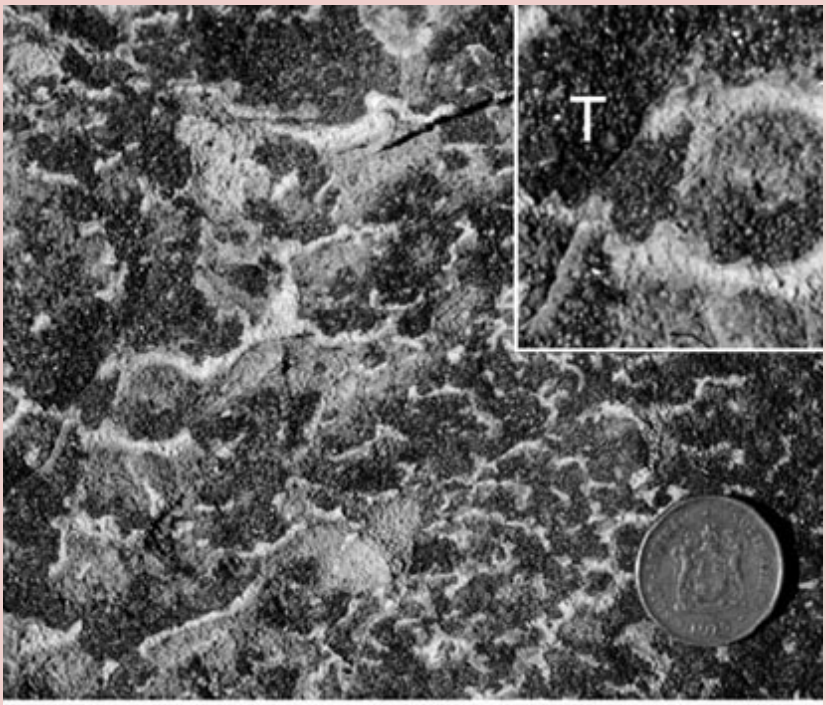
ATW070910

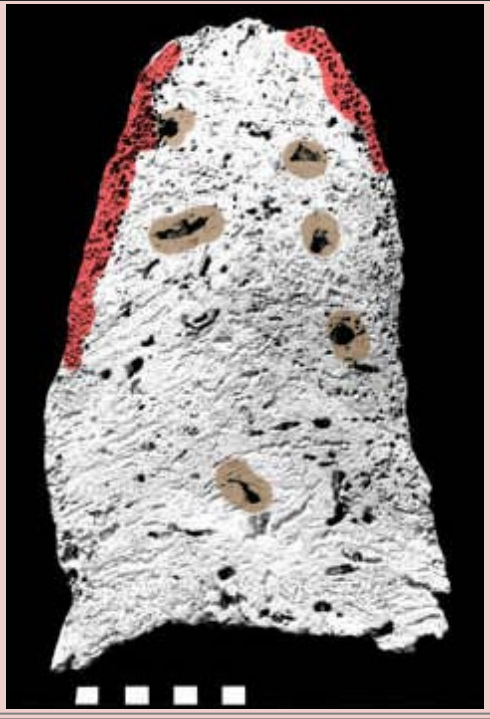
Irregulares- 2

```
PORIFERA
|--Archaeocyatha
|  |--Ajacicyathida
|  `--Irregulares
`--+--Stromatoporoidea
   `--+--Calcarea
      `--+--Hexactinellida
         `--+--Demospongiae
            |  |--Tetractinomorpha
            |  `--Ceractinomorpha
            `--+--Homoscleromorpha
               `--EUMETAZOA
```

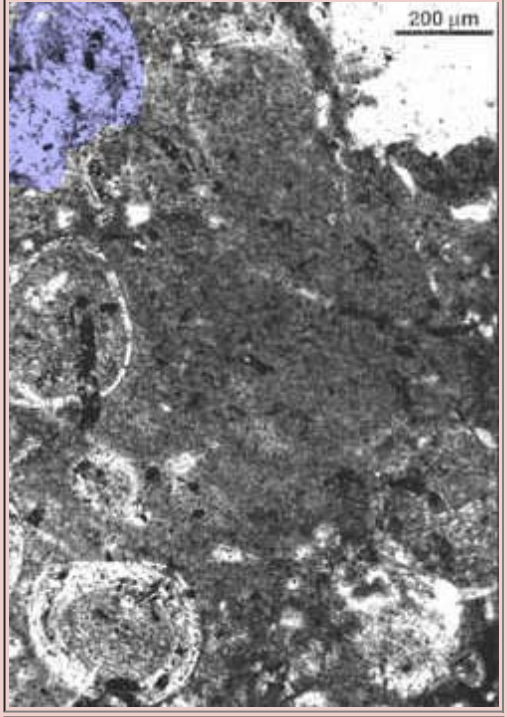
D. Detailed texture of the internal "mesoclot" texture of many thrombolites. Note (a) the two different scales of structure and (2) the fact that the clots are composed of curved plates with a fairly consistent vertical axis.

Ediacaran of Namibia. Grotzinger *et al*. (2000).



E. Exterior of thrombolite. Note the pores on the exterior surface (brown) and, again the texture of small cells where the surface is abraded away (red).

Recent of the Bahamas. **Cyanobacterial Image Gallery**.

		
F. Very common widening-upwards structure.	**G.** Thrombolite columns in cross-section. Note the peculiar structure in the upper left hand corner (blue) and, possibly, a similar structure on the lower right..	
Unidentified thrombolite from Dupraz *et al*. (2006).	Unidentified thrombolites -- Recent of the Bahamas. From the **Cyanobacterial Image Gallery**	

So, there you have it. Thrombolites, mostly simple cyanobacteria, can make all kinds of archaeocyath structures with no material help from hox genes or other body plan genetics. Thrombolites form hollow tubes, with interesting-looking mouths, external walls with pores, widening-upward cones, *reticular* systems of mineralized compartments, and mesoclot internal walls almost indistinguishable from the "thrombolitic" patterns of irregular archaeocyath septa. Sometimes, the walls appear to be doubled (not shown -- reference missing and presumed lost). We have not seen the cup-within-a-cup conformation as such, nor any convincingly *tabulate* structures, but neither of these features is present in the most basal archaeocyaths (Monocyathida), either. Thus every structure common to all archaeocyaths is also found in thrombolites, although there is no genetic commonality which can possibly explain the similarity.

So how do we pull the rabbit out of the hat?

Cyberthromboids: the Automata of Dupraz

The Automata of Dupraz sounds like a Twelfth Century treatise on alchemy, perhaps the work of a degenerate Florentine abbot, notorious for his unspeakable perversions. In fact, Dupraz *et al*. (2006) is an exceedingly Twenty-First Century paper, but somewhat magical for all that. The automata in the paper are not golems, but mathematical constructs which date back only to the work of John von Neumann. Dupraz and co-workers set out -- not to explain how cyanobacteria build such oddly complex structures -- but to see if they could *model* this behavior using a minimal set of mathematical rules.

Note that this is not paleobioloigy or paleoecology. Dupraz etc. do not try to guess what Neoproterozoic bacteria were actually like, or what their environment was. Theirs is simply a mathematical environment in which cellular automata move and form patterns according to a small set of rules. The rules imply no particular genetic program, no particular geochemistry, and no special ecological or trophic structure to the community -- just half a dozen rules. The rules contain parameters which can be varied. Those variations (on different runs, or in some pattern during runs) can mimic just about all general morphologies actually found in bacterial reefs. The parameters correspond, but only in a general way, to environmental constraints

If you're curious about details, see the link to this paper in the references section. The relevant point here is not

whether this particular model is "correct" or sufficient. The point is that Neoproterozoic reef structures -- including the features shown in the images above -- probably do not require unusual circumstances or particular organisms. We don't try to explain the topology of a particular sandbox surface by examining the genomes of the children who have been playing in it. Other things are far more relevant, e.g. their numbers, ages, and the availability of buckets, water, and parental supervision.

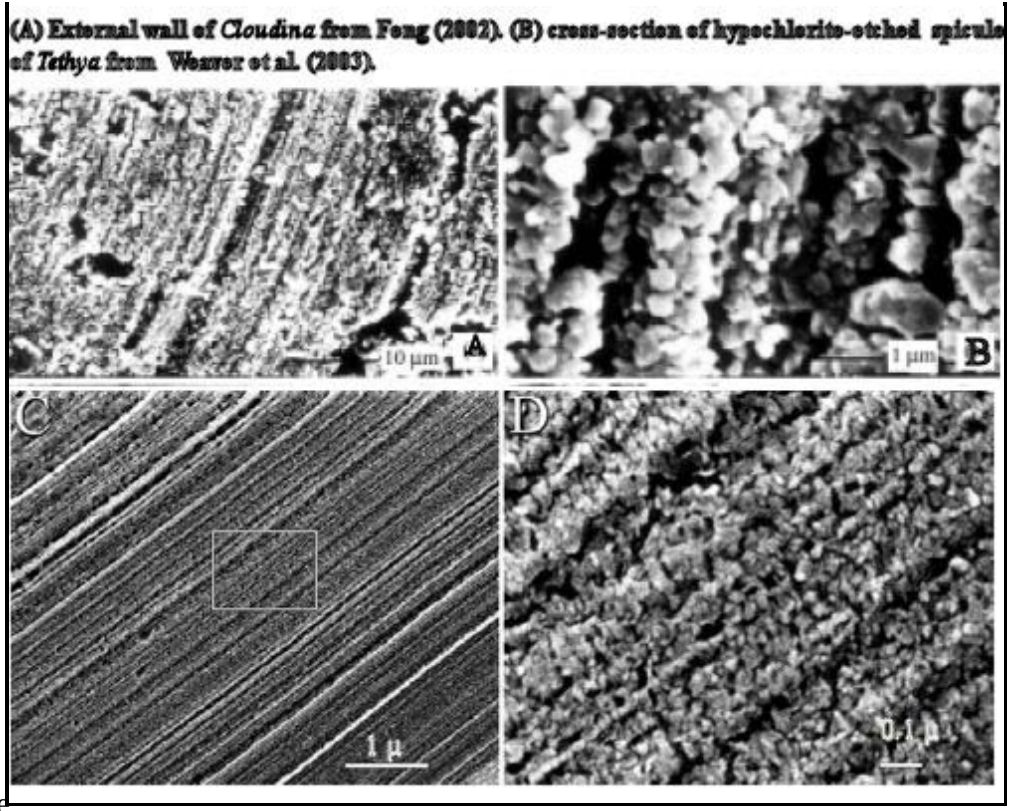
Likewise it probably made little difference whether the biota of these microbialites was entirely cyanobacterial, or whether some eukaryotic protists or even very simple animals were thrown in. The morphology of the resulting microbialite would be much the same because it was largely controlled by factors unrelated to details of community structure. As long as the bulk of the material was calcimicrobial, nothing else would matter a great deal. This also survives an intuitive reality check. By the Late Neoproterozoic, microbialites had already been around for one or two billion years, possibly even longer. Eukaryotes had existed for a minimum of half a billion years and potentially far longer. Bacterial reefs had already survived and adapted to an enormous number of environmental and biotic challenges. We would not expect them to change much, and they have not, even today. Accordingly, it seems much more likely that the earliest metazoans on the reef would adapt to the existing furniture, rather than immediately redecorating.

The Phylogeny of Epigenesis

So, our hypothesis is that early metazoans did not create body plans, so much as adapt to the pre-existing shapes of microbialites. Other than being physically possible, and parsimonious (since it does not require metazoans to invent body plans *de novo*), is there any evidence for this wild guess? Sort of. That is to say, it seems to be consistent with the very little we know about actual primitive metazoans. True, what we know is indeed little. Almost all of the Ediacaran animals are thought to be well off the main line of Metazoa, or outside Metazoa altogether. Worm-like trace fossils are not particularly helpful, either. They may represent the tracks of advanced, bilaterian animals. If so, they are irrelevant to the ancestry of sponges. Alternatively, some may represent the fossilized tubes of unknown things living below the surface. Whatever their relationships, we can know almost nothing about their morphology from the tubes alone.

This seems to leave two candidates, *Cloudina* and *Namacalathus* **[7]**. These two are often coupled in the literature, since they tend to be found in similar environments, i.e., on carbonate platforms and in association with cyanobacterial "build-ups." Almost all other animals from the Ediacaran are restricted to siliclastic sediments. Grotzinger *et al.* (2000). *Cloudina* and *Namacalathus* also have some degree of morphological similarity, although the resemblance is not particularly compelling. More interesting is the fact that these two animals, the only two regularly found on carbonate platforms are, probably by no coincidence, the only two Precambrian animals with carbonate mineralized skeletons.

Cloudina was only lightly mineralized, apparently by the precipitation of calcite in an organic template (Grant 1990). Grotzinger et al. (2000) **[6]**. That may be helpful. In fact the usual reconstruction of *Cloudina* looks a little like the cone-within-a-cone structure of an archaeocyath. The difference is that the stack of cones keeps on growing, like a column of paper cups. Recently, this interpretation has been challenged. Miller (2004). However, Miller's reconstruction of *Cloudina* differs mainly in omitting the "test-tube bottoms." The resulting structure is a continuous calcite tube which periodically gives rise to rings of flange-like protrusions, but otherwise looks a bit like Figure F above. Miller's three-dimensional interpretation of these rings is that they are the externally visible sign



of partially doubled or multiple walls, perhaps from repairs -- a bit like the arrangement in Figure C. If so, this is much more interesting. However, no one currently suggests that *Cloudina* had any of the intervallum intricacies that distinguish the archaeocyaths; and the actual living cells of an archaeocyath resided in the space between the two walls. Nevertheless, the presence of a partially double-walled, cup-shaped animal in precisely the environment which the archaeocyath would come to dominate a few million years later is, at least, a striking coincidence.

Another odd morphological similarity links *Cloudina* to sponges. The figure shows (A & B) part of the wall of *Cloudina* from Feng *et al*. (2002). C and D are cross-sections of a demosponge (*Tethya*) spicule taken from Weaver *et al*. (2003). The similarity is striking, despite an approximately 10-fold difference in scale. No doubt the structural resemblance could be due to the fact that there are only so many ways to build cylindrical objects from amorphous minerals. However, the possibility of homoplasy doesn't set us back.

Remember, we don't need to conclude that *Cloudina* and archaeocyaths are related. This is possible (see, *e.g*. Budd, 2003), but not necessary. Our point is that *Cloudina* and archaeocyaths both closely resemble thrombolites of various types. We are suggesting a common mode of evolution for sponges and *Cloudina*, not common ancestry. In fact, we have to be quite careful about trying to infer phylogenetic relatedness from morphology, if the more parsimonious interpretation is that morphology came before phylogeny. We'll worry about the mechanism for this peculiar reversal of the usual order in just a moment. For now, consider it simply as a reason not to jump to premature conclusions.

More or less contemporaneous with *Cloudina* is the tiny *Namacalathus*. If archaeocyaths are "ancient cups," then *Namacalathus* is an ancient goblet. The upper portion of *Namacalathus* is bowl-like, but with ovoid "port holes," usually six in number. In fact, Grotzinger *et al*. argue that *Namacalathus* actually had hexagonal symmetry. The bottom portion of the animal is relatively long and stem-like. At this point, it may be amusing to compare Grotzinger's reconstruction of *Namacalathus* with the ghostly outlines in the upper left-hand corner of Figure G above. This proves absolutely nothing, but it is interesting to contemplate that something similar to *Namacalathus* may have survived the end of the Proterozoic -- by over 540 My.

The principal non-thrombolite characteristic of *Namacalathus* is that, according to Grotzinger *et al*., the animal had a regular symmetry, specifically a more or less hexagonal symmetry about a central axis. This is particularly striking in cross-section. Extant sponges don't show this type of symmetry, nor do thrombolites. On the other hand, some *basal*

archaeocyaths do show this pattern (*Archaeolynthus* **[8]**, and perhaps *Dokidocyathus*, see Perejón & Moreno-Eiris, 2006) as do various blastula stage sponge embryos (Leys & Ereskovsky, 2006). In these latter cases, the symmetry is essentially an artifact, normally temporary and imposed by structural constraints during development. It is not the product of some hox-like genetic program. That is, early metazoan morphology was a matter of physical constraints, only later followed by genetic programming.

Evolving Cylindrical Rabbits

So, based on these whirlwind generalizations, we seem to have a peculiar puzzle. We asked earlier, "How do we get the rabbit out of the hat?" Actually, getting the rabbit out is no problem. He'll eventually leave on his own. The real issue is how he got there in there in the first place. Magicians have only minutes, but the metazoans had megayears. We suggest that these particular rabbits were in their hats because they evolved there.

The earliest metazoans had no particular shape, other than perhaps the generally spherical condition choanoflagellates have on the smallest scales. For such an organism, becoming trapped in a thrombolite on a bacterial reef would be an excellent thing. Surrounded by tasty bacteria, protected from environmental hazards -- who could ask for more? In this ideal environment, the major evolutionary pressures would be largely restricted to three factors: getting adequate circulation to receive food and remove waste, not outgrowing the space limitations, and dealing with environmental wear and tear on the thrombolite. Almost nothing else falls into the rather limited range of things which (a) matter to a small ball of cells and which (b) it could do anything about.

Very few of us know how to build a house from scratch; but almost everyone learns to make a few basic repairs. That requires much less skill. So, we suspect, the earliest metazoans had no expertise in general construction, but would gradually evolve the ability to make repairs by influencing the deposition of calcium carbonate, creating small holes for circulation, keeping the central region clear for the same reason, reinforcing the peripheral region, and ultimately creating a complete skeletal structure. The structure would, naturally, begin by looking more or less like a thrombolite. That is surely the most parsimonious expectation. The net result would ultimately be a collection of organisms which share some odd morphological characteristics with thrombolites, which are equipped with superficially similar biochemical toolkits for using calcium carbonate, but which do not seem to be very closely related to each other in other ways.

This leaves a great deal unexplained, but at least convinces us that there are reasonable explanations for what would otherwise be a remarkable series of odd coincidences at the base of the Metazoa and the dawn of the Phanerozoic. ATW070920.

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ATW070920

Archaeocyatha - 1

Early Cambrian to Furongian

```
PORIFERA
|--Archaeocyatha
|  |--Ajacicyathida
|  `--Irregulares
`--+--Stromatoporoidea
   `--+--Calcarea
      `--+--Hexactinellida
         `--+--Demospongiae
            |  |--Tetractinomorpha
            |  `--Ceractinomorpha
            `--+--Homoscleromorpha
               `--EUMETAZOA
```

Cross Reference Palaeos.org

Introduction

The Archaeocyatha are chiefly remembered for being the first Metazoan reef builders. They flourished briefly during the Terreneuvian and Cambrian Epoch 2, then declined drastically. A few survivors straggling on until the end of the Cambrian. Archaeocyaths had *calcareous* skeletons and lived attached to the sea-floor. They sometimes formed colonies, but were more often solitary members of reef communities actually dominated by mineralizing bacteria.

After a long history of phylogenetic uncertainty, the present consensus is that they were sponges. However, their placement as *stem* sponges is essentially arbitrary. The archaeocyath body typically consisted of two nested, perforate cones connected by a series of *septa*. Water flowed through the pores, into the space between the walls, and ultimately out through the central cavity. Work on the biomechanics of water flow through this structure suggests that archaeocyaths operated much like other sponges.

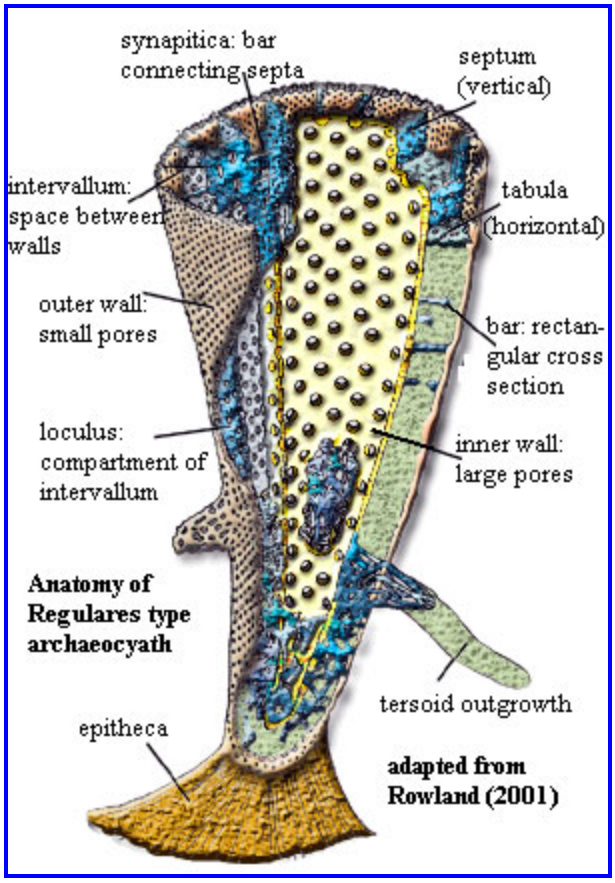
A word on nomenclature. In the days before Google, it didn't matter much how one turned nouns into adjectives. Now it does. About half the literature uses "archaeocyathan" as the word meaning "of or pertaining to the Archaeocyatha." We use "archaeocyath" as both the generic noun and the as the adjective. However, if you do any searching, try both. We missed some good sources on the first pass.

Special Credit: special thanks to Prof. Carlos M. da Silva of the Universidade de Lisboa, for posting really good

material on archaeocyaths; and to Lângia Colli Montresor, Universidade Federal de Minas Gerais, for help with the translation.

Special Discredit: a raised eyebrow goes to Kevin Zelnio and Christopher Taylor for their song *Receptaculites* -- surely the world's finest musical exposition of archaeocyath phylogeny. Kevin's sensitive interpretation of this moving *schwammlied* may be found **here**, a perfomance marred only slightly by the words, music, execution, etc. Unfortunately the guitar accompaniment also seems to have suffered some sort of diagenetic alteration...

Anatomy



Morphology: The essential body plan of the Archaeocyatha looks like pair of porous ice-cream cones -- or dunce hats -- one inside the other, forming inner and outer walls. The space between the calcareous cones is the *intervallum*. Both the inner and outer walls are porous. The two walls are joined by radially-arranged partitions (*septae*) which frequently look quite a lot like the septae of modern corals. Benton & Harper (1997); Rowland (2001).

This model implies an inverted conical shape, which is common, but archaeocyaths are also frequently cylindrical or even discoid. Rowland (2001). The size of archaeocyaths varies, normally between 1 - 2.5 cm in diameter and 8-15 cm high. However, giants species have also been found, 30 cm tall and about 60 cm in diameter.

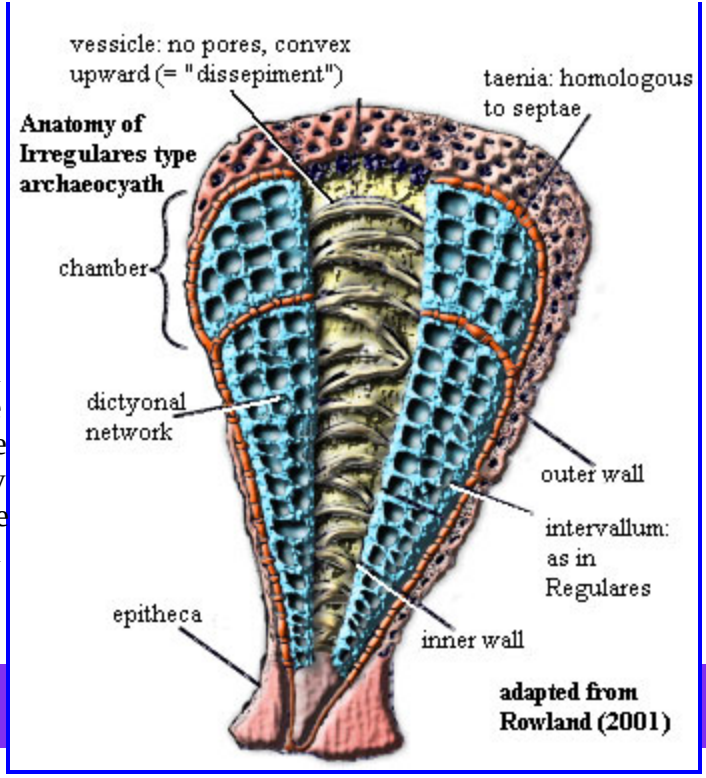
Exoskeleton and Outer Wall: The archaeocyath skeleton was *calcareous*; but, beyond that, things get a bit hazy. Some writers assert that this was a high-magnesium sort of calcite. Rowland (2001). Others observe that their fossils were extensively recrystallized, *dolomatized* (magnesium substituted for some of the calcium), or *silicified* during fossilization. Álvaro *et al*. (2002). In any event the skeleton was basically carbonate, not silicate.

The inner and outer walls are both extensively perforated by pores. Benton & Harper (1997). The pores are typically smaller in the outer wall, as in sponges. The outer wall may include outgrowths of various kinds (Rowland, 2001), *e.g*. *tersoid* (branches) or *rhizoid* (anchored to substrate).

Intervallum: The space between the inner and outer walls, the intervallum, is partitioned by a series of thin walls into hundreds of tiny, featureless compartments -- like an apartment in Moscow, only with better plumbing. The longitudinal walls are referred to as *septae*. Transverse (horizontal) walls, if present, are *tabulae*; and the individual compartments are *loculi*. These internal partitions are less porous than the walls, and sometimes lack pores altogether. Benton & Harper (1997); Rowland (2001).

Other structures occasionally found in this anatomical region include upwardly curved domed plates. These have been referred to as *dissepiments*. That term is now deprecated, by some, in favor of *vesicles*, in order to conform to sponge terminology. When present, dissepiments/vesicles lack pores and probably function as structural framing, as opposed to the drywall partitions created by septae and tabulae. One family of archaeocyaths, the Dokidocyathidae, also has spicule-like bars.

