Brachiopod Lecture notes

1. Brachiopods: “The Other Bivalves”

Reflects my interest in “orphan groups”

Not well represented in most collections

Turns out they’re pretty boring

2. What is a Bivalve?

Bivalve condition has arisen multiple times

3. Critters with two shells: Pecten

Most widely known are the bivalved mollusks, which have commandeered the name “bivalve.”

4. Critters with two shells: Ostracod

Tiny crustaceans, a few mm long.

5. Critters with two shells: Cladoceran

Another group of tiny crustaceans, also a few mm long.

6. Critters with two shells: Sacoglossan

Even snails have developed a bivalved version! True nature was not discovered until 1959, when living specimens were collected off Japan. Saccoglossan opisthobranchs. Since many people have never seen one, I’ve included a specimen in the show and tell. Begin life with a swimming coiled univalved operculate shell. When it finds a suitable alga, it settles, sheds its operculum, and the teleoconch splits. By four days post-hatching, it has a fully functioning hinged bivalved shell!

When you think about it, the operculum is a functional “second valve.”

**STOP!** I have a friend who brings me shells. She once brought me some small clam shells from the shore of a Texas lake that I was having difficulty identifying. I was finally able to identify them. Now move on.

7. Critters with two shells: Pistachio

Even plants can have bivalved shells!

**STOP!** Ask what the examples have in common, besides two valves. Looking for laterality. Now move on.

8. Critters with two shells: Brachiopod

Previous (not sure about pistachios) have all had left-right valves. Brachs are still left-right symmetrical, but valves are dorsal and ventral. Scallop, shown for bivalve mollusks has *functional* dorsal and ventral valves, but they are still left and right, and they lie on their sides, like flounders.

9. Shell orientation

Discuss plane of symmetry and relation to valves.

10. Critters with two shells: Box turtle

One final example of a bivalve, again with a dorso-ventral shell. This is actually a TRI-valve, with the main valves fused and the ventral valve secondarily divided to enclose the soft parts within the shell.

11. Comparison: Bivalve Mollusks vs. Brachiopods

Have not found information on histological or physiological processes of respective mantle. Will discuss lophophore and pedicle (also called peduncle) later.

12. Paleontological Distribution

Fully formed at the beginning of the Cambrian, when shelled fossils first arose. Have not been confirmed in pre-Cambrian, but without shell, how could you recognize a brach? Over 1600 fossil genera and >30K fossil species, compared to about 60 genera and 300-350 species today. Lingula is one of oldest genera, going back to Devonian, ca. 350 mya, but no living species goes back that far.

13. A Cambrian Seabed

Obligatory Cambrian diorama. Brachs are green spiriferids and orange discinids. Tall sponge-like structures are archaeocyathids. Trilobites. Brown “fishies” are Sidneyia (an arthropod of uncertain affinity), red “shrimps” are Candaspis. Blackish thing in lower left looks like Opabinia, a Burgess Shale creature of unknown affinity and no living relatives.

14. Fossil Brachiopods

Upper left, a craniid, which attaches by cementing to the underlying substrate, which in this case is an articulate brachiopod. Upper right, Mucrospirifer; wings allow it to live in relatively soft sediments without sinking into the sediments. Lower left: pyritized specimen. When a calcified shell is present, it is as calcite, not aragonite, so it is not displaced on fossilization.

15. Where do Brachiopods Fit in the Tree of Life?

So, where do the brachiopods fit among the other groups of animals?

16. What is a Brachiopod?

Brachiopods are a phylum, or basic “body plan” of animals. Approximately 35 phyla, depending on who’s counting. All but one are “invertebrates.” Here are the relative numbers of *living* species by phylum. Note that Brachiopoda is not among them. See that little sliver at the top? That’s the other 24 phyla lumped together. Let’s break that little sliver down.

