Laboratory V
Sponges, Archaeocyathans, Cnidarians and Lophophorates

Objective: This week begins a series of three labs in which you will be introduced to the main groups of fossil−forming marine invertebrates. You have two goals in this lab. (1) To understand the basic morphology of the group, and (2) to absorb the fundamentals of its classification. In lab, you will have a variety of specimens from most groups to examine. For each, you should observe the morphological features present in the fossils and link them to discussions of basic biology. You should also learn to identify the major groups.

READ: Chapters 12 and 13 in Prothero to accompany this handout. Bring your book to lab. The pictures will help!

NOTE: The dichotomous key for brachiopod orders will be due in lecture on Friday 22 February

Sponges

Sponges are animals on the cusp of multicellularity. Although they have a few specialized cells, they do not have tissue−level organization. Sponge cells are in such a loose confederation that they may be disaggregated and will reassemble themselves into new sponges. In fact, sponges may reproduce this way.

The sponge body is a porous cylinder. Water is drawn in through pores in the cylinder wall by flagellated cells called **choanocytes**. Coanocytes capture food particles as the water flows past them into the hollow interior of the sponge and out through an opening at the top. **Archaeocytes** in the sponge wall are responsible for digesting food and transforming into gametes for sexual reproduction.

The sponge is held rigid by a skeleton secreted by **sclerocytes** (secrete calcite or silica **spicules**) and **spongocytes** (secrete the protein **spongin**).

The fossil record of sponges is simultaneously great and poor. Spicules (calcite and silica) are common in the fossil record, but these can seldom be linked with specific sponge taxa. Consequently, spicules alone tell us little more than hexactinellid or calcarid sponges were present.

<u>Classification</u> [1]

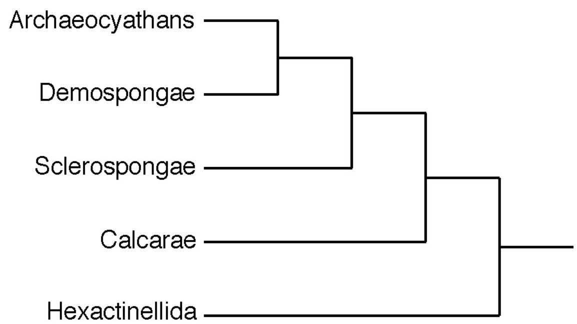
Class Hexactinellida (Cambrian − Recent) − glass sponges, characterized by six−rayed spicules with rays at 90° angles. Reef−builders in the late Devonian; suffered major losses in the Permian extinction, but recovered through the Mesozoic. Most charismatic member: Venus' flower basket (*Euplectella*).

[1] A general note on the classifications presented in labs. The classification of most of the groups we will study is in some form of flux. Most of this is due to the fact that phylogenetic analyses of the marine invertebrates have led to some surprises. Thus, as you read about the group in your textbook and elsewhere, you will find other classification schemes. Some older, some newer. Don't worry too much about which one is "right". Instead, focus on how they differ and why (i.e., what different types of data or methods give different results).

Class Calcarea (Cambrian − Recent) − calcareous sponges build a variety of spicule shapes. They may also secrete stony calcite skeletons not composed of spicules. Major reef−builders in the Permian and Triassic.

Class Demospongae (Cambrian − Recent) − skeleton composed of spongin although some produce a few silica spicules. Varied in shape and size; may live in freshwater or marine environment. These are the art and cosmetic sponges that you may know.

Class Sclerospongae (Cambrian − Recent) − these sponges tend to grow in encrusting layers and are likely relatives of the extinct **stromatoporoids** (Cambrian − Cretaceous). They may have calcite or silica spicules or have skeletons composed of organic material. Stromatoporoids were major reef−building organisms in the Silurian and Devonian, took a big hit in the Permian, and became extinct in the Cretaceous. Cenozoic sclerosponges are relatively minor contributors to diversity and reef construction.