Inner wall and Central Cavity: The inner wall often has larger pores, like the openings into the *spongocoel* of more conventional sponges. The vesicles may extend into central cavity. The upper end of the central cavity is open to the environment, and is 1-5 cm in diameter in at the wide end. The bottom narrows to a rounded base, and the entire system is attached to the substrate through an *epithecum* of uncertain composition and variable morphology. Benton & Harper



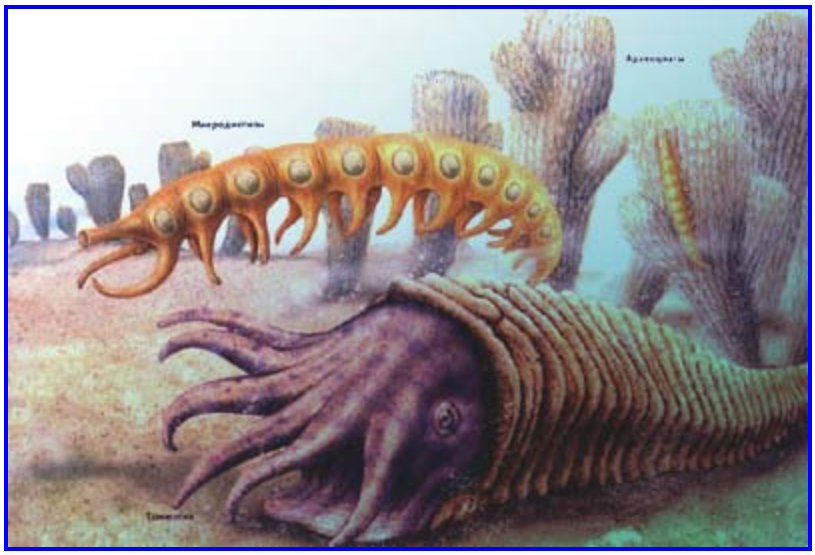
(1997); Rowland (2001).

Functional Morphology: The current take on archaeocyath functional anatomy is that they processed sea water in the same manner as other sponges. That is, water entered through the pores in the outer wall, bacteria and detritus were absorbed by *choanocytes* (or equivalent) as the water flowed through the intervallum, and waste was discharged through the central cavity. Rowland (2001).

Ecology

Environment: The Archaeocyatha were very common in tropical, shallow-water marine environments, almost always on carbonate substrates. Their ideal environment is reconstructed as being a stromatolite-covered carbonate shelf in a warm (~25° C.), open sea at a depth of 20-30 m, in water of moderate energy and high oxygen content. Isolated, solitary archaeocyaths occurred at paleodepths up to almost 100 m, but none deeper. As far as is known, all archaeocyaths were fully marine.

As mentioned above, some archaeocyaths were reef-builders. Benton & Harper (1997) observe that these reefs were "not very impressive;" but they're British (Benton & Harper, not the reefs), so it's hard to tell if this means anything. The archaeocyath reef was generally a mound no more than 3 m thick and 10 or 30 m in diameter. Some (even non-British) paleobiologists are so disdainful of these structures that they refer to them as "stromatolitic-archaeocyath build-ups," preferring to resort to awkward circumlocution rather than dignify these little complexes with the term "reef." Benton & Harper (1997); Rowland (2001); Álvaro *et al*. (2002).

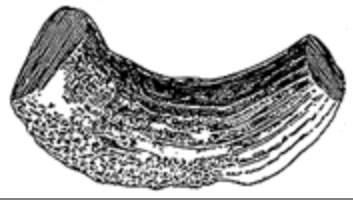


Distribution: Archaeocyaths were nearly ubiquitous in tropical regions during most of Cambrian Epoch 2. Wood (1998). So, for example, they were common in East Gondwana (Australia, East Antarctica), West Gondwana (Spain, France), and both coasts of Laurentia (eastern Canada, Nevada). *See, e.g.*, Rowland (2001); Álvaro *et al*. (2002); Corsetti & Kaufman (2003); Meert & Lieberman (2004); Wrona (2004).

Growth Habit: Despite their fame as early reef builders, archaeocyaths were more often solitary, and most of the actual building was done by calcareous bacteria in the surrounding stromatolite. In the nature of things, sponges cannot live too densely. They are extremely efficient at sucking up water with bacteria and spraying out water without bacteria. A really large growth of sponges would get in the way of its own exhaust stream and starve to death.

Archaeocyaths early exploited *cryptic habitats* -- in cavities and hollows below the bacterial mat. Wood (1998). One wonders what this may have contributed to the development of burrowing organisms and the eventual destruction of the firm, bacterial carpeting that covered the typical Proterozoic and Early Cambrian sea bottom within the *photic zone*.

Associations: Archaeocyaths first came to prominence in the Tommotian (Cambrian II), before the trilobites. Even at that time, the archaeocyaths were associated with other animals, *i.e*. the "small shelly fauna" which were almost all the fauna there were at the time. Maloof *et al*. (2006). As other potential associates became available over the later Early Cambrian (Atdabanian and Botomian), they were duly associated. Thus, in due course, archaeocyaths are found together with chancelloriids, calcareous sponges, stromatoporoids, hyoliths, trilobites, lingulid brachiopods and assorted echinoderms. Wood (1998); Álvaro *et al*. (2002); Müller *et al*. (2007); Sperling *et al*. (2006). Indeed, many of these associations were unusually close, in that the other organisms are found physically attached to the archaeocyaths.



Ethmophyllum whitneyi. Laurentia, Botomian age. Height about 2.5 cm. Moore *et al*. (1952)

Image credit: Tommotian community reconstruction from История нашей планеты.
Note: Russian-language web sites have an enormous amount of information on archaeocyaths, possibly more than the rest of the WWW put together. Even if (like us) you don't read Russian, run an image search on Археоциаты.

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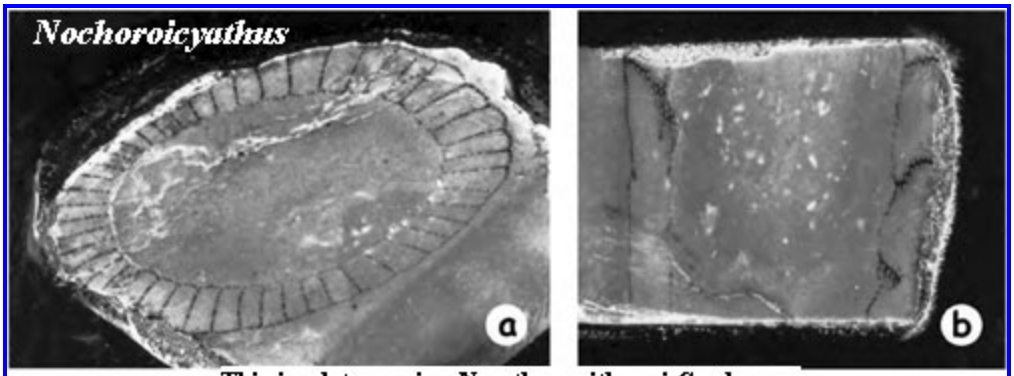
Archaeocyatha - 2

Phylogeny and Diversity



This is a late species, N. yathus, with peri-Gondwanan distribution. From Perejón & Moreno-Eiris (2006).

Origins: As stated above, the first known archaeocyaths are found at the beginning of the Tommotian. This turns out not to be a coincidence, because the base of the Tommotian on the Siberian Platform is often *diagnosed* by the first appearance of the archaeocyath, *Nochoroicyathus sunnaginicus*. Kouchinsky *et al.*, (2005). Archaeocyaths remain important stratigraphic bookmarks for the rest of the Early Cambrian.

Phylogeny: The phylogenetic background of the archaeocyaths is unknown. In fact, they almost out-mystify the conodonts, judging by the number of different taxa to which they have been assigned. Rowland (2001) was forced to resort to a sort of phylogram of phylogenetics in order to describe the evolution of thought about archaeocyath origins. Archaeocyaths have been classified as algae, Cnidaria, some sort of behemoth foraminiferan, and even as vascular plants. Some workers still assert that the archaeocyaths ought to have their own Kingdom. If Monaco can be a kingdom, why not Archaeocyatha?

As Rowland points out, the current dominance of the sponge school of thought (*i.e.* the spongiform encepahlo-party?) is due mainly to the discovery of structurally analogous modern sponges in the 1970's. These sponges have a massive calcareous base, but also spicules. See image of *Astrosclera*. However, these "Sclerosponges" or "coralline sponges" are

believed to be polyphyletic (Chombard et al., 1997), and we have so far turned up nothing that justifies the placement of the archaeocyaths on the stem lineage of the demosponges in particular. The idea seems to be based on a conference abstract describing some cladistic work in the early 1990's **[5]**.

Throughout their long history of wandering through the phylogenetic waste, the archaeocyaths have frequently been grouped with other taxonomic vagrants, particularly the receptaculitids and stromatoporoids. The current understanding (Rowland, 2001) is that the receptaculatids (whatever they are) were not close relativesof the archaeocyaths, but that the stromatoporoids probably are -- with both archaeocyaths and stromatoporoids being stem demosponges. This makes fairly good intuitive sense, if *Astrosclera* is a surviving stromatoporoid as suspected. In that case, we might suppose that the demosponge stem group started with both a massive calcareous framework *and* silicate spicules, with various groups specializing in one or the other skeletal system over time. However, once agin, there is no evidence that archaeocyaths are more closely related to demosponges than calcareous sponges. We take this matter up again later, in connection with the demosponges.

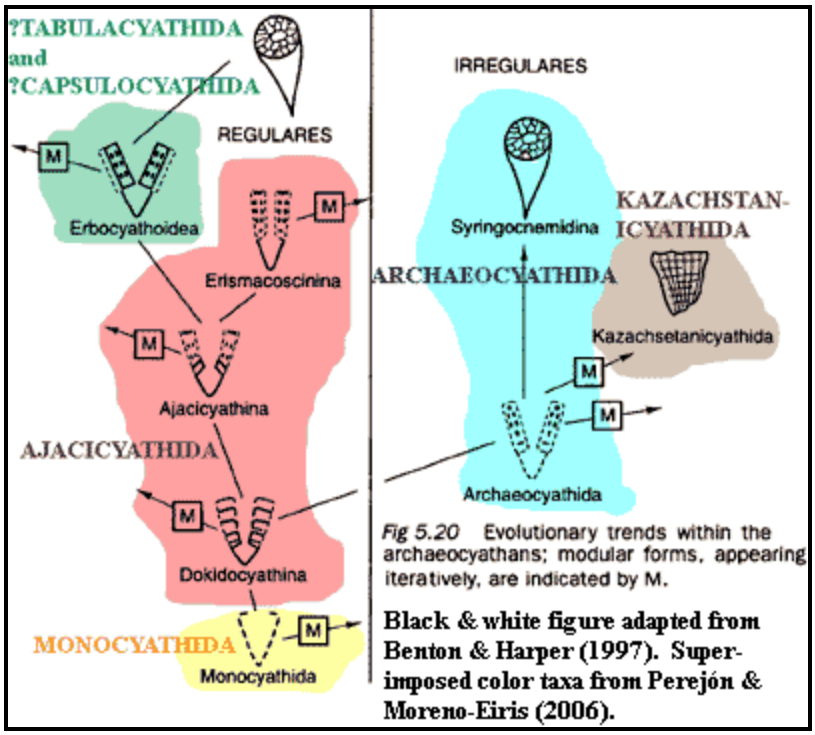


Fig 5.20 Evolutionary trends within the archaeocyathans; modular forms, appearing iteratively, are indicated by M.

Black & white figure adapted from Benton & Harper (1997). Superimposed color taxa from Perejón & Moreno-Eiris (2006).

Evolutionary History: Since the archaeocyath communities were already fully established at the base of the Tommotian in Siberia (Wood, 1998), it is likely that they evolved elsewhere -- or at least earlier. However, Siberia is where, and the Early Cambrian is when, they are first found. Benton & Harper (1997). Their distribution became worldwide, and their diversity grew to about 170 families in the Botomian (Cambrian IV), about 25 My later. Rowland (2001). Two waves of extinction in the later Botomian all but eliminated the entire group. Only one genus has been found from the Middle Cambrian, and another from the Furongian, both discovered in Antarctica. *Id.* No known archaeocyaths survived into the Ordovician. Their decline may be related to global cooling and the replacement of firm microbial substrates by soft, muddy bottoms over the course of the Cambrian. Bottjer *et al*. (2000); Álvaro *et al*. (2003); Dornbos *et al*. (2005).

Classification: Archaeocyatha have traditionally been divided into Regulares and Irregulares. Rowland (2001) describes the difference as follows:

> ...Irregularia included those genera in which aporous, concave-upward, curved plates called dissepiments always occur, and in which the dissepiments in the tip of the cup can be seen to have developed before the inner wall or any radial longitudinal elements had developed. Regularia, in contrast, included forms that may or not contain dissepiments, but, where present, they develop after the development of the inner wall and septa and/or tabulae.

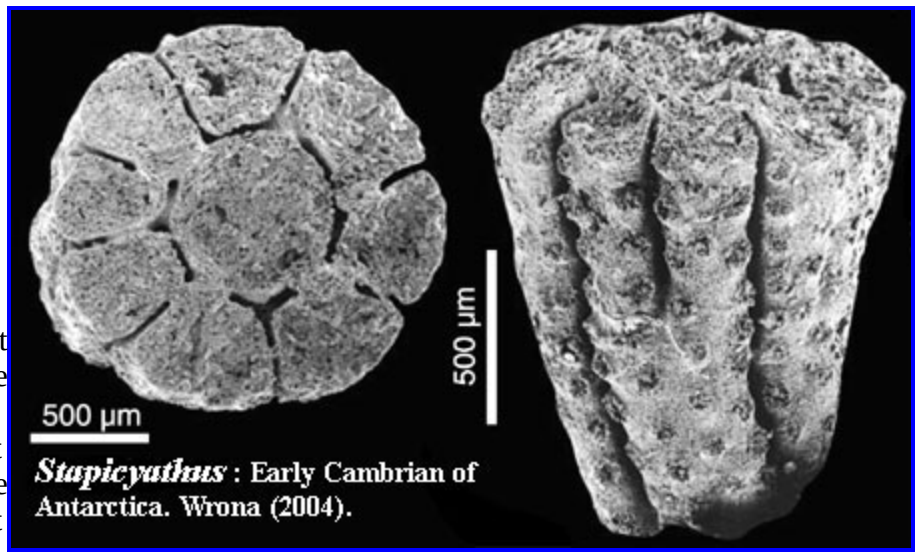
He goes on to explain that these are no longer regarded as phylogenetic groups, but that much of the literature still refers uses that terminology. So how might we arrange these groups in a somewhat more phylogenetically useful way?

We found two moderately recent attempts to reorganize things. They seem more or less consistent, as shown in the figure. Rather than look for trouble, we've decided to quit while we're ahead. Unfortunately, Perejón & Moreno-Eiris (2006) do not mention Benton & Harper's (1997) Erbocyathoidea. Similarly, Benton & Harper do not mention the

Capsulocyathida of Perejón & Moreno-Eiris. Worse, Benton & Harper apparantly put the tabulacyaths under Archaeocyathida.

However, by sweeping all those minor matters under the microbial mat, we can write an incomplete phylogeny something like this:

```
Archaeocyatha
|--Monocyathida
 --+--Dokidocyathina
   `--+--Ajacicyathida (Erismacoscinina >
Kazachstanicyathida)
      |  |--Ajacicyathina
      |   --Erismacoscinina
       `--Irregulares (Kazachstanicyathida >
Erismacoscinina)
         |--Archaeocyathida
          --+--Kazachstanicyathida
            `--Syringocnemidina
```



Of those taxa, Archaeocyathida is probably not monophyletic, and we're a bit dubious about the monocyathids. They may not even be archaeocyaths (one reason we still haven't ventured a definition of Archaeocyatha), but the rest look plausibly monophyletic. For a first guess, it will do. ATW070908.

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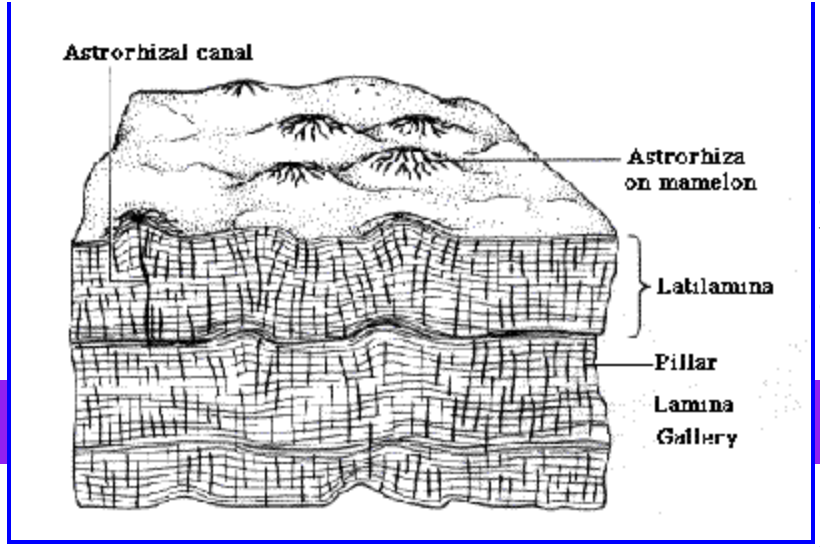
Stromatoporoidea - 1

Introduction

Stromatoporoids are best known for being the main reef builders of the Middle Paleozoic. Everyone seems happy with that statement, at least up to a point. Also, almost everyone agrees that they are sponges – which is almost meaningless since sponges are said to be merely a "grade of organization." The stromatoporoids have proven almost impossible to characterize beyond that point. The current, tentative, take on the group is that it is another "grade of organization," not a *phylogenetic* entity. It is often said that Stromatoporoidea is largely composed of *stem* sponges, or stem demosponges, massively *calcified*, with closely-spaced *laminar* or *tabular* layers and roughly vertical columns.

After that, things get really peculiar. For example, stromatoporoids are first found in the Tommotian (Wood, 1998), or perhaps the Botomian (Benton & Harper, 1997) ... or should that be Middle Ordovician (Webby, 2004)? Stromatoporoids flourished until the end of the Devonian, when they became extinct (Webby, 2004) -- except that they were also a major reef component in the Late Jurassic (Benton & Harper, 1997), and may not be extinct, even today (Rowland, 2001). Typically, we would now launch into a Philippic on the inevitability of such confusion when workers do not zealously guard against chaos by establishing careful phylogenetic definitions. However, we have already written too much on this topic and "as to the importance of a general zeal in the discharge of duty, believing you are convinced and satisfied, I say no more" **[9]**. The problem is that, in this specific case, it is nearly impossible to construct a testable phylogenetic definition. So "zeal in the discharge of duty" is going to do us about as much good as it did Demosthenes

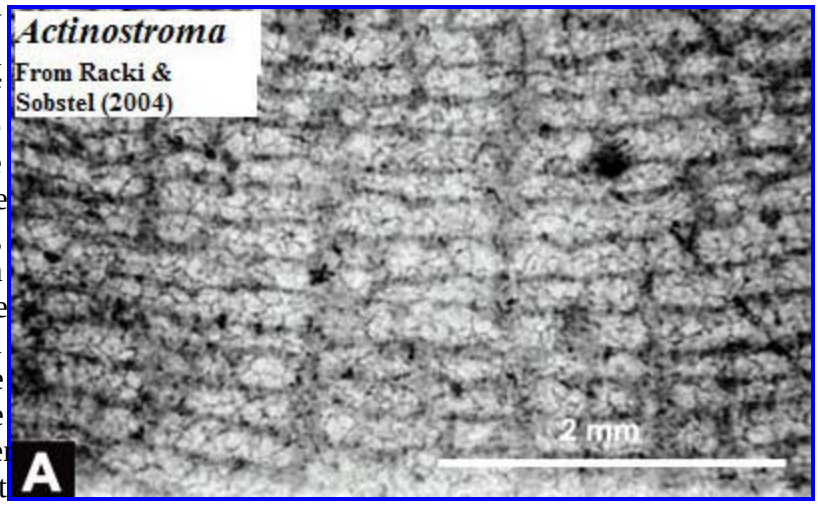


and his Athenians. However, also like Demosthenes, we refuse to allow piddling details to get in the way of exercising our traditional right to run off at the mouth on subjects we know nothing about.

Anatomy

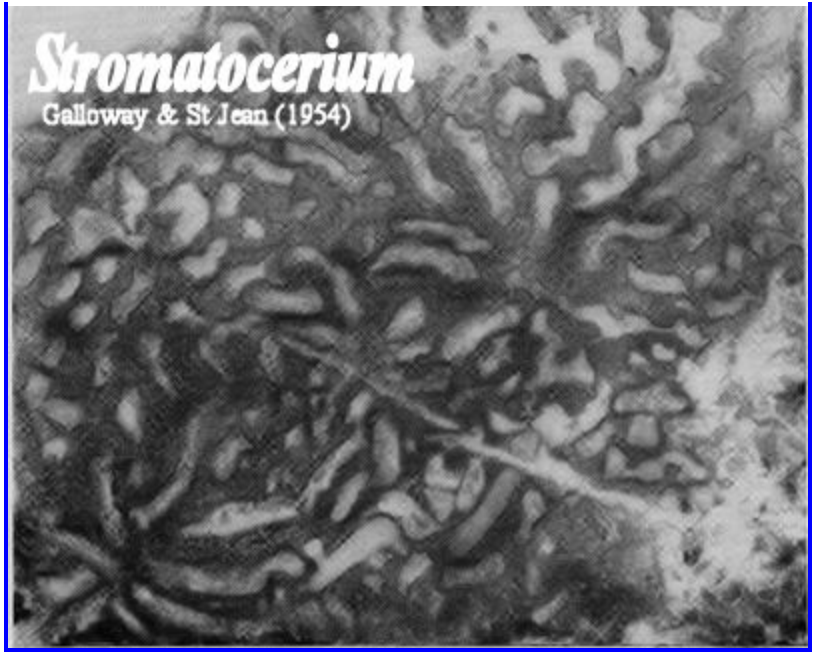
On the left is the usual sketch of a stromatoporoid. In fact stromatoporoid morphology is quite variable. They are best known, and most typically found as massive "domical" structures, but other types exist: conical, mushroom-shaped, columnar, branching, or even thin and reed-like. Benton & Harper (1997) Their skeleton (*coenosteum*) was *calcite* (or *aragonite*). Since they were both large and mineralized, they are frequently preserved as fossils. Stromatoporoids frequently formed reefs with bacterial stromatolites, which probably accounts for their name. Indeed, misidentifications of stromatoporoids for calcified bacterial mats, and presumably vice-versa, are still being corrected. Schlagenweit (2005); *c.f.* Igo *et al*. (1988).

Outer surface: *mamelons* and *astrorhizae*. Many paleontologists, even those who routinely work with stromatoporoids, seem to avoid trying to make sense of their anatomy. Most of these workers seem to believe that the living tissue of the sponge was restricted to the outer surface and one or a few levels down into the gallery. Benton & Harper (1997). Perhaps living tissues penetrated more deeply around the main channels of the water canal system. In any case, the outer surface is often organized around rounded projections called *mamelons*. A network of canals, the *astrorhizae*, radiate outward from the low peaks of the mamelons. Unfortunately, the details of the water canal system are rarely preserved, so it is hard to sort things out functionally. If stromatoporoids followed the usual pattern of sponge biology (and sponge physics), we might suppose that the astrorhizae were the incurrent openings, while the central region of the mamelons held the excurrent openings. However, the consensus view is that it was the other way around. Benton & Harper (1997); Webby (2004). Further, it is not clear that the mamelons had *any* particular significance since "[i]n many Recent 'sclerosponges' mamelon structures may be present or not within the same species (Hartman 1984)." Reitner & Engeser (1987).



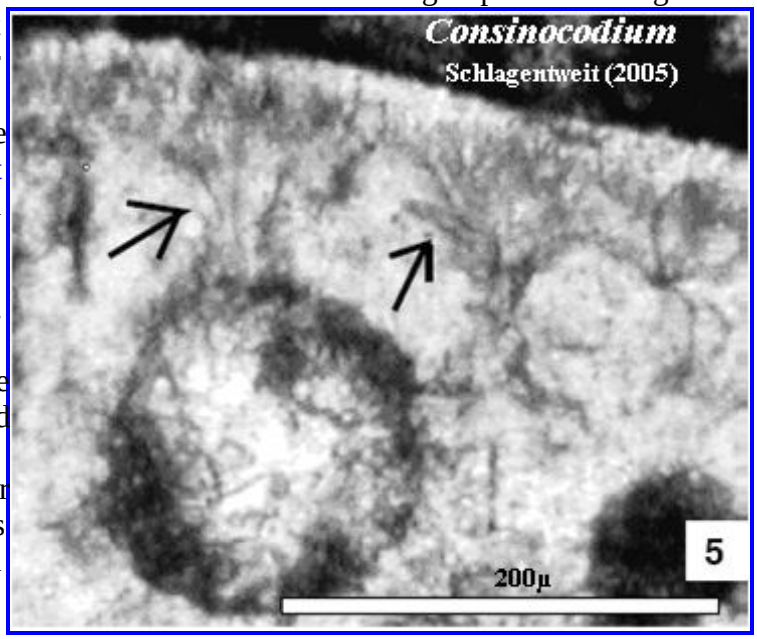
Inner Matrix: pillars and latilaminae. Webby (2004) aptly describes the inner mesh of the coenosteum as a "monotonous" gallery of vertical and horizontal elements. The vertical elements are inevitably known as pillars. In some cases, they may actually resemble pillars, as in the early Labechiida. *Id.* However, they may also form short, undulating walls, a bit like the septa of some Irregulares. Galloway & St. Jean (1954). Septum-like pillars also form the outlines of the astrorhizae.

The pillars are not necessarily continuous through the entire gallery. They frequently terminate at one of the *latilaminae*. *Id*. The latilaminae have been characterized as pauses in growth, like annual tree



rings. If so, this would imply a rather unsponge-like growth pattern. Sponges normally grow very slowly and are said to have lifespans measured in centuries, or even millenia (although no one we know has *quite* enough free time to keep a sponge under close observation for even a decade or two). However, it is also believed that Paleozoic sponge reefs had growth rates comparable to modern corals. Wood (1998).

Spicules: Mesozoic forms only. Paleozoic stromatoporoids apparently did not produce spicules. However, *silica* spicules have been observed in stromatoporoids from the Jurassic. In fact, the presence of spicules in Mesozoic stromatoporoids is one reason that these forms are thought to be unrelated to the Paleozoic groups. Others argue that that the entire skeleton may have be siliceous, but *diagenetically* transformed into *calcite*. Benton & Harper (1997). Neither argument is completely satisfactory. As the image shows, these spicules (indicated by arrows) are difficult to distinguish from ordinary pillars. Schlagintweit (2005). Consequently, any conclusions from this data would be ... spiculative.

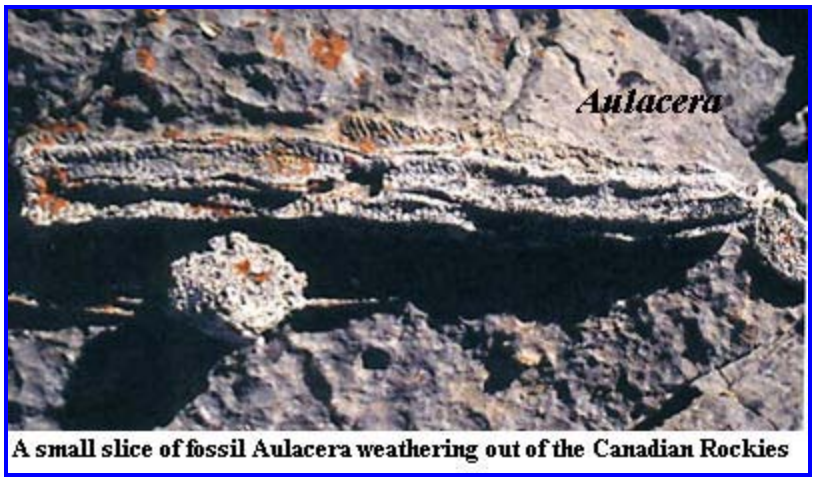


Water Canal System: poorly known, stromatactis-like. Schlagintweit's description of the Mesozoic *Consinocodium* shows that it is clearly more like a modern demosponge than a Paleozoic stromatoporoid. Note the large round cavities, possibly containing choanocytes or captive bacteria -- both common in demosponges. On the other hand, the extant *Acanthochaetes*, at the top of this page, is indistinguishable from a typical Paleozoic stromatoporoid in external view.

Other information on the inner workings of the water canal system is hard to come by. In doing our research, we saw a few brief descriptions and images, which looked suspiciously like *stromatactis*. Stromatactis is an "enigmatic" (Wood, 1998) material which looks like short, often interconnected, worm burrowings. It is usually assumed to produced by bacteria. Alternatively, stromatactis may be entirely abiotic. It is a common feature of Carboniferous marine cements, but has been reported from any number of other places, including Neoproterozoic methane seeps (Jiang *et al*., 2003).

From this brief description, you will have gathered -- correctly -- that we weren't able to find much anatomical information on stromatoporoids, and that we believed only about half of what we found. Stromatoporoid workers are a microscopic branch of a miniscule paleosponge community, and most of the serious effort has gone into the ecology of Paleozoic reefs. Unlike anatomy and phylogeny, we can only scratch the surface of this ecological material. Those scratches are as follows.

Ecology



A small slice of fossil Aulacera weathering out of the Canadian Rockies

Distribution: Middle Paleozoic, Mesozoic, and Recent. The archaeocyaths died off at the end of Cambrian Epoch 2. After that there were no metazoan reef builders, and few reefs of any kind, until the Darriwilian Age of the Middle Ordovician. The first stromatoporoid "mud mounds" appear at this time. These relatively small domical stromatoporoids usually occurred in warm, shallow, areas on carbonate platforms, shelves, and around islands, in water conditions of moderate energy and relatively little sediment. Webby (2004). At about the same time, a second ecotype developed, which had a more columnar form (*e.g.*, *Aulacera*). These were able to grow from soft, muddy substrates at greater depth. *Id.* This was a singular advantage, since there was a great deal of that sort of substrate lying fallow at the time.

In the course of the Ordovician, these two types increased in size and abundance. By the Hirnantian Period, columnar forms almost 2 m tall formed calcareous "forests" in some regions. However, they never reached a worldwide distribution, as Ordovician stromatoporoids are only found within 30° latitude of the paleoequator.

As you might expect, given this distribution, the stromatoporoids suffered badly in the end-Ordovician cold snap. However, they returned to form the gigantic Middle and Late Devonian stromatoporoid reefs, some hundreds of meters in height, known in Australia, Morocco, Sweden, and other locations. Whether or not they became extinct at the end of the Devonian is not clear, but no stromatoporoid-like sponges are known from that point until the Triassic.

Stromatoporoids never again dominated the landscape, but they formed an important part of various Mesozoic reef communities, particularly in the Late Jurassic. These Jurassic forms appear to have been a very different ecotype from their Paleozoic relatives (or analogues, as the case may be). The Mesozoic stromatoporoids tended to inhabit unstable, high energy, high-sediment regions, often in rather shallow, turbulent waters. Leinfelder *et al*. (1996); Benton & Harper (1997). They disappear again at the end of the Cretaceous until 30 years ago, when living species began to turn up in deep water at the height of the Cousteau Era in the 1970's.

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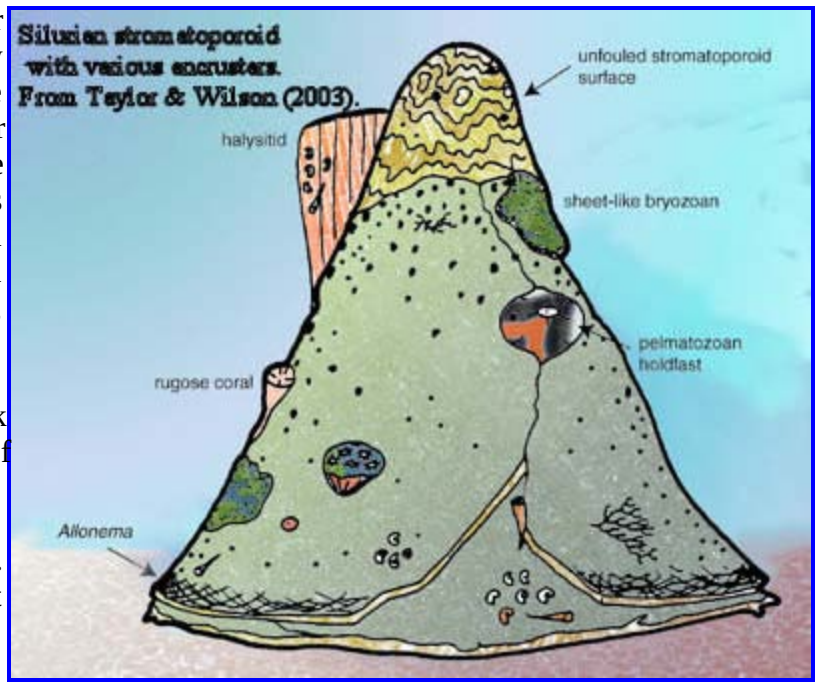
ATW070929

Stromatoporoidea - 2

Ecology (continued)

Growth Habit: the Calcite Empire. Like Romans or Englishmen, the stromatoporoids were colonial by nature, and often constructed edifices on a massive scale. These structures tend to be stratified, domal, or both. However (also like Romans or Englishmen), the very success of this monotonic system in gross depended on extraordinary adaptability and diversity in fine. Many stromatoporoids departed from the ground pattern and adopted other morphologies: bulbous, columnar, branching, or encrusting. Webby (2004); Benton & Harper (1997). And not just upper crust, either. One of the significant findings of recent work on reefs, ancient and modern, is the importance of cryptic communities -- organisms which lived under, within, or between the large calcifying elements. Wood (1998); Taylor & Wilson (2003). Stromatoporoids not only created these habitats, but sometimes lived in them as well.

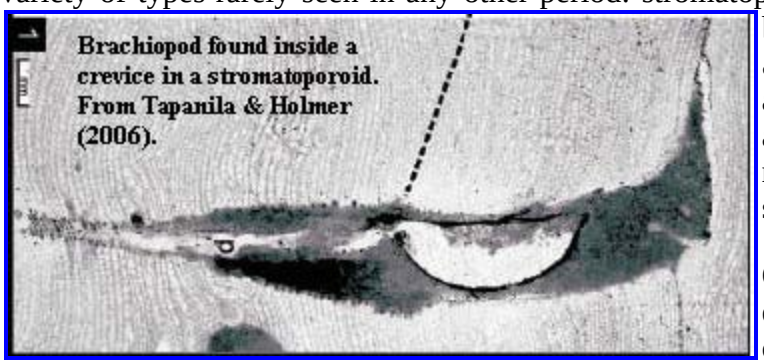


Associations: In Ordovician reefs, stromatoporoids are associated mainly with tabulate corals (and, less often, rugose corals), calcifying bacteria ("algae") lingulid brachiopods, spirorbid worms, pelmatozoans, and bryozoans. Benton & Harper (1997); Taylor & Wilson (2003); Tapanila & Holmer (2006).

The diversity of organisms associated with stromatoporoids increased in the Silurian and Devonian, as the group spread beyond its Ordovician equatorial range. New inhabitants included goniatites, several new brachiopod groups,

trilobites and crinoids. Tabulate corals remained important partners in building reefs, but rhodophytes (red algae) also became significant components of the complex. Stanley (2003); Wendt & Kaufmann (2006).

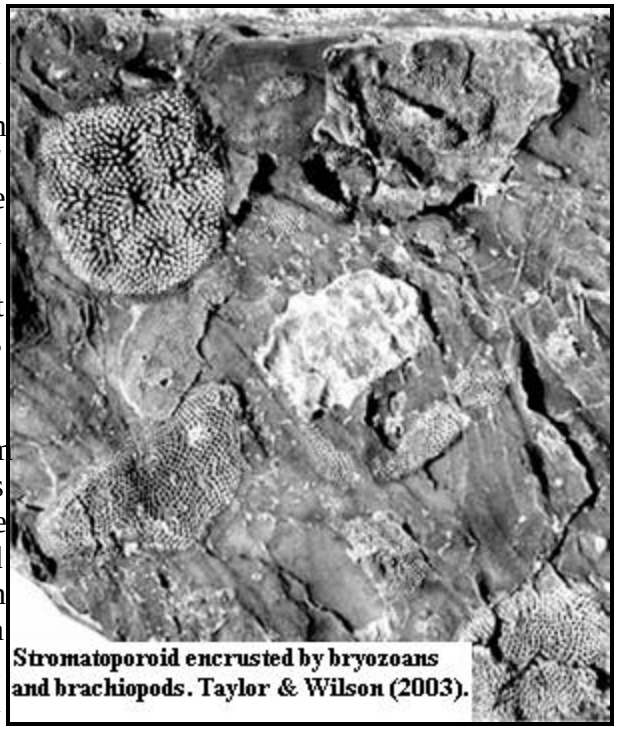
The Middle to Late Devonian was the zenith of reef-building -- not just for stromatoporoids, but probably for any biota, at any time in the history of our planet. Wood (1998). The stromatoporoids themselves produced a wide variety of types rarely seen in any other period: stromatoporoids which looked like mushrooms, or giant cabbages, or bushes, or sandcastles -- well perhaps not sandcastles, but almost (*see* Wood, 1998: 192, fig 3, item 7). It would, in any case, be pointless to list their associations. Almost anything that lived in the sea at that time was living in or near a stromatoporoid reef, unless it avoided the continental shelves altogether.



Brachiopod found inside a crevice in a stromatoporoid. From Tapanila & Holmer (2006).

One suspects that the main impetus for the evolution of enormous reefs in the Devonian may have been runaway competitive encrusting. Natural firm substrates were rare by the Ordovician, and became yet rarer. *But see* Taylor & Wilson (2003). The very success of the stromatoporoids and tabulate corals meant that they themselves gradually became the most widely available firm substrate in the oceans -- provided that an organism could encrust and outgrow the underlying sponge or coral, which was presumably not happy with the idea of becoming someone else's basement. Note that, the more that species *A* succeeded in encrusting and outgrowing species *B*, the greater the surface area it potentially provided to some third species *C*. That is, the more surface area *B* provided, the greater the selective reward to any other organism which could encrust and overgrow it.

This may explain several features of Middle Paleozoic reefs which are otherwise difficult to understand. ***(1) Size.*** These reefs increased in size in a roughly exponential way from the Middle Ordovician to the end of the Devonian. This is what we might expect of a system in which competitive success in outgrowing others necessarily *increased* selective pressure to grow yet more. To put it another way, the more you succeeded in overgrowing the neighborhood, the greater selection pressure on others to specialize in overgrowing you. ***(2) Growth Rate.*** According to Wood (1998), Upper Devonian reefs grew about as fast as modern reefs, even without photosynthetic symbionts. This follows logically from the previous point. ***(3) Morphology.*** One puzzling aspect of stromatoporoids is why they kept building enormous skeletons even when, as in columnar forms, the living organism scarcely grew at all. This strategy may have allowed stromatoporoids to grow rapidly, to defeat encrusters, without expanding beyond the available space. ***(5) Cryptic Habitats.*** A number of writers have noted the extensive use of cryptic habitats: space under, between, or even within, other mineralizing organisms. This is sometimes said to be a response to predation, as in Recent reefs. However, the cryptic growth habit goes back to the earliest archaeocyath reefs -- before predation was likely to have been a significant problem -- and perhaps even further back. It may be better explained as an adaptation to the trophic equivalent of "Class C" office space.


Stromatoporoid encrusted by bryozoans and brachiopods. Taylor & Wilson (2003).

However, none of this is to be taken too seriously. For reasons detailed by Taylor and Wilson (2003), it is very difficult to get reliable data on interspecific competition among reef dwellers.

The Mesozoic stromatoporoids were less impressive, but still important in rebuilding the reef system after the end-Permian. Late Triassic stromatoporoids combined with sphinctozoan sponges and the newly important scleractinian corals. Stromatoporoids like *Burgundia, Dehornella,* and *Acfinosfromaria* created reef communities with red algae and scleractinians along high energy northern borders of the Tethys and on both shores of the Atlantic Ocean, as it began to open in the Western Tethys realm.

Phylogeny

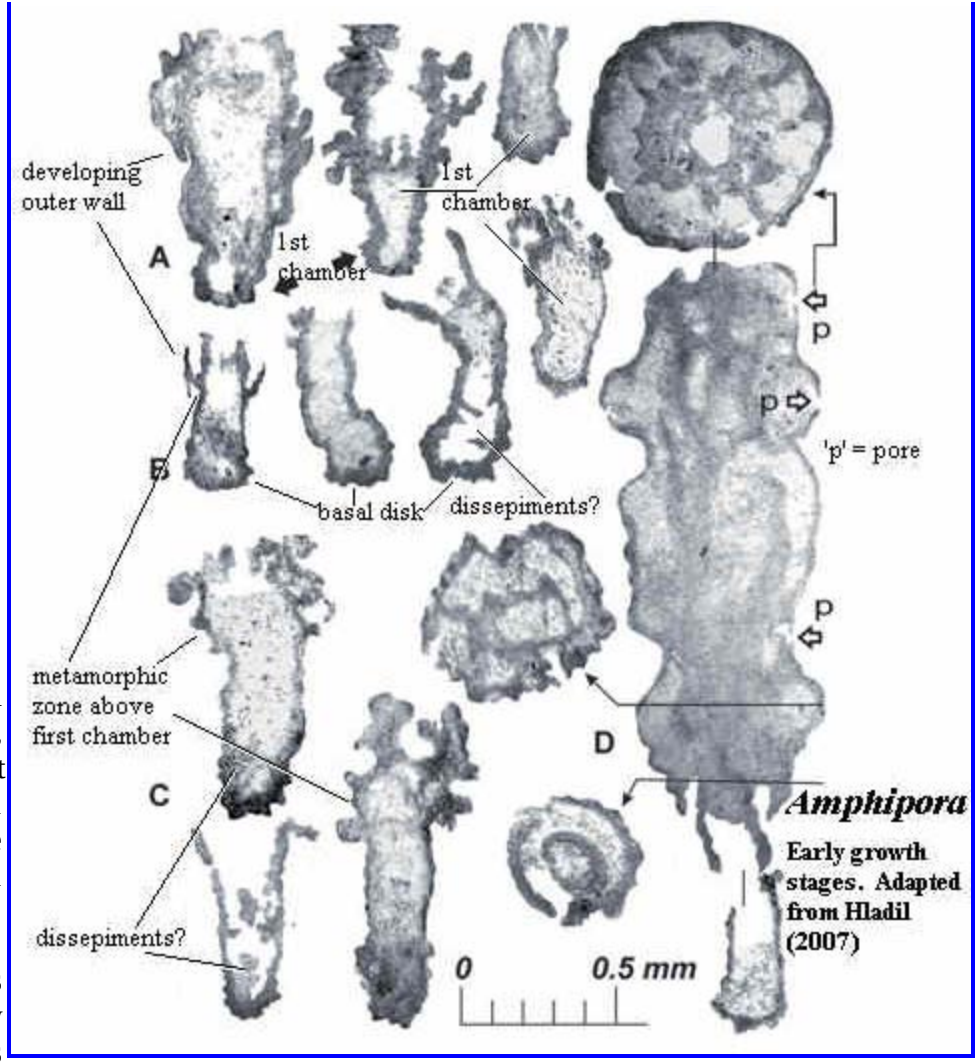
So, are Stromatoporoids a Clade? Stromatoporoids were historically grouped with the Archaeocyatha (Rowland, 2001), and later with the demosponges (Leinfelder *et al*., 1996). Happily, we can agree with both contentions. This might be the consensus view, i.e., placing both Stromatoporoids and archaeocyaths on the demosponge *stem*. However, there is considerable uncertainty about who ought to be included among the "true" stromatoporoids for this purpose. The earlier Paleozoic forms seem very much alike, and are assumed to be monophyletic. Webby (2004). Similarly, it is hard to doubt the affinities of at least some Recent stromatoporoidal demospoges with Mesozoic stromatoporoids assigned to the same genus. Reitner & Engeser (1987) (*Acanthochaetetes*). However, it is still unclear (a) whether the Mesozoic Stromatoporoidea are a natural group and (b) whether any of them are related to the Paleozoic bunch.

Unnecessary confusion has been added to this area by a tendency to overplay the molecular results of Chombard *et al*. (1997). The paper is frequently cited for the proposition that Stromatoporoidea is *polyphyletic*, with some stromatoporoids being demosponges, and others Calcarea. Worse, it is said to support the idea that stromatoporoids are merely a "grade of organization" without phylogenetic meaning. This time, we're not going to let that phrase pass without challenge.

First, this is a 1997 study. A great deal of methodological progress has been made since then. Chombard *et al*. used only 100-200 "informative" base pairs from the 5' end of the 28S "gene" of about a dozen species. This required throwing out a lot of data which wasn't parsimony-informative, or couldn't be aligned, and represents a rather small sample of organisms. Different primer combinations were used for different species, which tends to stack the deck. No genes were cloned. Rather, the tests involved direct cloning of PCR products -- risky when the underlying RNA has a complex secondary structure. The paper is vague on the extent of intraspecific sequence heterogeneity and the procedures used to resolve the discrepancies **[10]**. But, most fundamentally, this just isn't enough data on enough animals. *See*, for example, the remarkable effects of expanding the data and species numbers on the phylogeny of hexacorals. Daly *et al*. (2003). We are not questioning the conclusion that massive calcareous sponges are polyphyletic and "Sclerospongiae" an invalid taxon. We wish only to emphasize that this has absolutely nothing to tell us about stromatoporoids.

Despite having started out strong, we must finish weak. We lack even an amusing speculation to offer about either of the questions in the first paragraph of this section. Our sole purpose was to argue that these are still very much open questions. But now, rather than attempt to crawl laboriously out of this embarassing rhetorical pit in full view of the reader, exposed to his disdain and sarcastic shouts of encouragement, we will draw a curtain around thes matters while distracting the reader's attention with a brief discussion of Hladil (2007).

Hladil (2007) is not a "big" paper. It's a sort of "hmmm, *this* is interesting ..." kind of paper about the (mostly) Givetian-Frasnian stromatoporoid



Amphipora. *Amphipora* is an usual stromatoporoid which is tall and thin, somewhat like the head of a horsetail, but sometimes branched. Hladil has been doing stratigraphy and geology in the Czech Republic for several decades and has seen a great many specimens.

In essence, his thesis is that *Amphipora* is rather archaeocyath-like in early development. One of his key figures is reproduced at right. (Our re-labeling is more aggressive in interpreting the structures than Hladil's original, as we must make the point more quickly). *Amphipora* develops from a single-walled "first chamber" with a basal disk. Above this chamber is a metamorphic zone, in which the wall delaminates, through a series of irregular pustules, some of which develop openings or pores. Eventually, there are two walls.

Hladil also emphasizes that neither the inner nor outer wall in the metamorphic zone seems to be continuous with the original wall of the first chamber. If so, this provides a broad developmental hint, not only about the origins of the Stromatoporoidea, but also about the relationships of some archaeocyath clades. That is, it suggests that the Monocyathida are truly basal, and that their wall may not be strictly homologous with either inner or outer wall of other archaeocyaths. Rather the separate walls derive from (as Hladil notes) an irregular series of growths resembling calcite bubbles, and suggestive of an originally secondary repair system. We are particularly enthusiastic about this observation, since it flanges nicely with our thrombolite speculations.

Phylogenetic History: We have covered a good bit of stromatoporoid history above. We repeat it, with a few extra details, in case you weren't listening the first time.

Some reviews have indicated that stromatoporoids are first known from the Tommotian (Wood, 1998) or Botomian (Benton & Harper, 1997). However, *Pseudostylodictyon* from the Middle Ordovician of New York and New England may be the first "true" stromatoporoid. *Id.* Two distinct groups developed at that time, the Labechiida and the Clathrodictyida together with a few less well-known forms. The labechiids were particularly archaeocyath-like, with upwardly convex supporting plates. However, the water canal system is rarely preserved and is poorly understood. Webby (2004). By the end of the Middle Ordovician, large dome-like are found in North and South America. The labechiids were the dominant group in the Ordovician. They experienced two pulses of radiation in the Dariwillian and Sandbian, respectively. The Clathriodictyida also appeared in the Sandbian. *Id.*

The Labechiida declined in the later Katian and suffered further during the end-Ordovician glacial episode. The Clathriodictyida were the most successful group of stromatoporoids from that point until Famennian. *Id.* As discussed earlier, the Devonian was the high point of stromatoporoids. During this period, they formed vast reefs in association with red algae and calcifying bacteria (Wood, 1998; Stanley, 2003), sometimes hundreds of meters thick (Wendt &

Kaufmann, 2006). This reef system was badly, but irregularly, disrupted during the Kelwasser event at the Frasnian-Famennian boundary. Benton & Harper (1997); Stanley (2003); Bond *et al*. (2004). During the Famennian, the Labechiids made a small comeback, but the Stromatoporoidea as a whole seem to have disappeared at the end of the Devonian.

Stromatoporoid-like animals reappear in the fossil record during the Late Triassic, forming reefs with scleractinian corals, spongiomorphs, hydrozoans and calcareous algae. Stanley (2003). During Anisian and Norian time, sphinctozoan and "stromatoporoid-like" sponges were at least as important as scleractinain corals. *Id*. These stromatoporoids re-established themselves as significant (but rarely dominant) parts of various reef-forming communities in the Late Jurassic. However, they were gradually replaced by rudist bivalves during the Cretaceous, and again disappear at the KT boundary. *Id.*; Benton & Harper (1997). In 1967, living stromatoporoid-like sponges were discovered in deep submarine caves and other out-of-the-way locations. Unfortunately, they are rare, scrupulously protected, and have thus remained rather poorly known.

Conclusion

It is still very uncertain whether stromatoporoids are a clade or simply a body plan on which various groups of sponges have converged, from time to time. Our prejudice is that they are probably a paraphyletic grade, but (properly constrained) not grossly polyphyletic. Most can probably be confined to a series of branches on the sponge stem group, a group which diverged at about the same time as the Archaeocyatha, and from about the same region of phylospace. Despite considerable stratigraphic and ecological work, we know very little about stromatoporoid anatomy, much less phylogeny. Like many sponges, stromatoporoids leave numerous and sometimes massive fossils, but the information content per gram of fossil material is perhaps the lowest of any major metazoan taxon. At the present time, we see only two notable rays of light: the rediscovery of living forms (analogues or ancestors, as the case may be), and the early results of Hladil's developmental work. Unfortunately, to quote Hladil, "[t]he examination methods are simple, but laborious." This is an important area for early metazoan phylogeny. It is grossly under-investigated, but not likely to yield big results from either improved technology or the discovery of some unique fossil specimen. ATW071008.

Page Back | Page Top | Unit Home | Page Next

Calcarea

```
PORIFERA
|--Archaeocyatha
`--+--Stromatoporoidea
   `--+--Calcarea
      `--+--Hexactinellida
         `--+--Demospongiae
            |  |--Tetractinomorpha
            |  `--Ceractinomorpha
            `--+--Homoscleromorpha
               `--EUMETAZOA
```


Introduction

(Cambrian-Recent)

This class consists of marine calcareous sponges with a skeleton composed of massive calcite or separate calcareous spicules, not divisible into megascleres (larger) and microscleres (smaller). They have an asconoid, syconoid or leuconoid construction. Many are dull coloured -- and some are, admittedly, just plain dull. However, brilliant red, yellow, and lavender species are also known. In size they are generally smaller than representatives of other classes, most are less than 10 cm in height. They have a world-wide distribution, mostly restricted to shallow coastal waters. Possible Calcarea are known as early as the Tommotian. Wood (1998).

Representative Orders

classification according to Valid PMPD Orders (marine only)

```
Calcarea
     Heteractinida
     Calcaronea
     Pharetronida
     Sphaerocoelida
```

classification according to Synopsis of the described taxa of the world

```
Calcarea
     Innaecoelida      (extinct)
     Solenida          (extinct)
     Poratida          (no fossil record)
     Clathrinida       (no fossil record)
     Pharetronida      (extinct)
     Murrayonida       (no fossil record)
     Leucosoleniida
```

```
Heteractinida    (extinct)
Lithonida
Permosphincta    (extinct)
Sphaerocoelida   (extinct)
Clathodictyida   (extinct)
```

Permosphincta may be Demospongiae? (see Palaeontographica Canadiana No. 16 "Silurian Wenlock demosponges from the Avalanche Lake area of the Mackenzie Mountains southwestern District of Mackenzie Northwest Territories Canada."

Order Pharetronida

In this large group the spicules form a closely packed mesh of different sized "tuning forks", giving a rigid skeleton. During the Jurassic these sponges formed large reefs

(includes the genera *Stellispongia, Myrmecium, Elasmostoma, Corynella, Raphidonema, Peronidella, Porosphaera, Petrostoma, etc*)

Order Thalamida

(includes the genus *Barroisia*.)

Cladogram

```
<===o CALCAREA
   |--o CALCINIA
   |  |--o CLATHRINIDA
   |  |  `-- Clathrinidae*
   |  `--o LEUCETTIDA
   |     |-- Leucaltidae
   |     |-- Leucascidae
   |     `-- Leucettidae
   |--o CALCARONIA
   |  |--o LEUCOSOLENIIDA
   |  |  `-- Leucosoleniidae*
   |  `--o SYCETTIDA
   |     |-- Sycettidae
   |     |-- Heteropiidae
   |     |-- Grantiidae
   |     |-- Amphoriscidae
   |     `-- Lelapiidae
   |--o PHARETRONIDIA
   |  `--o INOZOIDA
   |     |-- Murrayonidae
   |     |-- Paramurrayonidae
   |     |-- Minchinellidae
   |     |-- Petrobionidae
   |     `-- Lepidoleuconidae
   `--o SPHINCTOZOA
      `--o PORATIDA*
         `-- Neocoeliidae
```

Links

Calcarea - Curt Smecher's summary

Parker, Sybil P. (ed.), 1982: *Synopsis and Classification of Living Organisms*. New York: McGraw-Hill Book Co., 2 vols.