Archaeocyathans

The archaeocyathans (Lower−Middle Cambrian) probably shouldn't get their own heading because most paleontologists now agree that they are an unusual sponge, probably sister to the demosponges. However, because they have an interesting place in paleontological history, we'll take special note of them here.

Archaeocyathan structure differs from that of most sponges in having a double, rather than single, skeletal wall. Archaeocyathans look like a pair of cones, one inside the other, separated by a system of struts. Apart from the atypical (for sponges) architecture of their skeleton, archaeocyathans appear to have functioned much like other sponges−filter feeding using a current of water drawn in through holes in their skeleton. Because they are known only from fossils, we don't know what cell types they possessed or how these cells may be related to those of other sponges and free−living choanoflagellates. Hence, the long−standing question about their affinities.

Despite their brief tenure on Earth, archaeocyathans left a major mark: they were the first organisms to build really substantial reefs. Although reef−like mounds were constructed by microbial communities in the Proterozoic, the archaeocyathans constructed structures that formed the physical basis for the first metazoan reef communities.

Cnidarians

Cnidarians are multicellular animals that have a simple body design. Imagine thrusting your fist into a closed plastic bag full of jello. The cavity left by your fist would form the interior of the animal. Cnidarians lack a complete digestive system (food enters and waste exits through the opening created by your fist), but they do have a rudimentary nervous system, muscles and specialized reproductive organs. Cnidarians are distinguished from other polyp animals by specialized stinging cells or **nematocycts**. Most cnidarians have both jellyfish−like (**medusa**) and **polyp** stages to their life cycle, although some species spend more time in one phase than the other.

Classification

Class Hydrozoa (poor fossil record) − free−living polyps, such as *Hydra*, that secrete no hard parts, thus have a very poor fossil record.

Class Scyphozoa (poor fossil record) − jellyfish. Because they too lack hard parts, they are rarely fossilized. However, there are notable exceptions in Lagerstätten like the Ediacarian localities of Australia (Neoproterozoic), the Burgess Shale of Canada (Cambrian) or the Solnhofen Limestone of Germany (Jurassic). Thus, we know they were present in the Proterozoic, which allows us to constrain the age of the clade.

Class Anthozoa − corals, sea anemones, sea fans, sea whips, and sea pens. Only the corals, because of their calcium carbonate constructions, have a good fossil record. The corals are useful ecological indicators because, like trees, the colony continues to grow and respond to environmental conditions. Thus, by looking from bottom to top in a colony (or individual) you can reconstruct the environmental history that colony experienced. New techniques, such as those that use ratios of stable oxygen isotopes, can reconstruct temperature variation experienced by ancient corals.

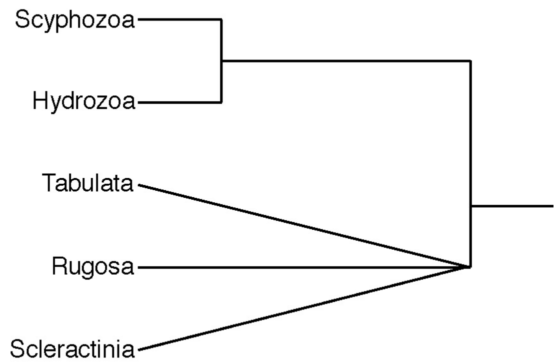
Order Tabulata (Early Ordovician − Permian) −polyps live in colonies composed of closely−packed calcite tubes (**corallites**) . Polyps secrete a series of floors (**tabulae**) in their tubes that allow the polyp to remain at the surface of the colony as the tubes grow upward. Tabulate corals were important reef builders during the Silurian and Devonian, taking over from bryozoa after the end−Ordovician extinction knocked out many of the important clades.

Order Rugosa (Middle Ordovician − Permian) − horn corals. This diverse group included solitary and colonial members. Individual polyps secrete a calcite corallites that increases in diameter as it builds upward to create the horn shape. **Septa** are inserted at regular angles in sets of four. These septa provide support for the polyp and give its muscles something to push against. Rugose corals were important members of Silurian and Devonian reefs and contributed to their physical structure, but did not build reefs on their own.