Invertebrate Zoology by Edward E. Ruppert, Robert D. Barnes

Calcarea

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uploaded on Kheper site 2 June 1999, transferred to Palaeos Site 12 April 2002
checked ATW031228, last modified ATW071211

Hexactinellida

Glass Sponges: Late Ediacaran to Recent

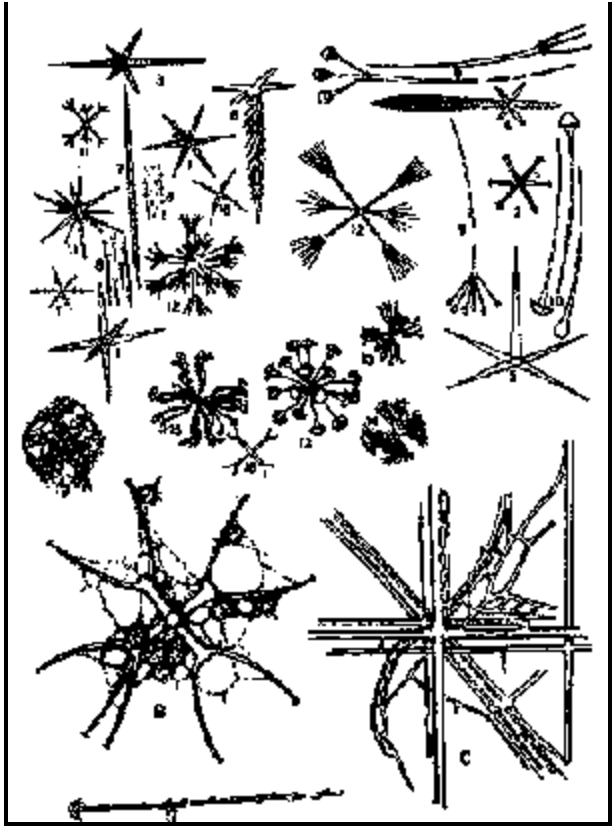
```
PORIFERA
|--Archaeocyatha
`--+--Stromatoporoidea
   `--+--Calcarea
      `--+--Hexactinellida
         `--+--Demospongiae
            |  |--Tetractinomorpha
            |  `--Ceractinomorpha
            `--+--Homoscleromorpha
               `--EUMETAZOA
```


Anatomy

Hexactinellids and their Spicules: Hexactinellids, commonly called "glass sponges", construct a skeleton composed of simple to complex 6-rayed *siliceous* spicules (left) with a fundamentally *orthogonal* symmetry. In extant heaxactinellids, the spicules are often fused into networks, with the entire structure appearing as an open mesh or an intricate, basket-like structure. Hexactinellids are exclusively marine, and in the modern oceans are usually found at depth (generally 450 to 900 m, but up to 5000 m).

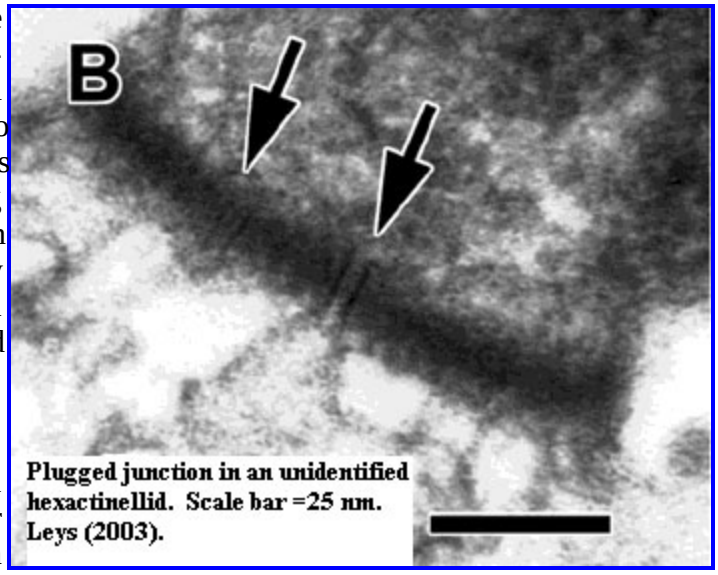
Some of the anchoring spicules produced by hexactinellids are extraordinarily large. The anchoring spicules of deep-sea sponge *Monorhaphis* can reach lengths of up to 3 m with a maximum diameter of only 8.5 mm. Hexactinellid spicules are produced in concentric layers -- up to 500 layers in the case of *Monorhaphis*. Each layer is thus 10-20 *μ* thick, composed of small grains of silicate within a matrix of undetermined composition (possibly *collagen*). The silicate layers are built on a core of amorphous silicate. The core, in turn, is built around a square axial channel containing a protein filament about 2 μ in diameter. Müller et al. (2007). Unlike other sponges, hexactinellids form spicules exclusively inside their cells.

Syncytial Organization. So, how can a sponge make giant spicules



inside cells? The hexactinellid sponges are said to display the *syconoid* pattern of organization. To put it mildly, this understates the weirdness of the hexactinellid body plan. In fact, hexactinellids have perhaps the strangest of all animal bodies. Most of the tissue consists of a single giant, multinucleate *syncytium*. This syncytium forms both "the inner and outer layers of the sponge and is joined by cytoplasmic bridges to uninucleate cellular regions." Leys *et al*. (2006). That is, a hexactinellid can make giant spicules because its body is composed largely of one giant cell. Compare the Xenophyophorea, gigantic rhizarian protists which have a somewhat similar structure.

This syncytial organization appears to be secondary, as the embryonic hexactinellid *Oopsacas* is cellular until well along into gastrula stage (yes, sponges have a sort of gastrula). However, the later merger of cells is fairly complete. Even the *micromeres* left at the outer surface are joined to the syncytium by cytoplasmic bridges or peculiar "*plugged junctions*" reminiscent of the pores plugged by *Woronin Bodies* in the septae between sections of fungal hyphae. Instead of *choanocytes*, hexactinellids have "collar bodies," with collars and flagellae, but lacking the usual cell bodies. The hexactinellids have no real pinacoderm. The syncytium forms a network of strands -- like a three-dimensional spider-web, which suspends numerous small chambers, lined with collar bodies, like the carcasses of so many bugs caught in the web. Each of these chambers is independently open to the water. The spicule-forming sclerocytes of the embryo develop in the usual way, but then become multinucleate and connect to the syncytium by cytoplasmic bridges. Leys *et al*. (2006). However, at least in some hexactinellids (*Dactylocalyx*), some of these specialized cells apparently remain entirely independent.



Plugged junction in an unidentified hexactinellid. Scale bar =25 nm. Leys (2003).

Anatomy and Physiology -- Leys (2003). Fortunately for us, hexactinellid anatomy and physiology has recently been summarized in an accessible, short review by Leys (2003), for which we provide the following **direct link**. As usual when we find a really good source of this kind, we will provide only bullet points:

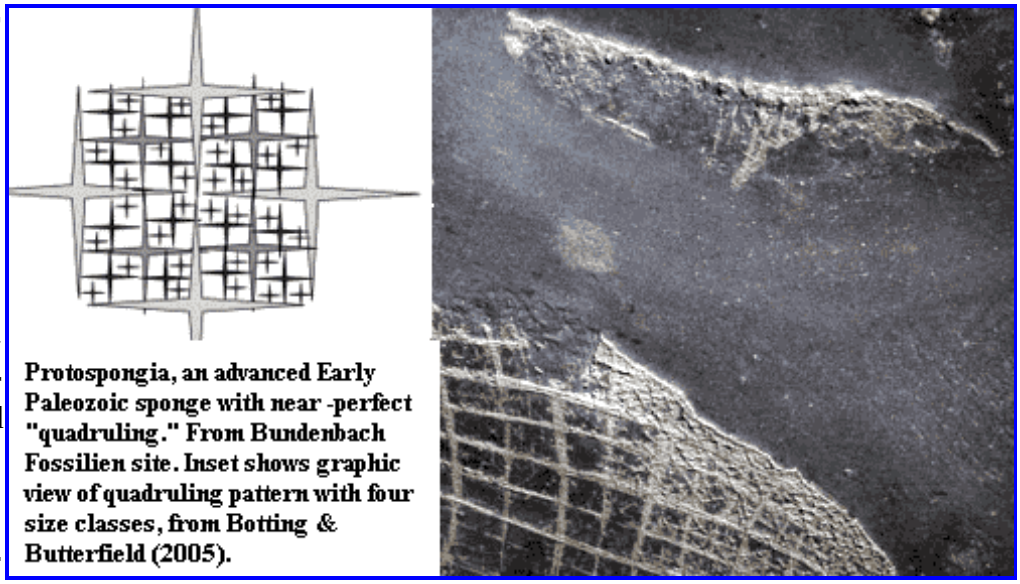
- ***Plugged Junctions***: The plug is not a membrane, but a three-layered disc pierced by cylindrical pore particles, like nanno-scale porocytes with a 5 nm channel and a ring of rods around the outside. Membranous vesicles have been seen squeezing through the pores, like politicians discovered at a brothel. Unlike a membrane, the barrier passes ions.

- ***Cytoplasmic Streaming***: The syncytium contains "highways" in which cytoplasm, inclusions, and organelles flow throughout the sponge at over 2µ/sec [fast enough for any given inclusion to reach any part of an average sponge in about half a day]. These streams are about 20 µ across, and probably involve microtubules, but the detailed mechanism is not known.

- ***Electrical Currents***: Hexactinellids lack a nervous system but transmit electrical currents (ion waves?) which trigger changes in water uptake rates.

Evolution

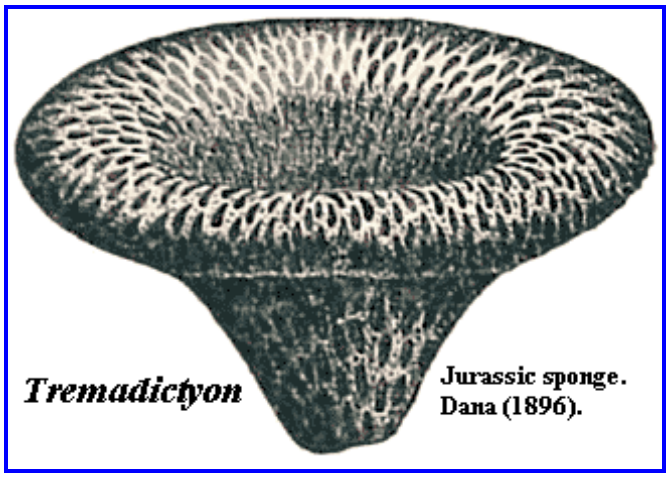
Early Hexactinellids had a one-Layer "Quadruled" Skeleton. Hexactinellids have a reasonably good fossil record, going all the way back before the Cambrian. As discussed elsewhere, they probably evolved from the basal radiation of "heteractinids." The fashion for all early sponges was to maintain a single layer of outer tissue, but increase spicule size with body size. However, it was considered rather bad form to simply stretch out the old spicule to a new size, as if it were a Spandex waistband. Rather, the prosperous sponge of Cambrian time grew spicules in an increasing number of size classes as it expanded, with each size class about 1.3 times larger than the last. Botting & Butterfield (2005).



Protospongia, an advanced Early Paleozoic sponge with near -perfect "quadruling." From Bundenbach Fossilien site. Inset shows graphic view of quadruling pattern with four size classes, from Botting & Butterfield (2005).

As it turns out, 1.3 is a convenient number, because $(1.3)^3 \sim 2.2$. Using every third size class thus lends itself to a structural pattern which Botting & Butterfield call "quadruling." This is illustrated by an actual hexactinellid sponge, *Protospongia*. *Protospongia* perfected the quadruling style in the Early Devonian, after which it quite sensibly became extinct. Later hexactinellids grew additional *layers* of spicule-supported tissue, but abandoned this unique, fractal mode of construction. *Id.*

Evolutionary History. The earliest sponges identified as hexactinellids are from Ediacaran exposures in Mongolia and India. Tiwari *et al*. (2000). Hexactinellids were relatively rare in Tommotian Chengjiang (Hagadorn, 2002), but were an important component of the Middle Cambrian Burgess Shale community. Unfortunately, it is not clear whether these earliest discoveries are, in fact Hexactinellida, or part of the basal "heteractinid" radiation. Botting & Butterfield (2005).

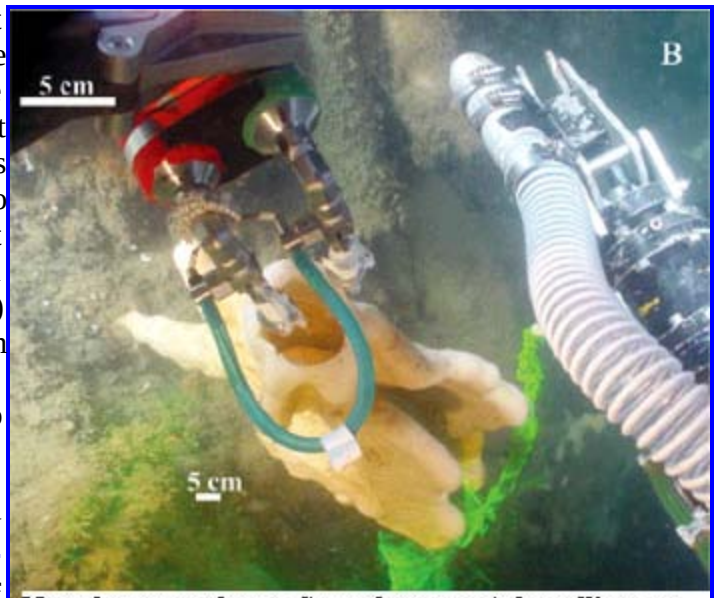


Certainly hexactinellids were important, and perhaps the dominant form of sponge, from the Middle Cambrian on, into the late Paleozoic (Tiwari *et al*., 2000), and occupied much shallower water than modern forms. After the extinction of protospongeoid, "quadruled" sponges in the Early Devonian, the hexactinellids evolved in two directions. By the Late Devonian, hexactine sponges had evolved a looser skeleton, while hexactinosans (hexactinellid "*lithistid*" sponges) created the massively fused siliceous skeleton more typical of Mesozoic and Cenozoic hexactinellids. Vishnevskaya *et al*. (2002). However, they declined in the Permian, along with other *sessile epifauna* and became increasingly restricted to deep waters. Wood (1998). Like most long-term trends, this one has not been entirely consistent. Hexactinellids made a considerable, perhaps dominant, contribution to the Late Jurassic reef system along the northern borders of the Tethys, extending from Central Asia to the southeastern United States – more or less from Tblisi, Georgia to Savannah, Georgia. Krautter (1998).

Phylogenetic Position is Uncertain. As discussed at various points elsewhere, the position of the hexactinellids is unclear. The traditional view (to which we still cling) is that hexactinellids are so peculiar that they must have branched very early. Quite possibly, we are making the error of confusing *symplesiomorphies* with *synapomorphies*. Yet molecular phylogenies have found nearly every possible grouping of the three major sponge groups and Eumetazoa. See, *e.g.*, Cavalier-Smith & Chao (2003); Rokas *et al*. (2003); Medina *et al*. (2001). Hexactinellids, as you might expect, are almost as notorious as nematodes for long-branch artifacts, so the credibility of molecular phylogenies is particularly suspect. *Id*. The best of this unavoidably bad lot is probably still Schütze *et al*. (1998), which finds the Hexactinellida to be the earliest-branching sponge group.

Tales of Silt and Carbon

Ecology?. Demosponges have evolved to handle soft substrates and mobile predators with a variety of subsurface anchors and unpleasant toxins. Hexactinellids lack these tools. They rely more on tightly woven spicules and the fact that their soft tissues are rather insubstantial. Hexactinellids are mostly silicate mesh and empty space. This design also provides a very high surface to volume ratio. Consequently, it has often been said that they are able to subsist on dissolved organic carbon, even when bacteria (the usual sponge fodder) are in scarce supply. On the other hand, this general design also makes hexactinellids rather sensitive to sedimentation, which can quickly clog their silicate meshes, or cause them to become top-heavy and topple over. For similar reasons, hexactinellids need a relatively low-energy environment. All of these factors favor a deep-water home, and probably explain why they still do well in such environments. Krautter (1998). The supposed ability of hexactinellids to live off dissolved organic carbon has also led to some elaborate theorizing about the evolution of metazoans. See, *e.g.*, Sperling *et al.* (2006).



More than meets the eye. Spongebot meets Aphrocallistes at 160 m. From Yahel et al. (2007).

.. or maybe not ... It therefore came as something of a shock when a very recent empirical study found that most of the last paragraph was myth. Yahel *et al*. (2007). Hexactinellids are, it seems, even more voracious than most sponges when it comes to removing bacteria from intake water, but they show no signs of interest in organic smoothies. Also, contrary to expectations, they are also partial to fine sediment, which they absorb, lick clean of adhering organics, and spit back out again. To be fair, this is only a single study. But it does illustrate some of the pitfalls of relying on scientific folklore which has never been empirically tested. Sponges are relatively little studied, and a remarkable number of accepted sponge facts turn out to be speculations by some Nineteenth Century worthy, who was simply giving us his best guess, with even less information than we have today.

Classification

We have not attempted to catch up with any recent changes in hexactinellid taxonomy. There are two main groups (clades or subclasses) and six orders, all of which have a fossil record. The oldest known species, and also the oldest known fossil sponge, is *Paleophragmodictya* from the Ediacaran of South Australia. That, and others in the Reticulosa, may or may not be "heteractinids," an informal taxon of basal sponges with a mosaic of demosponge, calcarean, and hexactinellid characters.

Hexactinellida

Amphidiscophora

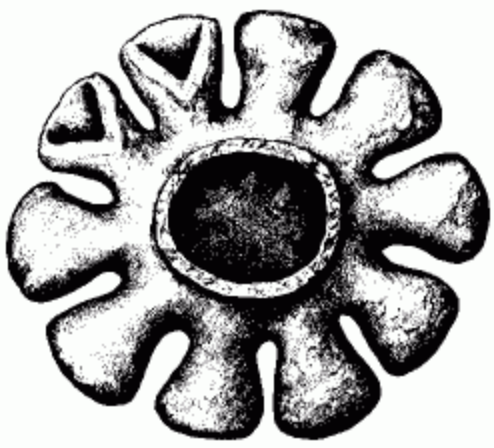

```
     Reticulosa    (extinct)          (Ediacaran - Permian)
     Hemidiscosa   (extinct)          (Carboniferous -
Cretaceous)
     Amphidiscosa / Amphidiscosida    (Ordovician - Present)

  Hexasterophora
     Lyssacinosa / Lyssacinosida      (Ordovician - Present)
     Hexactinosa / Hexactinosida      (Devonian - Present)
     Lychniscosida                    (Triassic - Present)
```

Classification according to Fossil Record of the Hexactinellida, Valid PMPD Orders and Synopsis of the described taxa of the world

Since the Reticulosa are presumably paraphyletic, the Amphidiscophora are also questionable. Accordingly, for working purposes, we draw the cladogram like this:

```
Porifera (Heteractinida)
|--Eifellia
 --+--Hexactinellida
   |   |--Protospongoidea
   |   `--+--Hemidiscosa
   |      |--Amphidiscosa
   |      `--Hexasterophera
   `--+--Demospongiae
      `--+--Calcarea
         `--EUMETAZOA
```



Brachiospongia digitata (Owen)
Trenton Limestone = ?Sandbian (Ordovician)
Kentucky, USA. (Laurentia)
diameter about 8 or 10 cm
order Lyssakida - family Brachiospongiidae

Brachiospongia digitata

image © C. L. & M. A. Fenton, *The Fossil Book*, p.64

Hydnoceras tuberosum Conrad
Chenmung = Late Frasnian (Devonian)
height about 12 cm
New York (Western/Central Euramerica)

image © xxxx

Titusvillea drakei Caster
A colonial glass sponge
Early Mississippian = Tournaisian
height of this specimen about 12 cm
Cussewago Beds, northwestern Pennsylvania (Western/Central Euramerica)

image © C. L. & M. A. Fenton, *The Fossil Book*, p.64

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last modified ATW070828

Class Sclerospongiae

leuconoid

This small class is sometimes included in the Class Demospongiae. It contains species usually found in grottos and tunnels in association with coral reefs. These leuconoid sponges (see diagram at left) are unique in having an internal skeleton of siliceous spicules and spongin fibers like those of the Demospongiae together with a massive calcareous basal skeleton

small sponge drawing © xxxx

Phylogeny

```
<===o SCLEROSPONGIAE
      |--o STROMATOPOROIDA
      |   |-- Astroscleridae*
      |   `-- Calcifibrospongiidae
      |--o CERATOPORELLIDA
      |   |-- Ceratoporellidae*
      |   |-- Tabulospongida
      |   `-- Acanthochaetetidae*
      `--o MERLIIDA
          `-- Merliidae*
```

References and Links

Sclerospongiae.

Parker, Sybil P. (ed.), 1982: Synopsis and Classification of Living Organisms. New York: McGraw-Hill Book

Co., 2 vols.

 ***Invertebrate Zoology*** by Edward E. Ruppert, Robert D. Barnes

 **Class Sclerospongiae** - short intro

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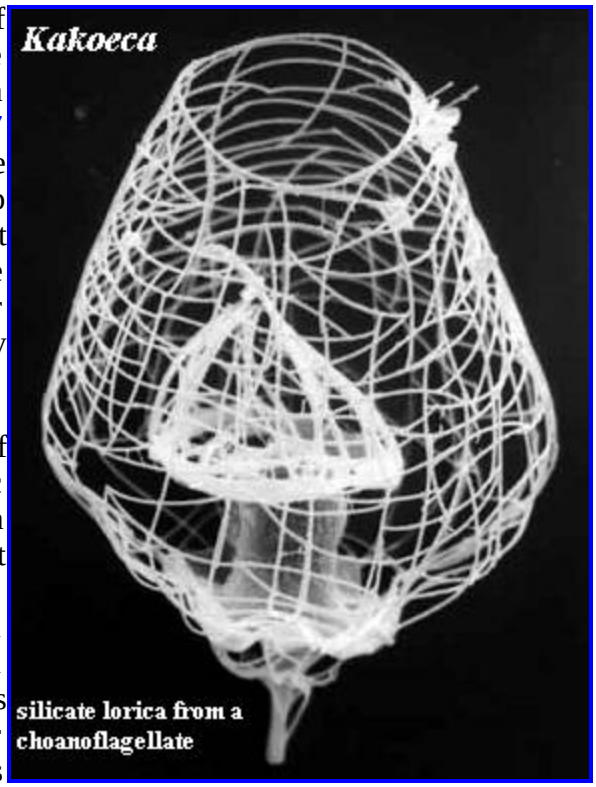
Demospongiae - 1

Introduction



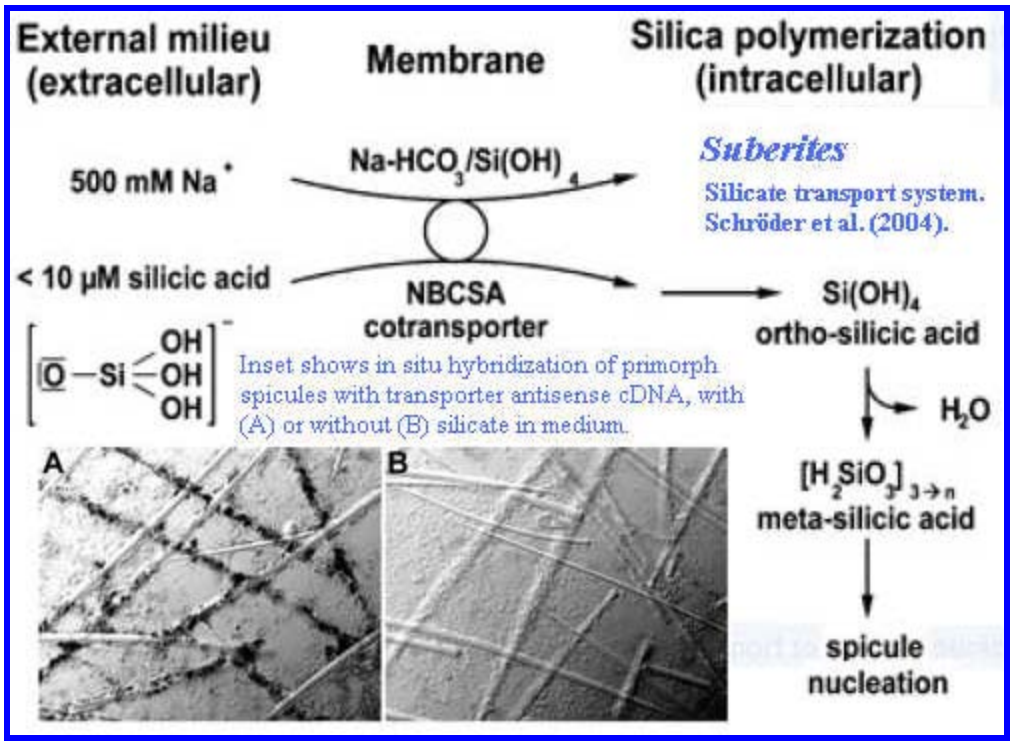
It is not a good sign when sponge experts cannot agree on the name of the most common large taxon of sponges. "Demospongiae" is by far the majority choice. However, there are some who insist on "Demospongia," (*e.g.*, Medina *et al.*, 2001; and Benton & Harper, 1997 -- sometimes) or even "Demospongea" (Benton & Harper, 1997 -- the rest of the time). This may be one of those Linnaean things, with deep significance for those concerned with taxonomic rank. It turns out that all of these spellings are good Latin. The *-ea* and *-ia* forms are alternate spellings of the singular, which is the actual (if unlikely) Latin word for sponge: *spongia*, or *spongea*, as the case may be. Still, the ambiguity portends problems; and there are a great many of them.

Here, we concentrate on a few areas which have generated a pile of recent papers. We thought they might be useful for phylogenetic purposes. As you may have gathered, sponge phylogeny is currently in a sorry state. In fact, we even found ourselves nodding and smiling at Maldonado (2004), whose ideas approach the downright weird. Maldonado argues that choanoflagellates may be descended from demosponges, rather than *vice-versa*. Weird or not, Maldonado makes a plausible case for the reverse arrangement. In fact, this scheme solves certain otherwise intractable problems in sponge phylogeny. For example, the fossil record (and other evidence, discussed later) suggests that carbonate skeletons came first, followed by silicate spicules. Botting & Butterfield (2005). However, as Maldonado points out, some choanoflagellates produce silicate *loricas* (Cavalier-Smith & Chao, 2003) **[11]**. Perhaps they inherited this ability from demosponge ancestors.

Not that we agree with Maldonado. It is not entirely clear that even Maldonado really agrees with Maldonado. Rather, he seems to be telling us, all too skillfully, to avoid the facile or "consensus" answers. Dissonance and contradiction lie in ambush for the hopeful sponge taxonomist. We could not evade all of these traps, but perhaps our mistakes may serve as a warning to others.

We will deal here with a subset of the issues -- spicule formation, development, and some associated biochemistry. These seem to lead to a phylogeny which mostly agrees with the fossil record, as interpreted by Botting & Butterfield (2005), but places the Eumetazoa on the demosponge branch. The track is tortuous and uncertain, with frequent excursions into dead-ends and suppositions, pasted together with guesswork. While this is not all that different from the rest of Palaeos, perhaps, it is even messier.

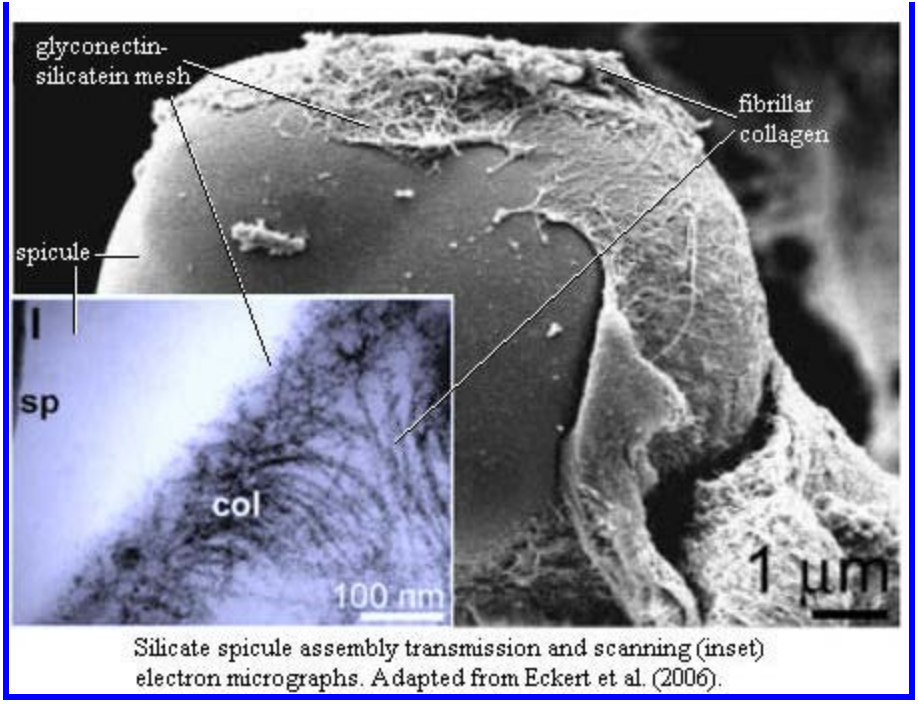
Spicules: a New Look



Classically, Demospongiae was a taxon held together by spicules. Almost anything sponge-like, with *siliceous* spicules, was deemed to be a demosponge. Needless to say, life has become considerably more complicated. To form their skeletal elements, different demosponges use varying combination of *spongin*, silica, *calcite*, or even *aragonite* -- or even none of the above, since a few demosponges have no skeleton or, like Americans, bulk up on debris without much regard for composition. The collagen protein spongin may prove to be a true *synapomorphy* of the Demospongiae. But even this is uncertain, because any sponge with spongin is *assumed* to be a demosponge. Most workers with a sophisticated knowledge of sponges -- and who would otherwise know better -- likewise assume that the molecule folks will take care of phylogeny, and have stopped writing about the phylogenetic implications of their results. Unfortunately, as we will see, sequence-based molecular phylogenies have little credibility for high-level sponge taxa.

The classical sponge taxonomies were based largely on spicule morphology. This was ultimately found to be an unsatisfactory tool for phylogeny. However, spicules have also recently become the subject of some serious molecular biology. These results suggest new approaches to phylogeny. Spicules are undeniably tempting as tools for sponge taxonomy because there are so many of them. Demosponges and hexactinellids may be over 75% spicule by dry weight. Müller *et al*. (2006); Barthel (1995). (Of course, there are not many dry sponges -- but it's just the kind of specious, pseudo-quantitative drivel you can throw around to amaze your friends.)

Silica Transport. Now, all of this spicule mass has to come from somewhere. The concentration of silica in sea water is highly variable, but typically less than50µM. Abe & Watanabe (1992). If we have kept all our decimal points in order, this means that a sponge must often suck *all* the available silicate out of almost 1000 liters of seawater to make a gram of silicate spicule. Carbonate, by contrast, is about 5-40 times more plentiful than silicate -- at least in modern oceans. Uriz (2006). More to the point, carbonate can be produced from carbon dioxide, a by-product of the metabolic activity of the sponge and its

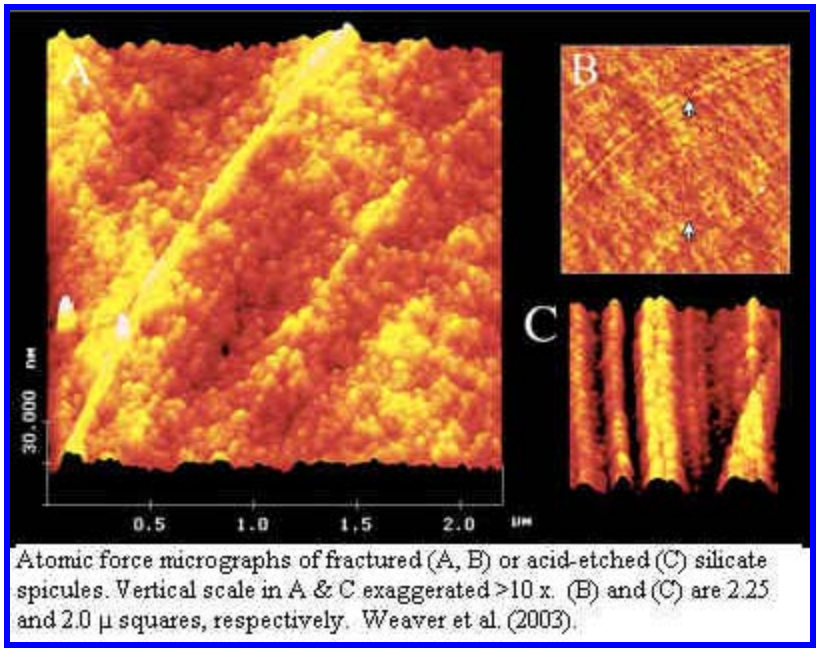


Silicate spicule assembly transmission and scanning (inset) electron micrographs. Adapted from Eckert et al. (2006).

bacterial symbionts. This is yet another pseudo-quantitative factoid, but it raises the following interesting question: if it takes considerably more work to collect silicates than carbonates, would this support the idea (Botting & Butterfield, 2005) that carbonate skeletons probably evolved first?

We thought we could shore up this speculation with a quick peek at transporter mechanisms, but we were wrong. As the figure from Schröder *et al*. (2004) shows, carbonate and silicate are imported from seawater using the *same* transporter. The assiduous reader may recall that this is not the only commonality between these spicule systems. Silicase, the enzyme that dissolves silicate and helps shape the spicules, is essentially the same as carbonic anhydrase, the enzyme which creates carbonate from carbon dioxide. Müller et al. (2007). Interestingly, eumetazoan homologues of this same transporter family are frequently associated with carbonic anhydrase, combining the two functions to regulate pH. Pushkin & Kurtz (2006). Whether this association between carbonate-silicate transporter and carbonic anhydrase also occurs in sponges is not known.

Spicule Assembly. Demosponges actually assemble spicules using a rather complex process described by Schröder *et al*. (2004) and Eckert *et al*. (2006). Parenthetically, Schröder *et al*. (2004) makes it onto our very short list of Amazing Sponge Papers, which we recommend reading at this **direct link**. Very briefly, the spicule is nucleated inside a cell vacuole on a core of *silicatein* overlain with a meshwork of *glyconectin*. After the spicule is a few µ long, it is extruded into the *mesohyl*. There it is surrounded, but never contacted, by fibrillar *collagen*. The collagen apparently serves to pattern additional net-like of meshes of glyconectin and, presumably, additional silicatein, which adds additional layers.



Atomic force micrographs of fractured (A, B) or acid-etched (C) silicate spicules. Vertical scale in A & C exaggerated >10 x. (B) and (C) are 2.25 and 2.0 µ squares, respectively. Weaver et al. (2003).

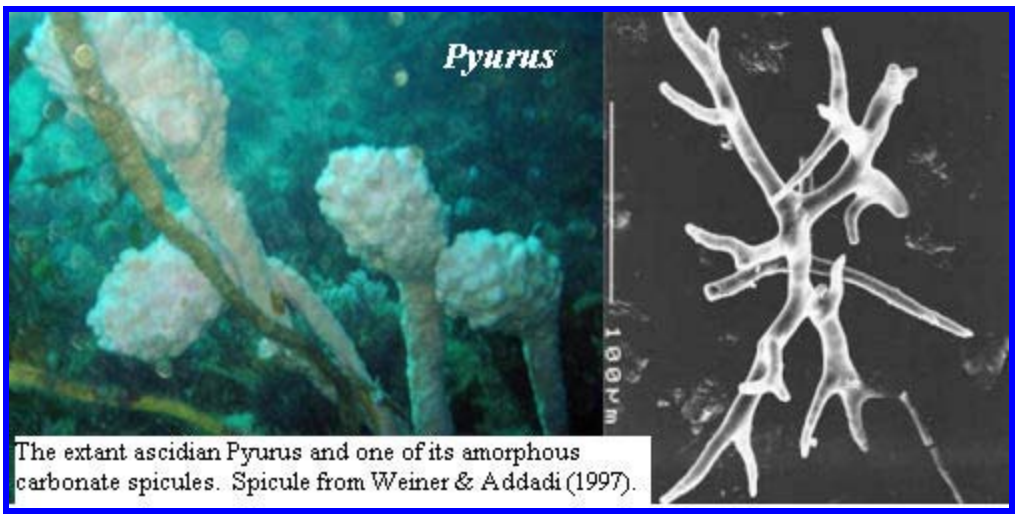
Remarkably, this work is consistent with even more detailed structural predictions made using low-angle X-ray scattering (Croce *et al*., 2004) , atomic force microscopy (Weaver *et al*., 2003) and magnetic resonance imaging (*MRI*) (Müller *et al*., 2006). For our purposes, the most important fact that all this stuff tells us is this: the component silicates are not at all crystalline. They are laid down as blobs of amorphous silicate trapped on grids of glycoproteins, the glyconectins. The blobs seems to be arranged carefully, in concentric layers, exactly one blob thick, and in a manner which does not permit adjacent blobs to merge.

Comparison with other Sponge Groups. How does demosponge spicule development compare with spicule formation in other sponge classes? It's a bit hard to tell, since no one has looked at the other groups in this kind of detail. The system in Calcarea is poorly known, but also seems to involve collagen fibrils densely packed around the growing spicule. However, unlike siliceous spicules, calcareous spicules are essentially crystalline and include comparatively little protein of any kind. The growing calcite spicule does have some sort of proteinaceous sheath which closely controls crystal growth, but the sheath is displaced by the growing spicule – not incorporated. Weiner & Addadi (1997), Botting & Butterfield

(2005). *See also* Uriz (2006).

Hexactinellids may produce spicules in essentially the same fashion as demosponges. However, hexactinellid spicules include a higher level (~15%) of organic materials than demosponge spicules (~10%), and the silicate blobs are less tightly packed. Croce *et al*., 2004. Maldonado & Riesgo (2007) have recently examined the formation of unusual "intra-epithelial" spicules in a homoscleromorph sponge. These spicules are not typical, being located inside certain epithelial cells. However, we do not see their description of spicule synthesis as being fundamentally different from the demosponge system, except that inner protein layers are more evident.

The Primitive Condition. With this background, we may repeat Botting & Butterfield's important question. Which is primitive for sponges, silicate spicules or carbonate spicules? Like most important choices in paleo or politics, we suspect that the dichotomy is false and the correct answer is "none of the above." Spicules are not primitive for sponges. Massive carbonate skeletons are primitive for sponges, as found in the Archaeocyatha and stromatoporoids. In any case, massive calcareous skeletons are primitive for nearly every other group which has evolved a mineralized skeleton. Why not sponges?



The extant ascidian Pyurus and one of its amorphous carbonate spicules. Spicule from Weiner & Addadi (1997).

Spicules vs. Skeletons. But massive carbonate skeletons are not carbonate spicules. Chemically, they could scarcely be more different and still be composed of the same ground substance. The carbonate spicules of Calcarea are essentially single crystals whose orientation seems to be controlled on a nanometer scale. Calcite crystallizes spontaneously under certain, biologically relevant conditions. A calcarean sponge needs no "carbonatein" enzyme, by analogy the silicatein of demosponges, to encourage the self-assembly of spicules; but the direction of growth must be carefully controlled.

By contrast, massive carbonate skeletons are composed of amorphous calcite. This requires a mechanism to *avoid* crystallization. Sponges do this by aggregating granules of amorphous calcite. This calcite is kept amorphous by an admixture of glycoproteins. Otherwise, it would transform into a crystalline morph very quickly. Weiner & Addadi (1997).

Phylogenetic Consequences. If we have this correct, the probable sequence of events is not difficult to reconstruct. Stem group sponges (archaeocyaths, Paleozoic stromatoporoids) had amorphous calcite skeletons. Subsequently one lineage (at least) developed spicules, radiating into a number of different types (e.g. *Eifellia*, chancelloriids). Note that amorphous calcite can be used to make spicules, as in the extant urochordate *Pyura*.

These early spiculate sponge groups probably used a variety of different "recipes" for making spicules. Some recipes included silicate. The use of silicate actually required little change because, as discussed, the silica and carbonate mechanisms for spicule construction have much in common. Ultimately, two spiculate groups dominated. One, the Calcarea, continued to use carbonate, but adapted to manipulate crystal growth, gradually reducing the expensive investment in glycoprotein additives. The other branch, including demosponges and hexactinellids, kept the basics of the amorphous mineral plus glycoprotein system, but switched to the structurally stronger and more stable silicates. Both groups retained the basic equipment for making massive calcareous skeletons, a trait which pops up now and again in both lineages.

Plausible? Let's see how it fits with other facts, and, if possible, whether it allows us to place the Eumetazoa somewhere...

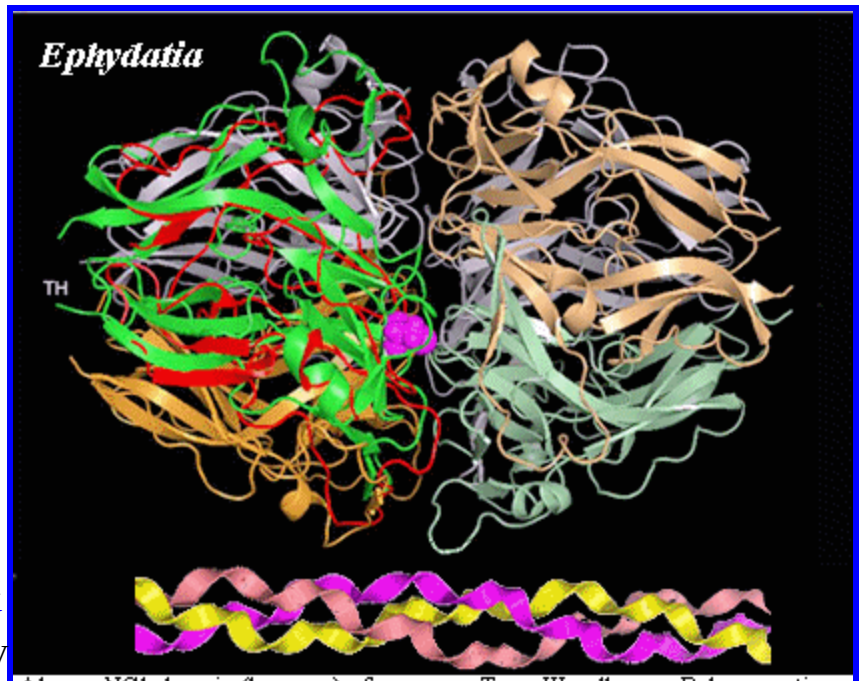
ATW071104

Demospongiae - 2

Sponge Skin

Special Credit: Special thanks to Profs. Sally Leys and Jean-Yves Exposito for answering questions without knowing how the information would be misused.

This section is actually about demosponge *collagens*. However, having adopted this alliterative title, we feel compelled to say something about sponge "epithelium" in general. As we have mentioned elsewhere, the term "epithelium" is placed in quotation marks because sponge skin generally has no *basement membrane*. It seems that, absent a basement membrane, quotation marks are needed to hold the tissue together.



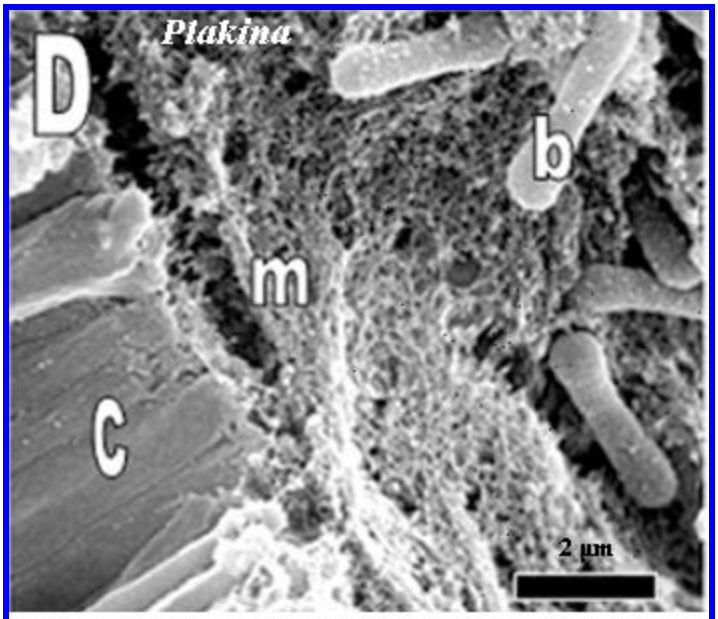
Above: NC1 domain (hexamer) of a sponge Type IV collagen. Below: portion of a typical fibrillar collagen. A similar structure would extend from the Type IV collagen at the point labelled "TH." Adapted from Aoucheria et al. (2006).

Homoscleromorpha have Type IV collagen. What *ought* to be holding the tissue together is *type IV collagen*. Every non-sponge animal has type IV collagens and basement membranes. However, among sponges, only the Homoscleromorpha (*Oscarella* and that crowd) have basement membranes and type IV collagen. Boute *et al*. (1996); Exposito *et al*. (2002). This is a very useful and important fact. It demonstrates that the homoscleromorphs are indeed very advanced sponges. The usual moral drawn from this data is that the homoscleromorphs are thus not demosponges as once thought, but more closely related to Calcarea --

consistent with the latest molecular sequence phylogenies. *That* is rubbish ... but perhaps we are being too subtle. It is not only wrong, but absolutely and perversely wrong.

Type IV collagen is similar to Spongin. Type IV collagens are indeed special -- and quite distinct from the fibrillar collagens found in all animals, sponge and non-sponge alike. On the other hand, type IV collagens are quite similar to *spongin*, a collagen thus far found *only* in demosponges. So, the proper conclusion is that homoscleromorphs are close relatives of demosponges, just as they appear by morphology, and that the collagen data is egregiously inconsistent with sequence phylogenies. Of course phrases like "quite similar" are mushy and often abused. However, any (hypothetical) readers can examine, for example, the review by Exposito *et al*. (2002) at this direct link and make up their own minds.

Recently, this dissonance has become even worse. It turns out that spongins are not merely *homologous* to type IV collagens. Rather spongin is itself conserved in Metazoa, as the basal family of a large class of short-chain collagens widely distributed in animals. Aouacheria *et al*. (2006). These short-chain collagens had escaped notice until recently because they are absent in the two largest and most-studied clades, Vertebrata and Ecdysozoa.



Homoscleromorph embryo: detail of basement membrane (m). From Leys & Ereskovsky (2006).

Type IV collagen is quite distinct from fibrillar collagens. It is worth some emphasis that type IV and short-chain collagens are so different from fibrillar collagens that they are scarcely collagens at all. The characteristic triple-helical domain of collagen, with its repeating GPP* (where P* = *hydroxyproline*) motif, seems to have been grafted onto one end of a very different protein which forms a series of folded ß-sheets, tightly interconnected by cystine disulfide bridges at moderately well-conserved positions (the NC1 domain). This non-collagenous domain has itself undergone duplication (NC1a and NC1b), further diluting the triple helical portion. The triple helical portion is also interrupted and terminated by two short additional non-collagen domains (NC2 and NC3, respectively) which likewise link to other elements via cystine disulfides. Aouacheria *et al*. (2006). In fact, some of these short chain species have no triple helical domain at all. *Id*. (see their Figure 1).

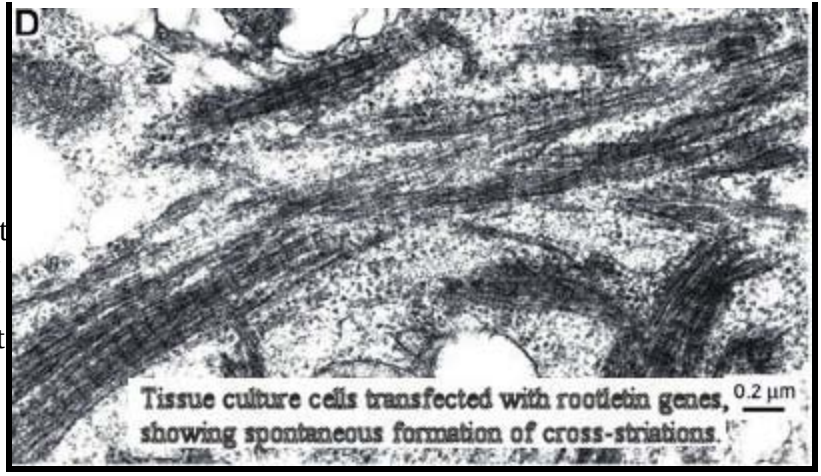
Finally, just to kick this dead horse one more time, Aouacheria *et al*. believe that the short-chain "spongin-like" collagen from at least one demosponge, *Ephydatia*, is in fact better described as a Type IV collagen. If so, the Homoscleromorpha no longer have a monopoly on these basement membrane collagens. Probable basement membrane layers have also been identified in larval demosponges and there are rumblings that this may be a character more widely distributed in the Demospongiae. Eerkes-Medrano & Leys (2006).

In the interests of full disclosure, we should mention that things are less clear than we would like. For example, it would increase our confidence a good bit if some homoscleromorph species made both type IV collagen *and* spongin. That may be the case, and the species is simply known as a demosponge, as were all homoscleromorphs until not long ago. On the other hand, nothing about sponge phylogeny is easy, so why should the collagen part be any different?

Homoscleromorphs are probably demosponges. The correct lesson to be drawn from this material is that homoscleromorphs are probably demosponges after all, or represent a closely allied clade. It seems likely that the molecular phylogenies are correct in placing Homoscleromorpha as the living sister group to Eumetazoa. Although, as we will briefly mention later, there is one other contender for this spot -- also a demosponge clade. The molecular sequence work cannot be reconciled with the collagen results, which appear far too tidy and far too complex to be the work of chance. But we have a number of issues to cover before drawing further conclusions.

Rootlets and Relationships

Cross-striated ciliary rootlets are the only morphological character joining Calcarea,



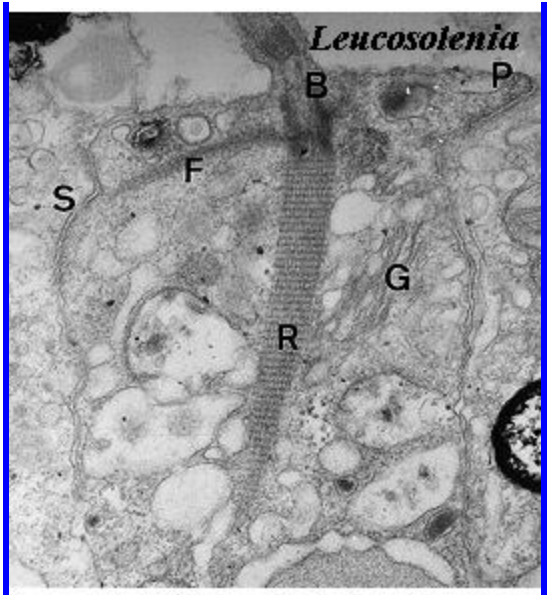
Homoscleromorpha and Eumetazoa. One of the many embarrassments faced by the sponge molecular sequence phylogenies is the paucity of plausible morphological synapomorphies uniting Calcarea and Homoscleromorpha. The thought seems to be that one sponge is pretty much like another, so homoplasy is probably rampant. That seems a counsel of desperation -- possibly correct, but we have not yet reached that level of frustration. However, the supposed clade Calcarea + Homoscleromorpha + Metazoa does have at least one arguable synapomorphy. Sperling et al. (2006). The rootlets of at least some cilia are banded, or in micro-speak, "cross-striated" with a periodicity of 40-80 nm. No such cross-striations are found in Demospongiae **[12]**. We don't mean to be too flippant about this issue. It is a serious problem for our hypothesis, and one for which we lack a complete answer. On the other hand, it isn't all that compelling an argument for a Calcarea-Homoscleromorpha connection, either.

Update: Cross-striated ciliary rootlets have now been reported in the demosponge *Asbestopluma*, making the rest of this argument somewhat needless. Riesgo, Taylor et al. (2007).