Order Scleractinia (Middle Triassic − Recent) − colonial corals responsible for most reef construction in the Mesozoic and Cenozoic. Scleractinian corallites are similar to rugosans in having septa at angles, but in scleractinians, septa are inserted in sets of six. Colonies come in all shapes and sizes. To some extent, colony shape varies with environmental conditions, mainly the degree of wave pounding. Many modern scleractinians have symbiotic algae (**zooxanthellae**) that provide a significant portion of the polyp's nutrition. Zooxanthellae may also aid in the secretion of aragonite (the main mineral used to construct corallites in this group). The zooxanthellae partnership may account for dramatic rates of colony growth reported among some scleractinian groups.

Some have speculated whether extinct corals−tabulates and rugosans−possessed zooxanthellae. Some evidence suggests that they may have, but these data are ambiguous. For example, in scleractinians, there is a relationship between polyp size and the presence of zooxanthellae: polyps that lack symbionts need to be larger because they have to collect their own food. Similar size variation is observed in tabulates, but this variation could be caused by many factors. Thus, polyp size alone is not strong evidence for symbiosis in extinct groups.

The polytomy in the anthozoa reflects real uncertainty about the relationships among the three major groups.



Lophophorates

The lophophorates include two lineages, the brachiopods (lamp shells) and the bryozoa (moss animals). Unlike the other animals we have studied in this lab, these animals have a **coelom** (internal, fluid−filled body cavity) and relatively complex organ systems. The lineage takes its name from the primary synapomorphy they share−**lophophore**, an arm−like structure with ciliated projections that sweep food particles out of the water and toward the mouth. Both groups of lophophorates are common Paleozoic fossils and can be used to age−date rocks throughout the epoch.

Brachiopods − Brachiopods are solitary animals that live on the sediment surface. They produce a two−valved calcite shell that surrounds their body's soft tissues. Brachiopods are easily distinguished from clams because their plane of shell symmetry runs vertically through the shell rather than between the valves, as in clams. The brachiopod shell attaches to the hard substrate during adulthood by a stalk or **pedicle**, fibers or cement. Some brachiopods also lived free on soft substrates. Some of these had spines or broad shell flanges that simultaneously prevented them from being swept away and buried in sediment. When the shell is agape, the lophophore conducts food to the mouth, where it passes through the closed digestive tract (the anus seems to have been lost secondarily). When too much waste accumulates, the brachiopod regurgitates it through its mouth. Two sets of muscles, adductors and diductors, close and open the valves respectively. This arrangement of muscles also distinguishes brachiopods from bivalves, which have only adductors. This explains why clams gape when relaxed (or dead) and brachiopods generally remain closed. In brachiopods, muscle contraction is requires to open, as well as close, the shell.

<u>Classification</u>
Class Inarticulata − these brachiopods do not have a tooth−and−socket hinge between their valves. Instead, valves are held together only by muscles.

Order Lingulida (Cambrian − Recent) − tongue−shaped shells characteristic of the living *Lingula*. This unusual brachiopod burrows (most of the rest live on the sediment surface) and tolerates brackish water (most of the rest do not). These features, plus its longevity in the fossil record, make it an excellent environmental indicator.

There are several other rare orders with in the inarticulates.

Class Articulata − these brachiopods have an elaborate tooth−and socket mechanism upon which their shells hinge. Valves are held together with ligaments and articulated with muscles. These constitute most of brachiopod diversity.

Order Orthida (Cambrian − Permian) − characterized by a long, straight hinge, a triangular opening in the hinge where the pedicle would have emerged in life, a broad **umbo** (the little hump near the beak on the ventral valve), and bi−convex shell shape. These brachiopods were extremely abundant during the Cambrian and Ordovician. Although they persisted until the Permian, they suffered a major loss of diversity in the end−Ordovician extinction and never recovered community dominance.