We lack the data draw phylogenetic conclusions based on ciliary rootlets. The problem results, in part, from lack of data. We aren't certain yet what causes the cross-striations. Ciliary rootlets are cable-like systems which attach at one end to the basal body of a cilium (= eukaryotic flagellum) and generally run to a point in the general vicinity of the nucleus, but sometimes elsewhere. The function of rootlets is uncertain. Recently, a group at Harvard has reported that the ciliary rootlets of some vertebrate tissues are probably a homopolymer of a novel protein they have called "rootletin." Yang *et al*. (2002); Yang *et al*. (2005). That's Harvard for you. Marvelous work, but they should never be allowed to name things. In any case, rootletin is a more or less distant cousin of myosin, and the cross-striations may result from the alignment of repeating rootletin units. Yang *et al*. (2002). Ciliary basal bodies are homologues of centrioles and, sure enough, it seems that the centrioles within the nuclei of non-ciliated vertebrate cells may also be joined by strands of rootletin. Yang et al. (2006).

As yet we know nothing about the presence or absence of rootletin in Demospongiae, or for that matter in any sponge. Perhaps rootletin has nothing to do with rootlet cross-striations in sponges. Perhaps it does, but the demosponges (for whatever reason) don't line up the rootletin fibers in a way which exhibits cross-striations. There are not all that many studies of the ciliary rootlets of sponges. Perhaps one or more groups of demosponges have banded ciliary rootlets, at least (like Calcarea), in the embryo and we simply haven't seen them. Finally, sponges react oddly to conventional preparations for electron microscopy. Thus, it is even possible (if unlikely) that the lack of cross-striation in demosponge rootlets is an artifact of preparation.

Cross-striated rootlets are homoplastic in Eukarya. The real problem with relying on rootlet cross-striation as a synapomorphy is that the trait is plainly homoplastic in the Eukarya as a whole. For example, cross-striated ciliary rootlets are also known from Alveolata, the heterolobosean amoebae, the parabasalids, the spironemid flagellates, and *Cryothecomonas* (a flagellate of uncertain affinities). Patterson (1999). This character may also be found in some choanoflagellates, although here the evidence is less convincing. Maldonado (2004); *but see* Sperling *et al*. (2006). In any event, if rootletin turns out to be the main link between centrioles, it will probably also turn out to be a key element in organizing mitosis. If so, it is hard to imagine that rootletin is entirely absent in demosponges. It must simply take on a form which does not show electron-dense bands in rootlets. Finally, so far as we can tell, no one claims that any animal completely *lacks* unstriated rootlets (i.e. has all rootlets striated). Thus the presence of *un*striated rootlets in Demospongiae is not a synapomorphy,



Cross-striated ciliary rootlet in the embryo of a calcarean sponge. Amano & Hori (2001).

either.

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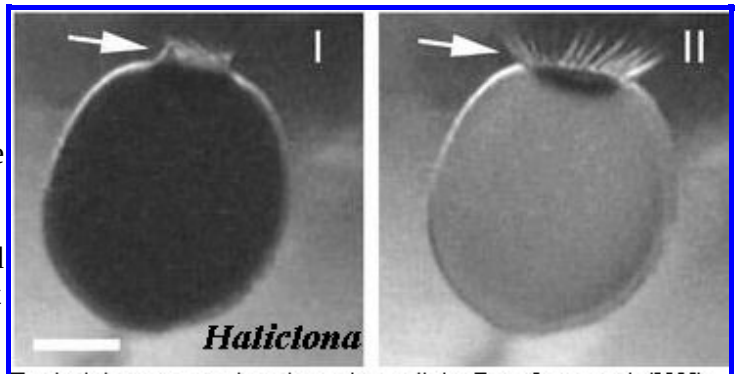
ATW071111

Demospongiae - 3

New Developments

I was present at an undersea, unexplained mass sponge migration.
--Ghostbusters (1984)

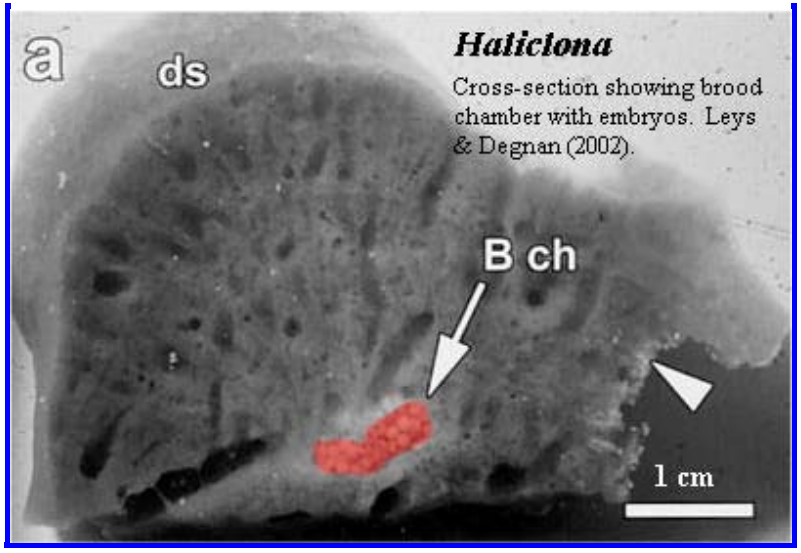


Typical demosponge larval reaction to light. From Leys et al. (2002).

Actually the matters we are *not* going to cover here include motility and photosensitivity. These are interesting topics, but have little phylogenetic potential. Slow motility, in the mm/day range, seems to be common to both calcareous and siliceous encrusting sponges. Not a great deal is known about this phenomenon in any sponge.

Larval photosensitivity is more promising. Some calcareous sponge larvae have exactly four "*cruciform cells*" evenly distributed about their equator. It has been speculated that these cells are photosensitive, but no phototaxis has been observed. Demosponge larvae, by contrast, have a very definite negative phototactic response. Light must be a traumatic experience for young sponges, as it causes their cilia to stand straight up on end. This reaction seems to be related to pigment located in the cell bodies of a subequatorial ring of cells with elongate cilia. A well-developed reaction to light thus may be unique to demosponge larvae. However, we have very little comparative data, particularly outside the demosponges. Leys & Degnan (2001); Leys *et al*. (2002); *c.f*. Amano & Hori (2001).

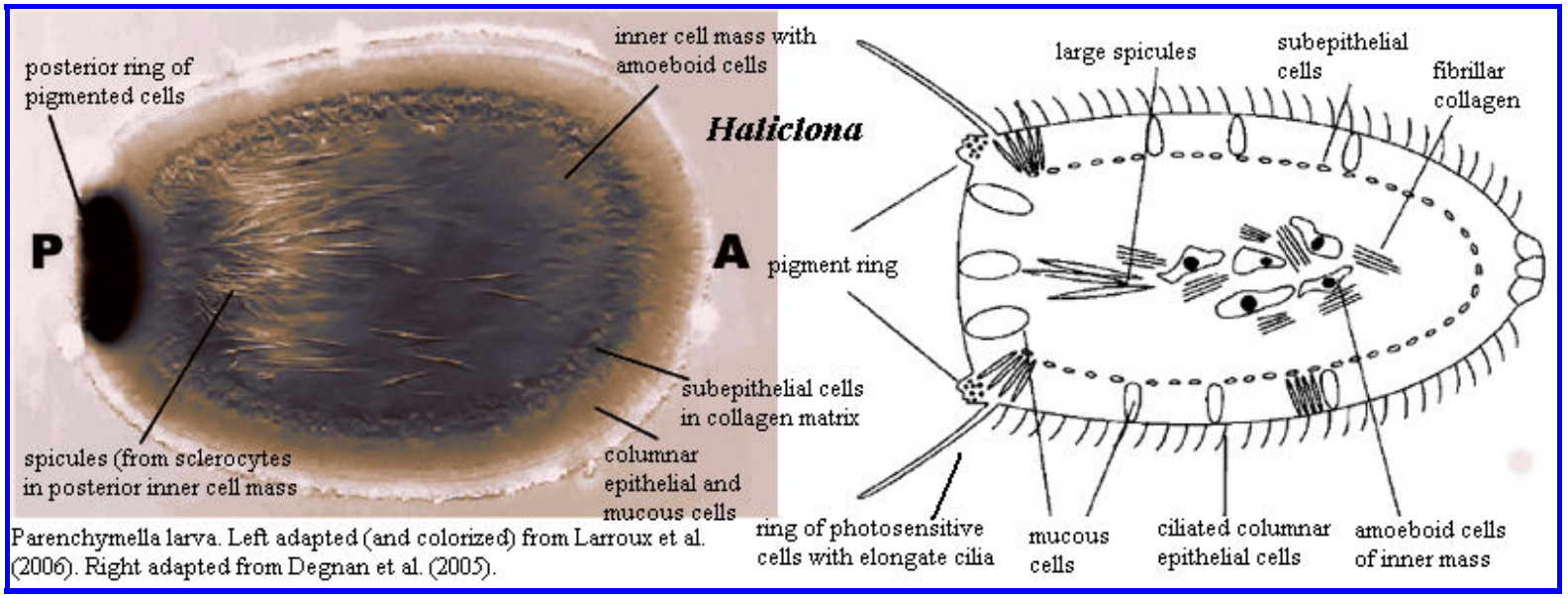
What we *are* going to discuss is sponge development. As we have just seen, sponges avoid the bright lights and don't run around much. They don't wear a lot of make-up. They settle down early, and usually get pregnant in a discreet manner -- so discreet that in many cases the male gamete has never been observed. It may seem peculiar that sponges should get pregnant and bear live young



(Leys & Ereskovsky, 2006). But, then, we've always felt that way about English majors, too. Somehow, one feels that they ought lay large, intricately colored eggs, like a Fabergé kiwi. In fact, some sponges *are oviparous*. Most or all of these oviparous sponges are also demosponges, but none are English majors -- although it may sometimes be difficult to make these fine distinctions by casual inspection.

This is only the first of many demosponge developmental peculiarities. Sponges in general have more developmental diversity than any other group of animals, bar none. For example, embryologists have been debating the existence and nature of *gastrulation* in sponges since Haeckel's time, despite the fact that Haeckel based the concept of gastrulation on the development of calcareous sponges. Not only do sponges differentiate "inside" and "outside" in a wild variety of different ways, but no one is absolutely sure which, if any, of these moves is actually homologous to gastrulation in bilaterians.

Perhaps we should approach this subject a little more systematically. Sponge gametes are generally formed from the *choanocyte* cell lineage, with some exceptions. Leys & Ereskovsky (2006). Some maternal tissue is usually released with the embryo, and even accompany the egg in oviparous forms. In addition, each embryo takes along a selection of maternal bacteria, like a folder of family recipes. While immaterial to the present discussion, note that this presents both theoretical and practical problems. The average sponge newborn has a good deal of functional DNA hanging around, bacterial and maternal, which is not part of its own genome.

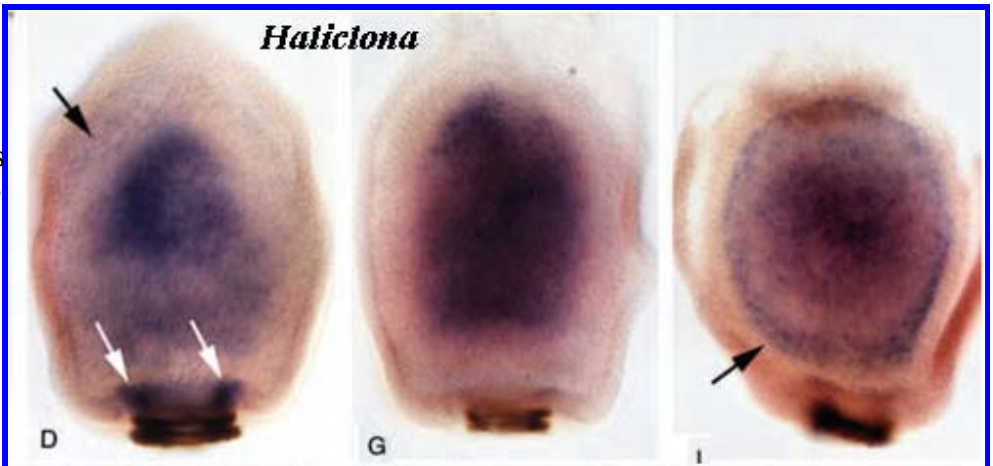


Parenchymella larva. Left adapted (and colorized) from Larroux et al. (2006). Right adapted from Degnan et al. (2005).

The usual demosponge larva is referred to as a *parenchymella*. Like sponge larvae generally, it has a distinct outer "epithelial" layer including small ciliated cells (micromeres) and a distinct front and back end. Whatever the sponge adult may look like, the sponge larva is always radially symmetrical. Development of the parenchymella larva of *Haliclona* (= *Reniera*) is very nicely summarized by Larroux *et al*. (2006). The following is essentially a quotation, but patched together from two separate parts of their paper. In addition, we have omitted citations and some express comparisons with metazoan embryogenesis.

> The haplosclerid demosponge *Reniera* [*Haliclona*] broods embryos throughout the year. After fertilization there is a period of cell division with little or no cell growth. Cleavage ends with an asymmetric cell division, which gives rise to two cell populations -- micromeres and macromeres -- which are initially mixed with each other. This is followed by a period of cell sorting that produces an embryo consisting of inner macromeres and outer micromeres. At this stage a number of

differentiating cell types are evident in the micromere population, specifically a large group of uniciliated cells, and smaller groups of pigmented cells and spicule-producing sclerocytes. Once on the surface, pigment cells and some *sclerocytes* begin migrating to the future posterior pole of the larva in a predictable manner. The pigment cells form an external ring that surrounds the posterior pole. The sclerocytes ingress [generally into the posterior half of the] inner cell mass. At this stage, a middle cell layer also forms. Embryogenesis culminates in a swimming larva composed of at least 11 cell types, each of which is allocated to a different cell layer and in some cases patterned along the AP axis, which is defined by the direction of larval swimming and can be readily identified by the posterior location of the pigment ring. At metamorphosis the larva undergoes dramatic changes that include the loss of overt body axes, the migration and transdifferentiation of specific cell types and the formation of choanocyte chambers



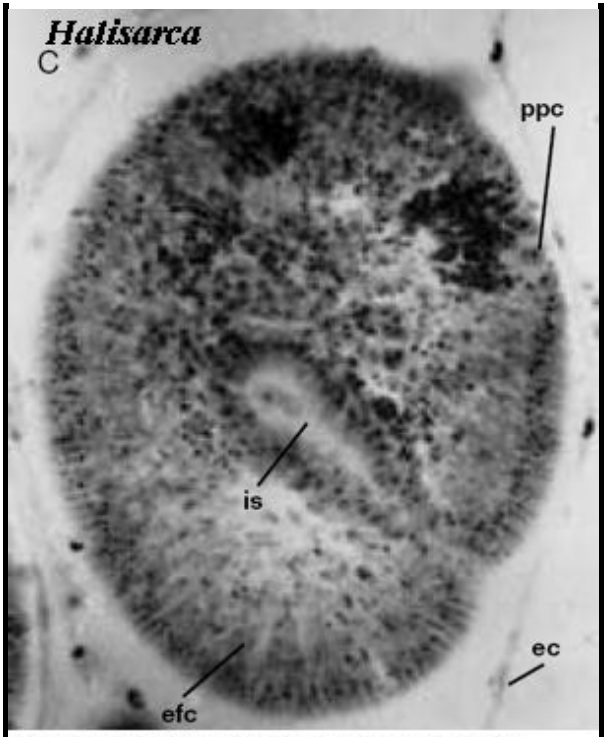
Parenchymella embryos hybridized in situ with probes for (D) procollagen lysyl hydroxylase, (G) galectin, & (I) an unidentified leucine zipper transcription factor. From Larroux et al (2006).

It is important to notice that all this shuffling of micromeres differs from *histogenesis* in most Eumetazoa. The micromeres are initially mixed in with everything else and seem to migrate as individual cells, not as a tissue. On the other hand, we know very little about cell-cell communications in sponges. We can't really tell whether these are free-market, Objectivist micromeres, influenced only by self-actualizing responses to an Invisible Hand, or, instead, class-conscious Socialist micromeres, marching forward to their destiny in histological solidarity. Cell fate does seem to be determined early, before migration, but even that isn't really clear. All we can say for certain is that sponges rarely practice histogenesis by differentiation of a particular mass of contiguous cells. Degnan *et al*. (2005); Larroux et al. (2006); Leys & Ereskovsky (2006). At the same time, the variable, and often chaotic, pattern of cleavage in the late blastula stage of many sponges also means that the blastomeres are not chained to their fate until at least the end of blastula. Degnan et al. (2005).

We have barely mentioned gastrulation, because, in respect of sponges, the mere utterance of that word has the same effect as a prefrontal lobotomy, shutting down volition, analysis and imagination. Thus, someworker sees three tissue layers, another utters the G-Word, and all nod vaguely. Then, for a minute or two, everyone peers vaguely into space, as if anaesthetized. Finally, discussion abruptly takes off again, on some completely unrelated tack. It's really quite peculiar.

Larroux et al. (2006) is something of an exception. We have methodological (and typological) issues with it, but it is another Amazing Sponge Paper. After finding the requisite three layers and invoking the G-word, they take a page or so of dithering to recover – but they go on. In particular, they go on with *in situ* hybridization experiments, the first in any sponge. It is quite clear from these experiments that there are *more* than three layers involved. There are either four or five layers. At a minimum, distinct expression patterns are found in an additional "germ layer" below (i.e. medial to) the subepithelial layer. In fact, this layer can even be faintly seen in the unstained embryo from the preceding figure. The authors refer to this as the "inner part of the subepithelial cell mass," but we have to wonder whether they do so because they are expecting to see only three layers. The cold hand of Ernst Haeckel still grips the world of sponges at times.

The point we are trying to make is that sponges are not a bunch of sullen failures who are still sulking after flunking the Eumetazoan Entrance Examination 600 My ago. Sponges were, and are, the base of the entire metazoan radiation, and we ought to be unsurprised to discover such diversity of developmental pattern. Also (with a nervous glance around for the ghost of Ernst Haeckel) this adumbration of layers is most unlike



Disphaerula larva with invaginating compartment.
From Ereskovsky & Gonobobleva (2000).

the Calcarea. The calcarean sponges have two unique patterns. The *calciblastula* type involves essentially direct development from blastula to adult. The *amphiblastula* begins as a cup, with ciliated cells at the bottom, the cilia on the inside – perhaps like an embryonic archaeocyath. The whole thing then flips inside-out, leaving the cilia facing outwards.. Ultimately, the non-ciliated macromeres overgrow everything. These modes do not bear any obvious relationship to Eumetazoa, or even Demospongiae.

What about the Homoscleromorpha? We thought you'd never ask. The homoscleromorph *cinctoblastula* is recognizably demosponge-like, but there are complications. In-and-out migration of individual cells, and cell migration along the outside, are both impossible due to the formation of the basement membrane. This has two results, one one of which favors a calcarean connection and one which does not. First, since epithelial micromeres cannot migrate laterally, metamorphosis into the adult form can only take place in the manner of some Calcarea. That is, the basal macromeres eventually overgrow the whole outer surface. Second, and unlike Calcarea, the micromeres can't migrate inward either, as happens in other sponge classes. Instead, multiplication of epithelial cells causes the outer layer to fold. Leys & Ereskovsky (2006). How much folding would it take to evolve an invaginating gut from one of those folds?

This is not a rhetorical question. Another group of demosponges, the Halisarcida, manage something quite like this, as the image from Ereskovsky & Gonobobleva (2000) shows. So is *this* gastrulation? It seems very unlikely. In fact, until we have a more sensible definition of gastrulation (which requires that we agree on what the homologies in gastrulation are), this is likely to remain a relatively meaningless question. What we may say, instead, is that the demosponge lineage seems to have a number of developmental characteristics shared with bilaterian gastrulation. These may, or may not, be synapomorphies; but, in any event, are characters which Demospongiae and Eumetazoa share with Homoscleromorpha, to the exclusion of Calcarea.

We may say all that -- but of course we may be completely wrong ...

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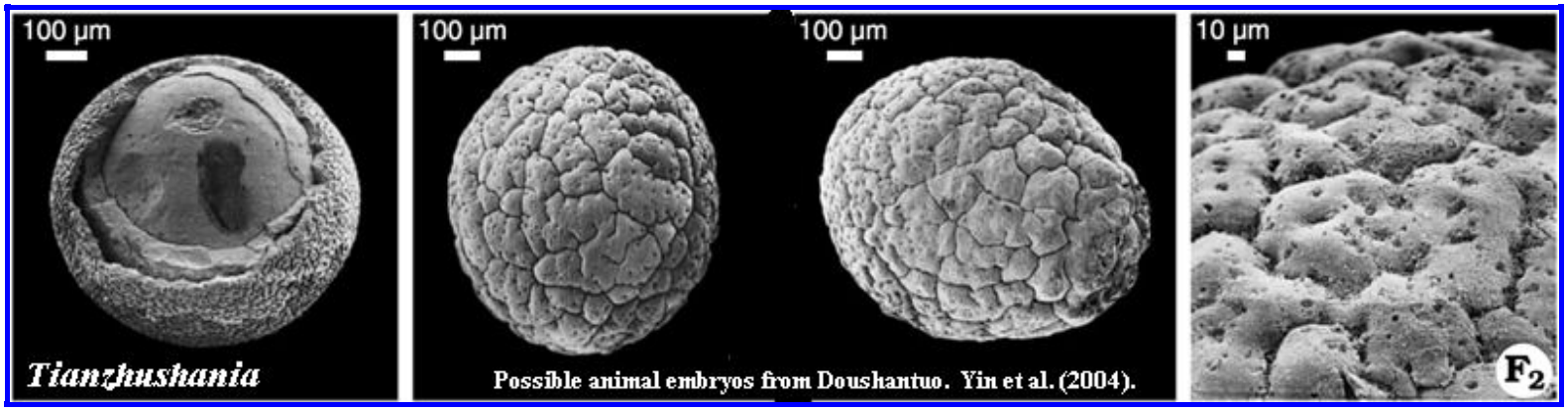
ATW071104

Demospongiae - 4

History



There is little doubt that some kind of sponges go back to the Early Ediacaran. Li *et al*.(1998). However, as Hagadorn *et al*. (2006) have noted, the (probable) embryos of the Ediacaran Doushantuo Formation may not be demosponges, since there is nothing resembling a parenchymella and little evidence of epithelium-like tissues. However, there is nothing which requires that these embryos have any relationship to the adult sponges of the Doushantuo. The adult sponges from Doushantuo are mainly globular, "but a few are tubular ... and range in size from 150 to 750 µ. Li et al. (1998). Only thin, *monaxonal* spicules are present, and these are randomly located and oriented. The spicules are between 0.5 and 1.0 µ in diameter, but as much as 60 µ long. The very largest are 4 µ in diameter and 100 µ long. *Id.* Li *et al.* believe these are demosponges based on the presence of silica and well-defined spongeocoels.

By the Terreneuvian, tubular demosponges, such as *Leptomitus*, *Leptomitella*, and *Paraleptomitella*

dominated the spiculate sponge fauna, together with spiny, funnel-shaped sponges such as *Choiaella*. Hagadorn (2002). Some of these were persistent, widely dispersed forms. The pictured example of *Leptomitus* comes from the Middle Cambrian of Spain, and similar examples are known from the Burgess Shale of early Middle Cambrian Canada. García-Bellido Capdevilla (2003).

As Dornbos *et al*. (2005) point out, many of these sponges were still essentially adapted to a firm Neoproterozoic-style substrate, held together as a bacterial mat. However, as the Cambrian progressed, this mat was looking increasingly moth-eaten and patchy, chewed up by "worms" and replaced by a soupy mud that left little purchase for attachment. As we've mentioned in connection with other early sponge groups, one of the key adaptations required for survival in these increasingly sloppy environments of the Middle and Furongian was the ability either to grow large quickly, or to grow attached to someone else who had already worked out a practical method for living in mud. As often as not, that "someone" was a demosponge, at least until the rise of stromatoporoids in the Ordovician. Accordingly, from the Furongian into the Silurian, demosponges literally supported a biota of bryozoans, unidentifiable worms, rugose corals, and articulate brachiopods. Taylor & Wilson (2003).

After stromatoporoids became a major factor, demosponges tended to adopt an encrusting habit and themselves become *epibionts*. With the extinction of Paleozoic stromatoporoids at the end of the Devonian, demosponges again became important as substrates for Carboniferous and Permian marine fauna. *Id*. During the Mesozoic, and particularly the Jurassic, demosponges evolved a large number if different types: new encrusters, massive lithistid forms, and perhaps also the Mesozoic stromatoporoid groups. They remain the dominant class of sponges today, and have even invaded fresh water habitats during the Cenozoic..

The Sequence of Sponges

All phylogenetic analyses using the basic morphological characters results in an animal tree with monophyletic sponges. Sperling et al. (2006). On the other hand, studies using molecular sequences have yielded just about every conceivable result except monophyly. *Id.* For a variety of reasons, we place relatively little faith in either approach. In some ways, the case against molecules is easier to make. We discussed it elsewhere, and nothing has happened in the last two years which signals any change in the foundations of statistics. Sequence phylogenies are not capable, even in theory, of sorting out lineages which diverged in a short period of time and the problem becomes worse when the lineage splitting events happened long ago. It isn't always a question of getting more DNA, more species, or improved calculations. We may be up against fundamental mathematical limitations. Rokas *et al*. (2003); Rokas *et al*. (2005). Worse, unless the fossil record is extremely good, we won't even know when we have crossed the border between low resolution and white noise. However, the continued failure of sequence phylogenies to yield consistent results is a strong indicator that we are over the frontier with the sponges.

At the same time, parsimony techniques using morphological characters are also likely to be futile. The lithistid sponge pictured above has so few characters in common with a fruit fly or zebra fish, that we have little basis for morphological comparison. Even where we can identify morphological similarities, it is rarely possible to tell homology from coincidence with any confidence. So how can we parse the evolution of demosponge, *Drosophila*, and *Danio*?

Here, as in many other places, we have tried to suggest a middle way. "Suggest" is perhaps a poor choice of words, since it implies that the idea was ours in the first place. It isn't. It is an approach which workers as diverse as Tom Cavalier-Smith and Sean Carroll have been converging on for over a decade. At the 2007 SVP meeting, several

graduate students I spoke with seemed headed in the same direction. Molecular sequences have a huge number of problems. Their real advantage is funding, and the fact that they don't require much knowledge of biology or evolution. But organisms don't live and die based on molecular sequence. The key in biochemistry, as in anatomy, is structure. We may be able to predict structure from sequence, but that doesn't help us if we continue to attempt to compare sequences instead of structures. While *gross* morphology changes too fast to compare organisms which are distantly related, or diverged long ago, the *structure* of their molecules, the morphology of cellular components, and various biochemical patterns of development, are more stable. What's more, the characters are frequently objective, reproducible, and involve unquestionable homology.