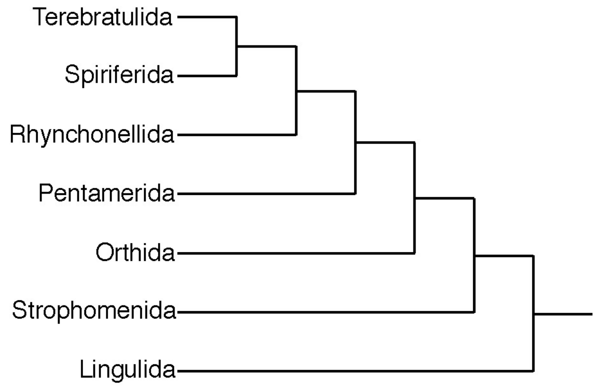
Order Strophomenida (Ordovician − Triassic) − valves are concave−convex or plano−convex with a long, straight hinge that gives them a distinct "D" shape. They apparently had no pedicle and thus must have rested directly on the substrate. Strophomenids are characteristic of Ordovician rocks, although they are present at low abundance. A Carboniferous lineage within this group, the **productids**, developed particularly deep ventral valves, covered with spines, and small, flat dorsal valves. These may have been adaptations to sitting directly on muddy bottoms, where the deep ventral valve acted like a boat with the spines as pontoons to help buoyancy in soft sediment.

Order Pentamerida (Cambrian − Devonian) − the most distinctive morphology in pentamerids occurs inside the shell. Here, a series of septa divide the shell into five segments. Externally, pentamerids have bi−convex shells with a short, curved hinge and a small pedicle opening. This group never accounts for significant diversity, but may be locally abundant.

Order Spiriferida (Ordovician − Jurassic) − bi−convex shells with a very long, wing−like hinge and prominent **fold−and−sulcus**. This lineage radiated dramatically in the Silurian and is the most common form in the Devonian. They survived the Permian catastrophe, but just barely, and finally became extinct during the Jurassic.

Order Rhynchonellida (Ordovician − Recent) − characterized by a short, bent hinge and pointed **beak** that gives the back of the shell a distinct "V" shape. Deep fold−and−sulcus and prominent growth ribs give the commissure a toothy grin.

Order Terebratulida (Devonian − Recent) − strongly biconvex valves with a large pedicle opening give this form the characteristic "lamp shell" shape. Shell is generally smooth with no fold−and−sulcus.



Bryozoa − Bryozoans are small, colonial poly organism with a coral−like lifestyle. However, unlike corals, bryozoans have a complete digestive tract with lophophore−bearing tentacles encircling the mouth and the anus outside of the tentacle ring. Bryozoans have a muscle system that allows them to retract their tentacles. They secrete calcite **zooecia** with floors much like tabulate corals, but bryozoan zooecia are much smaller than those of corals. Bryozoans grow in a wide variety of colony shapes and require a hard substrate. Thus, they are commonly seen encrusting other shells.

Most of the features that characterize bryozoan groups can been seen only in thin section, thus, you may find identifying the major groups in hand specimen a little frustrating. Use a hand lens for best viewing.

Class Stenolaemata (Ordovician − Recent) − the most common Paleozoic group, stenolaemates had highly calcified zooecia that tend to be long and narrow. Individual tubes continue to lengthen throughout the life of the colony.

Order Trepostomata (Ordovician − Triassic) − characterized by robust, calcite colonies that come in a wide range of shapes from hemispheres to delicate branches. Trepostomes are distinguished based on their three pore types: large (which contained generalized polyps), medium (which contained a reduced, specialized poly), and spines. Trepostomes were important contributors to reef construction in the Ordovician, suffered significant losses in the Devonian and limped through the Permian extinction to become extinct in the Triassic.

Order Cryptostomata (Ordovician − Permian) − this group is characterized by shorter tubes with wider openings than those of the trepostomes. Their colonies are smaller, more delicate and seldom branch. Some forms have abundant spines that may come in two sizes and occur on ridges between the zooecia openings.

Order Fenestrata (Ordovician − Permian) − characterized by the distinctive lacy appearance of the calcified colony. Zooecia are short and perpendicular to the open latticework of the colony. Fenestrates grow in a variety of fan shapes, but the most common is *Archimedes*, where the latticework fans spiral around a calcified central core that resembles the water screw of Archimedes, the Greek mathematician.

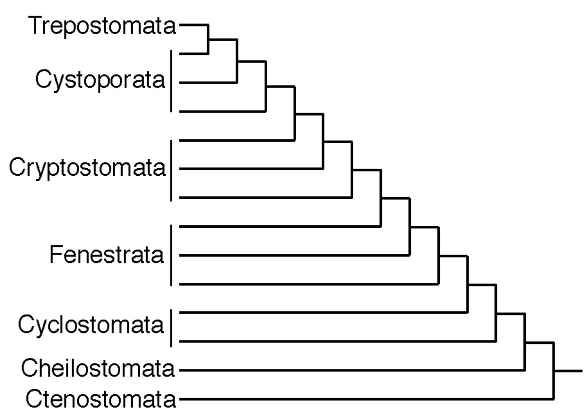
Order Cyclostomata (Ordovician − Recent) − this encrusting form is common on seaweed and other stranded material at the beach. Zooecia are simple and short, looking like clusters of erect bathroom tissue tubes on the surface. This group took big hits at all the major Phanerozoic extinctions, but diversified after each to contribute to recovery diversity.

Order Cystoporate (Ordovisian − Triassic) − similar to cyclostomes except that the floors of cystoporate tubes are bubble−shaped instead of flat. Some have star−like projections radiating from zooecia openings.

Class Gymnolaemata (Ordovician − Recent) − instead of being tubular and ever−growing, gymnolaemate zooecia are box−shaped, with a lid, and of finite size. The colony can only grow by adding more discrete zooecia.

Order Ctenostomata (Ordovician − Recent) − zooecia lid is open and walls are uncalcified.

Order Cheilostomata (Jurassic − Recent) − most diverse and common living group. These have well−calcified boxes with a solid, hinged lid.



Sadly, the classification of bryozoans is not in the best of shape, phylogenetically speaking. As you'll see below, all but three of the major groups (ctenostomes, cheilostomes, and trepostomes) are paraphyletic. However, more work on the phylogeny is needed before we're ready for a major overhaul of the classification.

In lab? In lab you have three main tasks.

(1) Examine specimens of the major groups discussed above. Sadly, we don't have representatives of each, but we do have examples of the most common. Make drawings in your notebook that will allow you to recognize these major groups again if you were to see them, say, on a quiz. Also make some written notes about how to distinguish major groups.

(2) Add the ranges of all of these groups to our course time line.

(3) Develop a dichotomous key for the orders of brachiopods discussed above. A dichotomous key is a series of questions arranged in a decision tree. If each of the questions is answered correctly, the user should arrive at the correct identification of the taxon. For example, here is a dichotomous key for the students in this class:

1. Male (go to 2)
   Female (go to 3)
2. Blond (**Trevor**)
   Brown hair (go to 4)
3. Blond (go to 5)
   Brown hair (go to 6)
4. Loves ⁕ (**Jay**)
   Ambivalent about ⁕ (**John**)
5. Graduating soon (**Marie**)
   Not graduating for a while (**Annie**)
6. Sophomore (**Sarah**)
   Junior (**Jen**)

Questions for Further Thought

1. We have no fossil record of hydrozoa, but their relationships with other members of the cnidaria allow us to put a minimum age on the clade. Based on the information in this lab, what is that minimum age? Explain. HINT: Think about the issue of ghost lineages.

2. Consider the range of brachiopod shell morphology that you observe in lab. What does this variation suggest about the range of environments inhabited by Paleozoic brachiopods?

3. Track the relay−race of reef−builders in the Paleozoic, beginning with the Archaeocyathans in the Cambrian. Who succeeds them when they go extinct? Then who?

4. Is the bryozoan Class Gymnolaemata monophyletic, paraphyletic or polyphyletic?