We have deliberately refrained from giving this approach a catchy name. That's a job for others who have earned the right to make names stick. We can only hope that they do not work at Harvard. Here we've tried to look at a few of the appropriate characters: spicule formation, collagen structure, ciliary rootlets, and a bit of embryology. Unlike sequence analysis, this stuff requires lots of biology. As sponge amateurs, our ability to analyze the facts is limited. It seems to fit together in a reasonable way, which has encouraged us to crawl far out on an unorthodox phylogenetic limb. With luck, that limb will begin to bend under the burden of weightier opinions. ATW071125.

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ATW071122

Subclass Tetractinomorpha

(Cambrian-Recent)

Cliona celata
Yellow Boring Sponge
Size : about 2.5 cm in diameter
Class Demospongiae - Subclass Tetractinomorpha - Order Hadromerida - Family Clionidae
specimen from Barkley Sound, Canada

These are encrusting massive or branching sponges, which range from intertidal habitats to abyssal depths of at least 5500 meters. While the 6 orders comprising this subclass share common features it is probable that the assemblage is polyphyletic. [ref: Curt Smecher]

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<===o TETRACTINOMORPHA
   |--o ASTROPHORIDA
   |   |-- Stellettidae
   |   |-- Geodiidae
   |   |-- Calthropellidae
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    |   |-- Pachastrellidae
    |   |-- Theneidae
    |   |-- Thrombidae
    |   `-- Jaspidae
    |--o SPIROPHORIDA
    |   `-- Tetillidae*
    |--o LITHISTIDA
    |   |--o TRIAENOSINA [DESMOPHORINA]
    |   |   |-- Theonellidae
    |   |   |-- Corallistidae
    |   |   `-- Pleromidae
    |   |--o RHABDOSINA
    |   |   |-- Scleritodermidae
    |   |   |-- Neopeltidae
    |   |   `-- Siphonidiidae
    |   `--o ANOPLINA
    |       |-- Leiodermatiidae
    |       |-- Desmanthidae
    |       `-- Vetulinidae
    |--o HADROMERIDA
    |   |-- Suberitidae
    |   |-- Polymastiidae
    |   |-- Spirastrellidae
    |   |-- Clionidae
    |   |-- Latrunculiidae
    |   |-- Placospongiidae
    |   |-- Timeidae
    |   |-- Tethyidae
    |   |-- Chondrosiidae
    |   `-- Stylocordylidae
    |--o AXINELLIDA
    |   |-- Axinellidae
    |   |-- Bubaridae
    |   |-- Trachycladidae
    |   |-- Desmoxyidae
    |   |-- Hemiasterellidae
    |   |-- Sigmaxinellidae
    |   |-- Raspailiidae
    |   |-- Euryponidae
    |   `-- Rhabderemiidae
    `--o AGELASIDA
        `-- Agelasidae*
```

References and Links

 Curt Smecher, *Tetractinomorpha* Levi - distinguishing characteristics in note form.

 Parker, Sybil P. (ed.), 1982: *Synopsis and Classification of Living Organisms*. New York: McGraw-Hill Book Co., 2 vols.

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cladogram by Mikko Haaramo

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Tetractinomorpha

Introduction

The current party line on Tetractinomorpha is that they are likely to be *polyphyletic*. That is, most of the main groups making up the Tetractinomorpha seem to be good *clades*, but few sponge workers are still willing to bet that all of these clades are more closely related to each other than to any of the ceractinomorphs. While it is entirely possible that some stripped-down group of tetractinomorph sponges is monophyletic, the current refusal to commit to any particular phylogenetic scheme is, based on our present state of ignorance, undoubtedly wise as well as prudent.

Traditionally, distinction between Tetractinomorpha and Ceractinomorpha was often based largely "on an oviparous

versus viviparous strategy of reproduction, [a distinction which] has been rejected by all molecular phylogenies produced so far." Boury-Esnalt & Solé-Cava (2004) (*see*, *e.g.*, Schmitt, 2002). However, oviparity is not completely useless for phylogenetic purposes. Since all Calcarea and Hexactinellida are viviparous, as are Homoscleromorpha. Thus any oviparous sponge is almost certainly a demosponge, even if we draw no other conclusion.

The free-living larvae of tetractinomorphs are *parenchymella* or "creeping blastula" larvae. The latter is a form which slowly rolls along the bottom, using successive rows of cilia to pull itself across the substrate. Tetractinomorphs have both large (*megasclere*) and small (*microsclere*) spicules. The megascleres are frequently a mixed population of *tetraxons* (4 axes) and *monaxons* (1 axis). Tetractinomorph microscleres include star-shaped (asterose) spicules. This microsclere morphology, like oviparity, is only found among traditional tetractinomorphs. However neither oviparity nor star-shaped microscleres are universal in this group. One early report states that tetractinomorph collagen may differ in several respects from collagen in other demosponges. Diehl-Siefert et al. (1985). However, this needs to be confirmed with more details and a broader sample of taxa. Blumenberg's (2003) useful and thought-provoking survey of sponge (except Calcarea) lipid chemistry notes that tetractinomorphs show considerably less variation than ceractinomorphs in the structure of their sterols, and usually synthesize an $18C\,\Delta^{5,9}$ unsaturated fatty acid which is almost unique to the taxon.

The sponges included in the Tetractinomorpha vary a bit from author to author, but generally include the Astrophorida (or Choristida), Hadromerida, and Spirophorida, as well as some or all lithistid sponges. ATW071227

ATW071227

Ceractinomorpha

Introduction

Cambrian-Recent)

Stylissa stipitata

Trumpet or Vase Sponge
Size : 12 to 15 cm tall
Class Demospongiae - Subclass Ceractinomorpha - Order Axinellida - Family Axinellidae
This photo shows a top view of vase shaped sponge, looking down the flute.

These sponges are frequently branching but may be encrusting, massive lobate fan-shaped or cuplike, and bizarre symmetrical shapes may occur among deep-sea species. They range in depth from intertidal habitats down to at least 7000 meters. [ref: Curt Smecher]

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<==o CERACTINOMORPHA
   |--o DENDROCERATIDA
   |   |-- Halisarcidae
   |   |-- Aplysillidae
   |   `-- Dictyodendrillidae*
   |--o DICTYOCERATIDA
   |   |-- Spongiidae
   |   |-- Thorectidae
   |   `-- Dysideidae
   |--o VERONGIIDA
   |   |-- Aplysinidae*
   |   |-- Aplysellidae*
   |   `-- Aplanthellidae*
   |--o HAPLOSCLERIDA
   |   |-- Haliclonidae
   |   |-- Niphatidae
   |   |-- Callyspongiidae
   |   |-- Oceanapiidae
   |   |-- Spongillidae
   |   |-- Lubomirskiidae
   |   `-- Potamolepidae
   |--o PETROSIIDA
   |   `-- Petrosiidae*
   |--o POECILOSCLERIDA
   |   |-- Mycalidae
   |   |-- Hamacanthidae
   |   |-- Cladorhizidae
   |   |-- Biemnidae
   |   |-- Esperiopsidae
   |   |-- Coelosphaeridae
   |   |-- Crellidae
   |   |-- Myxillidae
   |   |-- Tedaniidae
   |   |-- Hymedesmiidae
   |   |-- Anchinoidae
   |   `-- Clathriidae
   `--o HALICHONDRIDA
      |-- Halichondridae
      `-- Hymeniacidonidae
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References and Links

The above cladogram is based on Parker, Sybil P. (ed.), 1982: *Synopsis and Classification of Living Organisms*. New York: McGraw-Hill Book Co., 2 vols.

For an alternative (and more recent) classification, see Curt Smecher, The Systematics of the Sponges. Also (from the same site) Demosponges of British Columbia (systematic list of species), and *Ceractinomorpha* Levi

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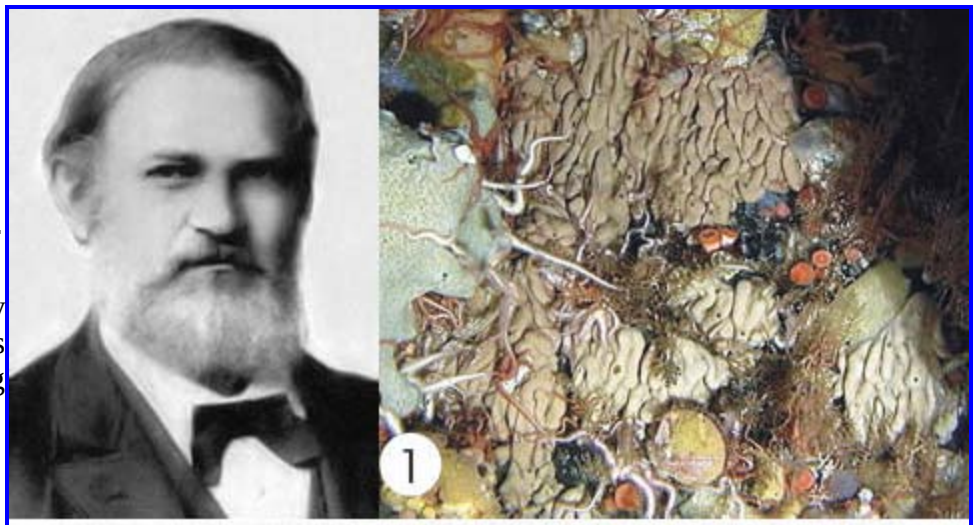
Homoscleromorpha - 1

(= Homosclerophorida)

Introduction


Franz Schulze with a new species of Plakina, the latter from Lehnert et al. (2005).

Homoscleromorphas are a small clade of encrusting sponges. Homoscleromorphs (or, sometimes, "homosclerophorids") are usually encrusting sponges, found all over the world in cool to tropical marine environments growing like underwater lichen on the surface of hard substrates. Ecologically, they usually favor relatively shallow marine shelves, but some species may also be found at depths approaching 1000 m. Muricy *et al*. (1998). They are anatomically simple, and often small and delicate, with few spicules -- or even none at all. Homoscleromorphs are said to be confusingly similar to the halisarcid demosponges. Fortunately, we ave no actual experience with the Halisarcida and are thus too ignorant to be deceived. In any case, you are unlikely to encounter a homoscleromorph, both because they usually grow in hidden (*cryptic*) places and because they are uncommon. Only a few genera are assigned to this group, the best-known being *Oscarella* and *Plakina*.

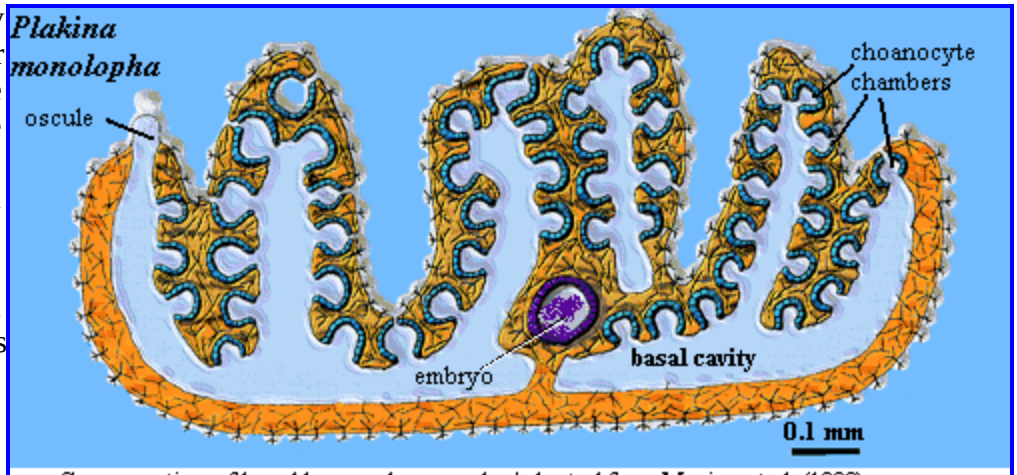
They are historically important and may be the sister group of Eumetazoa. Although homoscleromorphs are an obscure and uncommon little group of sponges, they have sometimes played a pivotal role in the history of

"spongology." Franz Schulze (who named the Plakinidae, the only homoscleromorph family) and Claude Lévi (who named the Homoscleromorpha), both well-known sponge workers of *circa* 1870 and 1970 **[16]**, respectively, both thought that the homoscleromorphs might be good approximations of the most primitive sponges. Leys & Ereskovsky (2006). However, in recent years, Homoscleromorpha has returned to center stage as a candidates for the living sponge taxon most closely related to the Eumetazoa, *i.e.*, to all animals other than sponges. As discussed in tedious detail below and elsewhere, this suspicion is based on a number of characters which the homoscleromorphs share with higher animals, but not with other sponges. The theory is that sponges are *paraphyletic*. In other words, sponges are not just a side-branch of early animals. Rather, all animals actually evolved from among the sponges. According to this view, we aren't just *related* to sponges. We *are* sponges, merely highly evolved sponges.

We have discussed some of the fine points of this theory, and a good deal of related stuff on biochemistry and embryology, in connection with the Demospongiae. The idea of sponge paraphyly has a lot of merit, and we have adopted it for purposes of the Palaeos cladogram. However, be aware that the concept of sponge paraphyly is still new and relatively untested. New ideas can only be tested slowly in sponge work, simply for lack of manpower. Here, we hope to take a somewhat less technical look at these potentially important animals, although we will inevitably slip into some discussion of our own peculiar (and probably wrong) ideas about sponge phylogeny.

Special Credit: special thanks to Dr. Ana Riesgo of the Centro de Estudios Avanzados de Blanes, Spain for help with sponge *acrosomes* and information on their phylogenetic distribution.

Anatomy

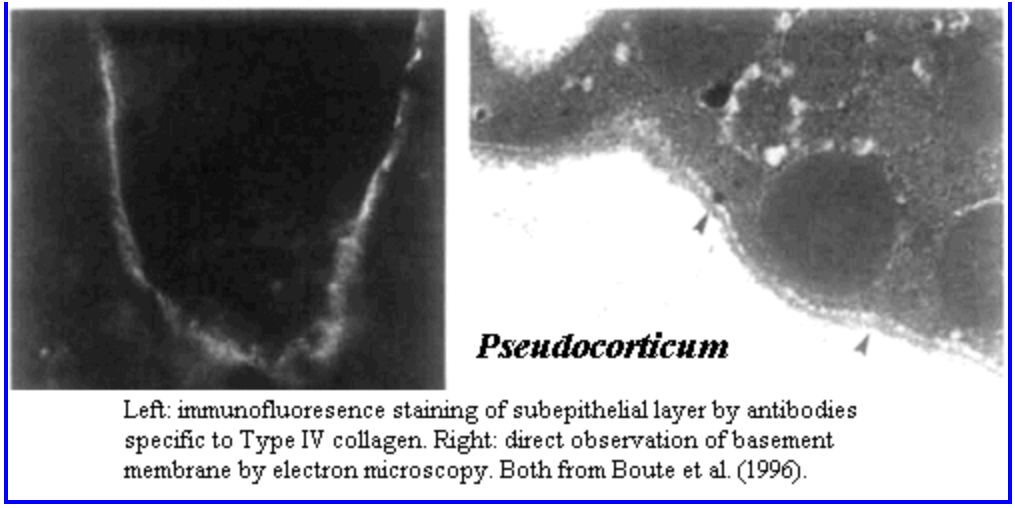


Cross-section of basal homoscleromorph. Adapted from Muricy et al. (1998)

As usual, it is almost impossible to say anything useful about what a particular sponge group "looks like." The image of *Plakina* above is a good deal more typical than *Oscarella*. From the outside, the usual homoscleromorph sponge looks a bit like a dense collection of candle drippings. On the inside, the basic homoscleromorph body plan is ... rather basic. Its gross anatomy simply doesn't have any distinctive features. Like most encrusting sponges, homoscleromorphs have "top" and "bottom" surfaces which are quite different. The basal surface is flat and bears protruding spicules, specialized for attachment. The upper surface consists of a densely pleated/folded *pinacoderm* which supports flagellated *pinacocytes*. Embedded in the pinacoderm are numerous ovoid to spherical *choanocyte* feeding chambers. The choanocyte chambers may open into the external medium, into an internal cavity, or into both. Bergquist & Kelly (2004). Wastewater is directed into a basal cavity and out through an *osculum*.

Basement Membrane

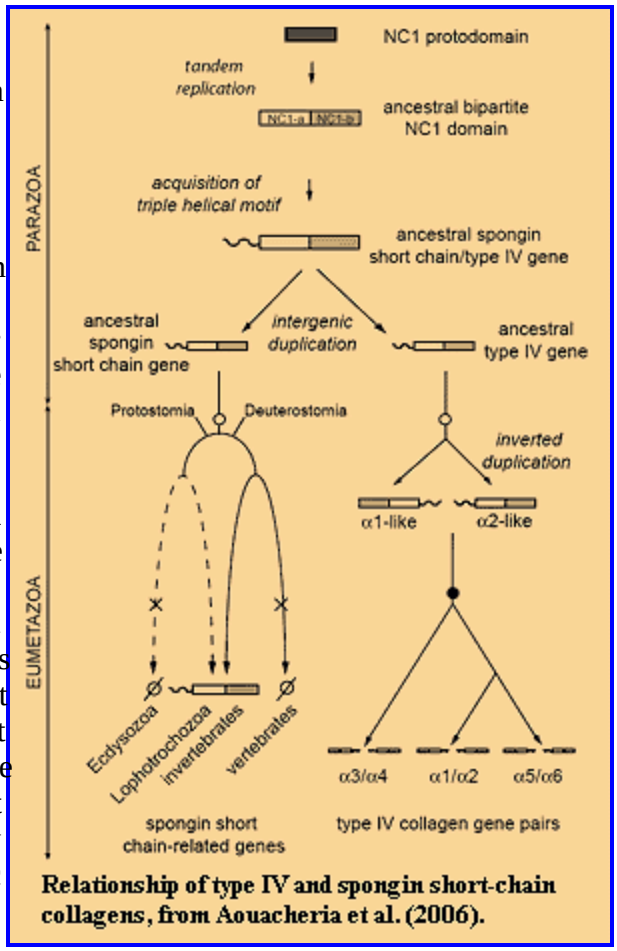
Eumetazoan-like basement membrane with type IV collagen. As



Left: immunofluoresence staining of subepithelial layer by antibodies specific to Type IV collagen. Right: direct observation of basement membrane by electron microscopy. Both from Boute et al. (1996).

we have said in innumerable other places, the homoscleromorphs are unique among sponges in having a basement membrane and, therefore, a true epithelium. We know this is a real basement membrane because it is composed largely of *Type IV collagen*, a protein not yet identified in any other group of sponges. Boute *et al.* (1996). We have extruded a large volume of words on the distinctive biochemistry of this stuff in a discussion of sponge skin. As if that were not enough, we have exhorted readers to examine Exposito's exposition on the subject (Exposito *et al*., 2002).

This requires significant changes in epidermal metabolism. The basement membrane in adult homoscleromorphs underlies the pinacoderm (outer surface) and the choanoderm (feeding chambers). Bergquist & Kelly (2004). As Maldonado (2004) points out, the existence of this barrier must have significant effects on sponge biology. In most sponges, cells of the pinacoderm are easily recruited from, and recycled to, the *mesohyl*. But homoscleromorphs have little mesohyl and the basement membrane makes migration between epidermis and mesohyl awkward. To the best of our knowledge, there is no substantial literature on the metabolism of the epidermis in homoscleromorphs, but it must necessarily be a more metabolically active and biochemically independent region than the outer skin of most sponges, i.e., more tissue-like and similar to the epidermis of eumetazoans. So, for example, *Corticium* develops tiny spicules which remain inside the cells of its epithelium, because the epithelial cells are separated from the internal *mesohyl* by the basement membrane. Maldonado & Riesgo (2007).



Relationship of type IV and spongin short-chain collagens, from Aouacheria et al. (2006).

Some demosponges may also have a basement membrane. While a biochemically well-characterized basement membrane has only been identified in homoscleromorphs, morphologically similar structures have been described from at least one demosponge larva (*Crambe crambe*, see Maldonado, 2004), "and it is likely that other demosponge larvae also have this layer" (Eerkes-Medrano & Leys, 2006). No such structure is known from calcareous sponges. *Id*.

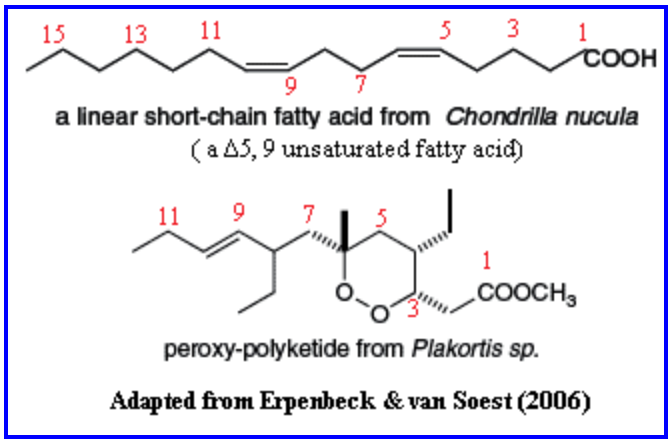
Spongin is related to both type IV and short-chain eumetazoan collagens. The closest known relative of the basement membrane type IV collagen among non-homoscleromorph sponges is *spongin*, the characteristic collagen of demosponges. There are important structural relationships between spongin and Type IV collagen, as discussed in Exposito's review. Yet, judged by sequence alone, that relationship is fairly distant. We happen to think it peculiar – in fact perverse -- to prefer sequence over structure when assessing the phylogenetic importance of a structural protein such as collagen. But only a tiny minority of biochemists seem to share our view, and it may be that we are mistaken in believing that this evidences a phylogenetic relationship between homoscleromorphs and demosponges. It is harder to dismiss the more recent work of Aouacheria *et al*. (2006). Aouacheria and co-workers (a group including Exposito) have shown that spongin is, in fact, *not* unique to demosponges. Short-chain spongin collagens are quite widely distributed among the Eumetazoa. However, nothing resembling either type IV collagen or spongin is known from the Calcarea. Thus, the natural conclusion is that homoscleromorphs, demosponges, and all non-sponge animals are more closely related to each other than any of them is to the Calcarea.

Homoscleromorphs also have many eumetazoan adhesion proteins. Another, perhaps related, suite of characters also unites homoscleromorphs with non-sponge animals. Homoscleromorphs have a nearly complete set of

eumetazoan cell adhesion receptors and proteins which join the components of the cytoskeleton (microtubules, microfilaments, etc.). Nichols *et al.* (2006). Morphologically, homoscleromorphs have *septate junctions* between adjacent ciliated larval cells. Eerkes-Medrano & Leys, (2006). Again, these may also be present in some demosponges. Maldonado (2004). However, there is insufficient comparative data for this information to have much phylogenetic significance.

"Chemotaxonomy"

Possible artifacts related to sponge-associated organisms. We were so enthusiastic about the possibilities of tracing phylogeny through biochemicals that we spent several days plowing through unpublished dissertations in German, notably Blumenberg (2003). Since we speak no German whatsoever, this was a non-trivial exercise and came perilously close to doing actual work. It might have been wiser to read Erpenbeck & van Soest (2006) (in English) before launching into this project. Those authors carefully explain the numerous pitfalls of "chemotaxonomy" -- pitfalls which are particularly deep when the technique is applied to sponges. Sponges are true animals, not just clonal aggregates; but they may also be viewed as cheap rooming houses for bacteria, protists, and fungi, along with other transients and undesirables. These boarders each bring their own metabolites and enzyme systems, and their population varies by sponge, by season, by reproductive state of the host sponge, or simply at random. So, chemotaxonomic statements have to be made with caution, and after broad sampling. As a practical matter, studies normally cannot be done with enough rigor to make indisputable statements. **[17]**.



Excessive concern for autapomorphies. Another limitation of chemotaxonomy seems to be entirely self-imposed. As discussed elsewhere, traditional taxonomy looks for autapomorphies, while phylogenetics looks for synapomorphies. The former are unique characters which can be used to identify an organism. The latter are shared characters which can be used to identify *relationships*. One relevant example is a very odd family of compounds known as peroxypolyketides. Historically, these were regarded as unique to homoscleromorph sponges. Erpenbeck & van Soest, however, conclude that these compounds are now taxonomically useless. Why? Because, forsooth, peroxypolyketides have recently been isolated from three orders of demosponges, including the Haplosclerida -- sometimes suspected of sharing other traits with the Homoscleromorpha. Someone seems to have missed the point here. However, there are other reasons to be wary of relying on these particular compounds for phylogenetic purposes **[18]**, so we will say no more.

Demosponges and homoscleromorphs are united by $\Delta^{5,9}$ unsaturated fatty acids. In the last analysis, the only chemotaxonomic statement in which we place some tentative confidence is one we have mentioned elsewhere: Blumenberg's observation that $\Delta^{5,9}$ unsaturated fatty acids seem to be found in hexactinellids, demosponges, and homoscleromorphs, but not in calcareans. Blumenberg argues that this is significant, because the synthesis of $\Delta^{5,9}$ fatty acids requires a very specific enzyme system which is not known in the Calcarea. We like this result, but need to mention three problems, also discussed by Blumenberg. First, the substrate for the creation of medium- and long-chain $\Delta^{5,9}$ fatty acids is a short-chain (saturated) bacterial fatty acid. Possibly, the Calcarea just don't associate with the correct bacteria, although this seems unlikely. Second, homoscleromorphs produce only a few, medium-chain (20-21C) varieties. They do not seem to synthesize the long-chain fatty acids made by demospongesand hexactinellids. Finally, the biochemistry of calcareous sponges is not exactly well-studied. Who knows what may be out there? Still, we count this as a modest point in favor of a demosponge-homoscleromorph sister-group relationship.

Also, possibly, by $\Delta^{6,X}$ unsaturated fatty acids. In addition, but with less confidence, Blumenberg notes that some odd $\Delta^{6,X}$ unsaturated fatty acids are found only in demosponges and *Plakortis*, a homoscleromorph. However, these may be entirely bacterial. Finally, he points a likely difference in the ability of sponge groups to synthesize sterols and probable marked differences in the sterols made. For example, aminosterols appear to be unique to homoscleromorphs. However, once again, comparative data from the Calcarea is insufficient to draw any conclusions. The literature on sponge biochemicals in general is sometimes obscure, but certainly large. At the same time, the coverage remains phylogenetically spotty.

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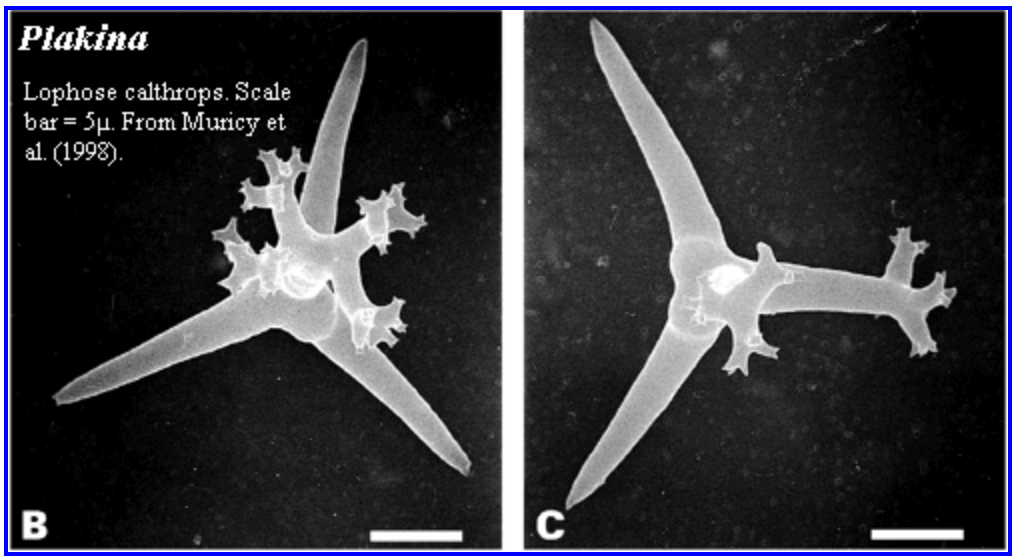
Homoscleromorpha - 2

Spicules



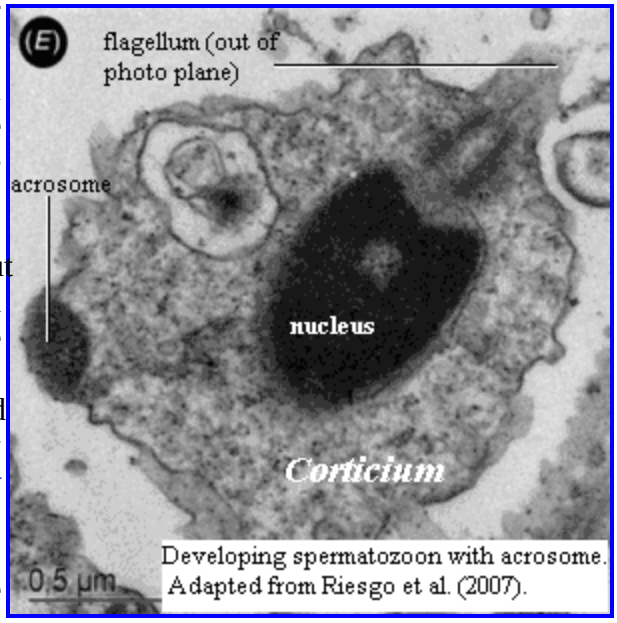
All homoscleromorphs have reduced skeletons, and some lack spicules entirely. When spicules are present, they are all generally of the same size -- hence the name *homoscleromorph*. Bergquist & Kelly (2004). Homoscleromorphs apparently do not have separate, sharply-defined size-classes of spicules. In this respect they differ from all three of the other main sponge groups.

The homoscleromorph spicule complement includes silicate *tetractines*, just as in most demosponges. The homoscleromorph tetractine is of the type referred to as a *calthrop*. A "caltrop" or "calthrop" was an evil-looking medieval landmine, consisting of mainly of four short, sharpened spikes radiating from a common center at equal angles. These were scattered in front of defensive positions and covered under a thin layer of dirt, where they tended to inconvenience charging knights. Homoscleromorph tetractine spicules often have the same generally plan, albeit with considerably less military value. Fortunately, in practice, sponges are rarely called upon to receive the assaults of heavy cavalry, as such tactics tend to be ineffective in a marine setting.

As indicated in the image, the genus *Plakina* is characterized by having *lophose* calthrops -- calthrops with branched spines. Muricy et al. (1998).

Reproduction & Development

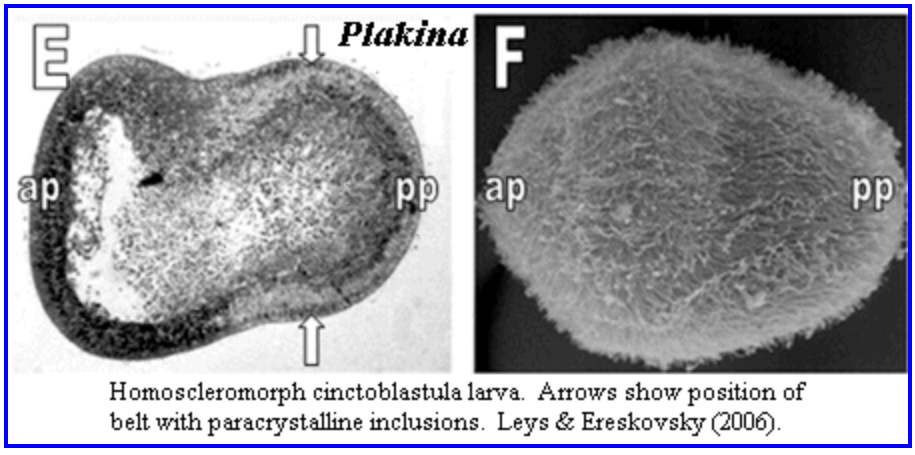
We have previously touched on the development of homoscleromorphs. There, we described it as generally similar to demosponge development. In retrospect, it seemed to us that we could have been just a tad more specific. So, although we can do little more than paraphrase Leys & Ereskovsky (2006), we supply some additional details here.



Developing spermatozoon with acrosome. Adapted from Riesgo et al. (2007).

For a number of reasons, we do not normally talk much about reproductive biology **[19]**. However, one frequently-mentioned character of homoscleromorphs falls into this category. The spermatozoa of many sexually reproducing eumetazoans bear an *acrosome*, the biochemical equivalent of an armor-piercing warhead to aid to fertilization. One of the folk-tales of spongeology is that only homoscleromorphs have acrosomes. Boute *et al*. (1996), Exposito *et al*. (2002), Leys & Ereskovsky (2006), Sperling *et al*. (2006). This belief appears to be mistaken. Acrosomes in calcareous sponges have been known for a long time. See, *e.g.*, Gatenby (1927). Definitive evidence of acrosomes in demosponges has only recently been obtained. Riesgo, Taylor et al. (2007) (*citing* Riesgo & Maldonado, in press). *Proacrosomal vesicles* have been observed in yet other demosponges. *Id*.

As in the development of most sponges, cleavage of the fertilized egg starts out in an organized manner: *holoblastic*, equal, and synchronous. As in the development of almost everything else in the universe, matters quickly become disorganized, asynchronous and rather random. The result is an apparently haphazard solid ball of cells, the morula. Leys & Ereskovsky (2006). At this point, the details become a bit obscure -- at least to us -- but the essential moves are (a) rapid division of the cells on the surface, combined with (b) outward migration of cells in the interior. Ereskovsky & Gonobobleva (2000), Maldonado (2004), Leys & Ereskovsky (2006). These two maneuvers transform the solid morula into a hollow sphere of cells enclosing a cavity populated by symbiotic bacteria and collagen fibrils. Maldonado (2004). This method of forming a hollow ball of cells ("multipolar egression") seems to be unique in the Metazoa. Leys & Ereskovsky (2006). It is often described as *gastrulation*. As previously discussed, we are not comfortable with that description.



Homoscleromorph cinctoblastula larva. Arrows show position of belt with paracrystalline inclusions. Leys & Ereskovsky (2006).

Within limits, the story so far may seems like a stripped down version of demosponge development. The main difference is that all migration is outward, rather than the complicated cell-sorting dance of the demosponges. Later events are even more like those occurring in demosponges:

(1) All, or almost all of the cells on the exterior become ciliated. As in demosponges, a small posterior region of the surface may be covered by larger cells which lack cilia. Maldonado (2004).

(2) As in many demosponges the rapid division of the epithelial layer causes the surface to fold or wrinkle – to become *plicate*. Ereskovsky & Gonobobleva (2000); Leys & Ereskovsky (2006).

(3) The larva develops an equatorial belt of cells with a *paracrystalline* inclusions in their nucleus. Maldonado (2004). These cells may or may not be homologous to the light-sensitive belt of cells in demosponges.

(4) The collagen in the internal cavity gathers under the epithelial layer to form a "felt." In homoscleromorphs, this structure becomes the basement membrane. Maldonado (2004).

(5) The outline of the embryo becomes somewhat pear-shaped, as in demosponges and hexactinellids. Leys &

Ereskovsky (2006).

After the larva settles, the posterior cells gradually overgrow the ciliated cells of the anterior surface and form the adult epithelium and pinacocytes. The blanketed anterior cells differentiate into the choanocytes and adult internal cells. Maldonado (2004). The belt of cells containing paracrystalline inclusions proliferate to form the excurrent canals the excurrent canal system. *Id*. In general, homoscleromorph metamorphosis resembles the same process in demosponges.

Relatively recent ultrastructural and biochemical work on homoscleromorphs shows that these sponges are surprisingly similar to non-sponge animals in characters relating to cell-cell communication and adhesion, such as the structure and extent of cell junctions and *basic helix-loop-helix* proteins, in addition to the famous basement membrane. Nichols *et al*. (2006); Simionato *et al*. (2007). As previously mentioned, comparative data are hard to come by. Consequently, these findings may suggest that Homoscleromorpha are close to the Eumetazoa, or simply that sponges are more similar to other animals than was once thought. Our bet is that both statements are correct.

Phylogeny and Diversity

The general feeling, at least as of this writing, seems to be that homoscleromorphs cannot be included in any of the three traditional groups of sponges. Until the late 1990's they were always included among the demosponges, and many workers still place them there. Even some RNA phylogenies tended to locate the clade within the demosponges, *e.g*., Shmitt (2003). However, most recent molecular phylogenies have nailed them outside the demosponges, either as demosponge sisters, or (perhaps more often) near-neighbors to the Calcarea (*e.g*. Sperling *et al*., 2006). The most sober and recent assessment is that neither morphology nor molecules have adequately resolved their relationship to the major sponge classes (Erpenbeck & Worheide, 2007); but no morphological study places the homoscleromorphs anywhere near the Calcarea. The two groups share no credible synapomorphies, while the homoscleromorphs have numerous similarities with demosponges.

On the other hand, both the molecular studies, comparative biochemistry, embryology, and ultrastructure all suggest that Homoscleromorphs have a special relationship to the Eumetazoa. Consequently, as argued here at really tiresome length, the most probable arrangement is that (a) homoscleromorphs diverged from near the base of the demosponges, and (b) this same branch ballooned into the Eumetazoa.

The homoscleromorphs have a miserable fossil record due to their reduced skeleton. They date back at least to the Mississippian. Unfortunately, they are not the only sponge group with calthrop spicules, and identification is difficult. They have probably never been numerous, and currently include only seven genera. Lehnert *et al*. (2005). Species are distinguished on the basis of texture, color, spicule size, branching pattern, and the structure of the water-canal system. *Id.*; Muricy et al. (1998). Not surprisingly, some of these identifications later turn out to be problematic. ATW080119

Porifera Cladogram

```
METAZOA
|--Choanoflagellata
`--PORIFERA
   |--Archaeocyatha
   `--+--Stromatoporoidea
      `--+--Calcarea
         `--+--Hexactinellida
            `--+--Demospongiae
               |  |--Tetractinomorpha
               |  `--Ceractinomorpha
               `--+--Homoscleromorpha
                  `--EUMETAZOA
```

Summary of Sponge Phylogeny and Early Animal Evolution

Originally, we had a neat little diagram here with links to the literature for the phylogenetic position of each taxon. This fastidious arrangement degenerated into swirling chaos when we had several changes of heart while writing a number of the individual sponge essays. Ultimately, we hit on a completely different phylogeny which satisfies us, but would probably be dismissed as pathological by more knowledgeable folks. Consequently, most of the citations had to be dropped from the cladogram.

At the tail end of our research we discovered that at least a few others may be sympathetic with some of our more radical rearrangements. If so, we look forward to being vindicated eventually. We remain optimistic since, as with other primates with keyboards, the laws of probability require that we will sometimes get one right. Although, having just finished de Waal's **Our Inner Ape**, we have the unsettling suspicion that certain apes might resolve the phylogeny faster than ourselves.

The story that emerged begins on the calcite "reefs" created by mineralizing bacteria in the Neoproterozoic. We discuss how small protoanimals took up residence in bacterial thrombolites and eventually adapted to mimic the form of these structures. In fact, this may have happened more than once, if archaeocyaths, *Cloudina*, and *Namacalathus* are all unrelated. In any case,

the outcome of that process was a generally "thrombolitic" structure: a cup-like, sessile, calcareous organism with internal septae and a sponge-like way of sucking water in from external pores and shooting exhalant water from a central osculum. All three lineages also begin with an essentially single-walled body plan. All, even *Namacalathus*, tend to become double-walled at some point above the base. Archaeocyaths show a similar tendency in an evolutionary sense, with increasing development of the inner wall and elaboration of tabulae and septae into a regular set of box-like chambers between the walls.

It turns out that stromatoporoids may well have developed in the same fashion, as discussed by Hladil (2007). In fact, it isn't all that easy to tell juvenile specimens of some stromatoporoids from archaeocyaths, or even a *Namacalathus*. However, other stromatoporoids responded to a unique set of ecological pressures in the Furongian and Ordovician, by becoming flat and massive. This trend was both slow and progressive, so we can be relatively certain that it represented a true evolutionary trend. We discuss some of the reasons why this may have occurred.

Other sponges retained the "cyath" body plan, but found a new, and less mineral-intensive, way to support it – by using spicules. Note that most Paleozoic sponges had quite regular body plans, all derived from the cyath system of external pores, an "intervallum" with living cells, and a wide central space with open osculum. See, for example, the various Paleozoic sponges discussed in connection with hexactinellids and demosponges. We outline some of the key biochemistry and molecular biology which unite the synthesis of calcareous and siliceous spicules, and unite both with the chemistry of the massive calcareous skeletons formed by stromatoporoids and archaeocyaths, in general agreement with the hypothesis of Botting & Butterfield (2005). Eventually, these spicules removed the necessity for maintaining a regular body plan of any type.

Homoscleromorphs are key players because they seem to share synapomorphies with eumetazoans. However, some studies based on molecular sequence data (e.g. Sperling *et al*., 2006) have united Homoscleromorpha with Calcarea, rather than Demospongiae. We explain why this arrangement is unworkable. The single morphological character that supposedly united calcareans with homoscleromorphs, the cross-striated ciliary rootlet, is plesiomorphic ("primitive") and known from any number of eukaryotes. Very recently, a cross-striated ciliary rootlet has also been identified in a demosponge. Riesgo, Taylor et al. (2007). Thus, this character cannot support a clade of Calcarea + Homoscleromorpha + Eumetazoa. Conversely, the characters which tend to unite homoscleromorphs with non-sponge animals are all traceable to developments in the demosponges (and generally *not* in Calcarea): for example the key collagen types, various aspects of embryology (see also here), and fatty acid structure.

Thus, when we'd walked this road as far as we could, we arrived at a phylogeny very different from the one we had in mind when we set out. In a general way, the whole phylogeny can be interpreted as a series of different strategies for physical support -- clearly the first and most obvious problem for multicellular organisms. After the choanoflagellate-like ancestral forms evolved the basic machinery for adhesion, metazoans adapted to take advantage of pre-existing physical supports. It seems likely that thrombolites were merely the most succesful of many structures adopted as templates. These bacterial structures provided a transition mechanism and medium through which the early metazoans could easily develop the cyath body plan.

However, the thrombolitic structure is workable only in environments which favor microbialites in the first place. Thus, selection would favor sponges which could either (a) out-mineralize the cyanobacteria on their home ground, or (b) adopt a lifestyle which would allow the sponge to live elsewhere. Stromatoporoids perfected the first approach, while the spiculate sponges tried the second. As argued by Botting & Butterfield, the evolution of spicules probably involved a host of different molecular strategies, with the crystalline calcareous spicule and amorphous silicate spicule representing only the two most succesful systems. Both strategies eventually permitted sponges to abandon the cyath body plan, although traces remained in the structure and development of the stromatoporoids, as well as the regular morphology of early spiculate sponges.

Collagen is used in the assembly of all spicules. At some point on the demosponge stem lineage, sponges evolved spongin from this starting point. Spongin proteins could be used, without mineralization, to supplement spicules. The homoscleromorphs diverged at this point, evolving a long-chain Type IV collagen which aggregated to form basement membranes, allowing a further reduction or (in many cases) elimination of the spicule-generating mechanism. The basement membrane, in turn, permitted the evolution of novel kinds of cell-cell interactions

Ultimately, at least one lineage evolved to derive physical support from the interactions between cells as much as the basement membrane in which the cells were embedded. The stability of cell-cell connections in a basement membrane also permitted the evolution of more specialized tissues. However, this step required regular symmetry in the adult. The maintenance of numerous specialized tissues is most easily accomplished if the tissues have predictable

geometrical relations to each other and to the medium. Similarly, the balance between numerous specialized tissues can only be maintained through long-range structural interactions (mediated, *e.g.*, through neurons and contractile fibrils). Long-range interactions, in turn, require long-range order -- a precondition met most easily through symmetry, and perhaps acquired by building on the symmetrical morphology of the homoscleromorph cinctoblastula embryo, with its large central cavity.

Thus, the Eumetazoa evolved as a natural and straightforward consequence of a series of evolutionary changes favoring structural stability under differing conditions. With some relatively arbitrary additions (Chancelloriidae) and speculations (*Namacalathus*), the whole *gemisch* looks like this:

```
METAZOA
|--Choanoflagellata (basic cell-cell connectivity and communications)
`--+??Cloudina  (adaptation to/of thrombolitic cyath body, amorphous carbonate)
   |--Namacalathus?
   `--+--Archaeocyatha
      |  |--Monocyathida
      |  `--+--Dokidocyathina
      |     `--+--Irregulares Kazachstanicyathida > Erismacoscinina)
      |        `--Ajacicyathida (Erismacoscinina > Kazachstanicyathida)
      `--+--Stromatoporoidea (only Paleozoic forms?) (strongly mineralized reefal forms)
         `--+--Chancelloriidae (basal spiculate forms)
            `--+--Eifellia
               `--PORIFERA (crown group) (homoplastic loss of cyath body plan)
                  |--Calcarea (crystalline carbonate)
                  `--+--Hexactinellida (amorphous silicate)
                     |  |--Protospongoidea
                     |  `--all other hexactinellids
                     `--+--Demospongiae (spongin)
                        |  |--Ceractinomorpha (polyphyletic)
                        |  `--Tetractinomorpha (polyphyletic)
                        `--+--Homoscleromorpha (Type IV collagen & basement membranes)
                           `--Eumetazoa (= "Radiata") (multiple tissues, long-range symmetry)
                              |--CNIDARIA
                              `--BILATERIA
```

Porifera References

```
METAZOA
|--Choanoflagellata
`--PORIFERA
   |--Archaeocyatha
   `--+--Stromatoporoidea
      `--+--Calcarea
         `--+--Hexactinellida
            `--+--Demospongiae
               |  |--Tetractinomorpha
               |  `--Ceractinomorpha
               `--+--Homoscleromorpha
                  `--EUMETAZOA
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Notes

[1] For an explanation of mtDNA phylogenies, and an interminable diatribe about their weaknesses, see Insectivora. We've been railing against the use of mtDNA phylogenies almost as long as people have been doing them. As it turns out, we were mostly correct (although not always for the right reasons). This is rare enough that we've made the most of the opportunity -- perhaps our last chance to kick this particular dead horse.

[2] But not all. Schütze *et al*. (1999) note that choanodermal cells of Calcarea lack the distinctive collar of choanoflagellates, and that many details of sponge ultrastructure differ from those of these probable poriferan ancestors.

[3] We, of course, take issue with this point because we regard spicule formation as closely related in all sponge taxa, as discussed earlier. In fact, we assert elsewhere that spicules were developed exactly once. However, we tend to agree that chancelloriids are indeed sponges, largely for the other reasons cited by Sperling *et al*. (2006).

[4] *Oscarella* is actually aspiculate. The Homoscleromorpha in general have silicate spicules.

[5] The UCMP site cites to Reitner J (1990), *Polyphyletic origin of the "Sphinctozoans"* **in** K Rutzler (ed.), **New Perspectives in Sponge Biology, Proceedings of the Third International Conference on the Biology of Sponges (Woods Hole)**. Smithsonian Institution Press, pp. 33-42. However, we have not read this paper.

[6] Grotzinger *et al.* cite to Grant SWF (1990), *Shell structure and distribution of* ***Cloudina****, a potential index fossil for the terminal Proterozoic*. **Am. J. Sci.** 290A: 261–294 as their basic text on *Cloudina*.

[7] We expect this statement to become obsolete very quickly.

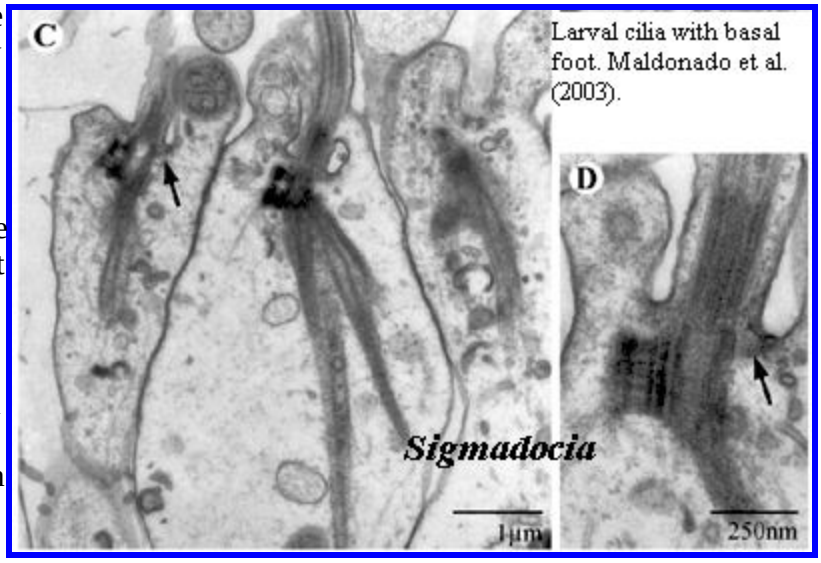
[8] *Archaeolynthus* could also assume a growth pattern of branching, tube-like structures, somewhat like Figures A and B.

[9] From the First Phillipic of Demosthenes, directed against Phillip of Macedon in 351 B.C. (Middle Holocene of Europe).

[10] "Each PCR product was sequenced from a minimum of two clones [so they stopped after *two* if the sequences agreed?]; when contradictions in the sequences of several clones could not be resolved [how would one resolve them?], the corresponding positions were coded according to the UPIAC code. The two strands were sequenced for the main part of the sequence length, with special attention ["main part"? What is *non*-"special attention"?] to the D2 domain where strong secondary structures of the molecule cause compressions in the sequence migration [how do they know it's restricted to D2?]." Chombard *et al*. (1997: 361). What this might mean is: "We had some troubling problems with inconsistency, and ran out of time/funding, but we think the errors were not too significant." Quite possibly, that conclusion is correct. On the other hand, it isn't the sort of painstacking accuracy we might expect with the improved methods available today -- nor the kind of thing on which we should rely for mapping fundamental branches in the phylogeny of the Metazoa.

[11] As do certain nucleariid amoebae (Patterson, 1999), also thought to be on or around the metazoan stem. However, this may well be a convergent specialization. For the moment, we will ignore the nucleariids.

[12] It is interesting, if probably irrelevant, that some demosponge larvae, which lack a cross-striated ciliary rootlet, also have a ciliary "foot" which *does* appear to have cross-striations. Maldonado et al. (2003).



Larval cilia with basal foot. Maldonado et al. (2003).

[13] Prof. Leys has expressed the view that the "plugged pores" of hexactinellids are not at all like Fungi. We think she's probably correct on this, but opinions vary.

[14] We discuss three of these features (basement membrane, flagellum, and embryonic development) in much more detail in connection with the Demospongiae. As discussed in that section, and in the section on Homoscleromorpha, *none* of these characters support a supposed clade composed of Calcarea + Homoscleromorpha + Eumetazoa, various papers to the contrary notwithstanding.

[15] One bizarre phylogenetic possibility raised by this similarity is that spicules evolved as a by-product of embryogenesis. Demoponge embryos frequently have spicules and, oddly enough, those spicules may be shed at metamorphosis. Maldonado *et al*. (1997). Sponges are also usually viviparous. Thus, we might imagine a *Cloudina*-like form, with internally growing embryos. Some embryos are released as young (and later shed their "baby spicules"), while others are retained to transdifferentiate into internal supports. This is pure speculation. But, in sponges, nearly anything is possible; and this would account for two sponge peculiarities at once.

[16] It's a bit hard to put any particular date on Prof. Claude Lévi. His first publication was in 1951. He retired from the MNHN (Paris) in about 2000, but we understand that he is still consulted on particularly difficult taxonomic calls.

[17] Oddly, this concern for contamination has never been addressed in the published sponge sequence phylogenies. Perhaps it is of less concern in such cases, for some reason.

[18] Briefly, (1) these polyketides look as if they may be derivatives of $\Delta^{5,9}$ unsaturated fatty acids. These are better dealt with on their own terms and are discussed below. (2) Some members of this family are branched, which is rare among animals, but more common in bacterial metabolites. (3) The creation of peroxy derivatives is not only unusual, particularly for animals, but means that the resulting substance is probably quite unstable -- a bad thing when one is looking for potential presence/absence characters. For what it may be worth, our suspicion is that peroxypolyketides are an incidental by-product of the reaction of sponge enzymes evolved for the metabolism of $\Delta^{5,9}$ unsaturated fatty acids with improper substrates, perhaps derived from fungi or dietary bacteria.

[19] (1) Reproductive biology reminds us of all the incredibly tedious stuff that bored us into catatonia during high school biology. (2) Characters of reproductive biology are wildly variable, seldom carry much long-range phylogenetic signal, and virtually never fossilize. (3) The subject requires a clear understanding of endocrinology and population genetics, both of which we lack because of item #1. (4) Finally, and perhaps most significantly, the subject requires a vocabulary which causes content censor programs to go into cardiac arrest and, conversely, attracts attention to the site from various types we like to avoid.

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