17. Brachiopoda’s Place among the “Minor” Phyla

Here are the 24 phyla represented by that little sliver in the previous chart. Brachiopoda has been “exploded.” About 335 living species, according to the source where I got these figures. To put that into perspective, there are about 10K spp of bivalved mollusks, about 750 species of chitons, about 700 species of cephalopods, and about 600 species of scaphopods. Note that I ran out of room in the legend to list all of the phyla; there are two phyla (Placozoa and Cycliophora) with only 1 species each.

18. What are the Brachiopods’ Closest Living Relatives?

One early name for brachiopods was “anomie”; Linnaeus placed the known brachiopods in his genus Anomia, which is the jingle shell, though of 27 names, 6 are Anomia, 1 is an oyster, 4 are living brachiopods, and 16 are fossil brachs.

The name Brachiopoda is credited to Duméril in 1807. “Brachium” is arms; it was thought that the “arms” of the lophophore were mobile, like a molluscan foot, so could be extended to move the animal about. Turns out to be false.

Orbigny developed the idea of a group “Molluscoidea,” to include the brachiopods, bryozoans, barnacles, and tunicates. This concept lasted well into the early 20th century. If you look at “mollusk” papers from that time, they will also include brachs and barnacles, and sometimes tunicates. But we’ve already seen that brachs are functionally very different from clams.

The lophophore is an elaborate structure that ties together the three phyla Bryozoa, Phoronida, and Brachiopoda. Brachs’ closest relatives are probably the shell-less, wormlike phoronids. In the great “tree” of invert life, there are two main branches: protostomes (arthropods, annelids, and mollusks) and deuterostomes (echinoderms and chordates). The lophophorates, of course, show characteristics of both groups, so they are either basal to both or perhaps near where the deuterostomes diverged from the protostomes. There is some evidence now that bryozoa are closer to mollusks, leaving phoronids and brachs as mutually closest relatives.

19. Living Brachiopods

Where brachiopods occur, they can be abundant. This was taken off Massachusetts, depth not known. Hemithiris has a U-shaped dorsal valve, see lower right. Terebratulina is more classically “clam-like,” as at upper center.

20. An Inarticulate Brachiopod

It is traditional and convenient to divide brachiopods into two groups: articulates and inarticulates. Both were present among the earliest fossils, so neither is more “primitive” than the other. The inarticulates lack a hinge, and the valves do not interlock (or articulate). It was pointed out that Lingula (Latin for “tongue”) is a strange name for an “inarticulate” creature. Note the pedicles in this photo of living Lingula in an aquarium.

21. An Inarticulate Brachiopod in Life

Lingula lives in a burrow, like many bivalved mollusks, anchored by the pedicle. The pedicle can be contracted to withdraw the animal into the safety of the burrow. They are capable of limited movement and reburial. Do not have siphons, like bivalved mollusks, but create inhalant and exhalant currents with lophophore and bundles of setae that extend beyond margin of shell.

22. An Articulate Brachiopod

Articulate brachiopods “articulate” with a hinge bearing teeth and sockets. The large shell is not a brachiopod, but a bivalved mollusk. Given the species, it is probably about an inch across. The brachs are the little specks attached, and enlarged here, along with a polychaete tube.

23. An Articulate Brachiopod

These Gwynia are full grown at about a mm across.

24. An Articulate Brachiopod in Life

Here is a drawing of two species of articulate brachiopods in life. This is from an old (1887) drawing, which confuses developmental and functional dorsal and ventral. The ventral valve *developmentally* is the larger and bears the pedicle, while the dorsal valve *developmentally* is smaller and sits within the ventral valve. In life, however, the animal “sits on its head” with the “ventral” valve dorsal and the “dorsal” valve ventral! Hence the contorted pedicles seen here. Articulate pedicles cannot reattach, and the animals cannot move if pedicle is torn, will become buried. This also illustrates the common name of “lamp shell,” as the shell gives the appearance of an “Aladdin’s lamp.”

25. The Brachiopod Shell

Here is a diagram of an articulate brachiopod shell, showing the life position in more realistic perspective. Since fossil brachs are common and important in correlating stratigraphy, an elaborate nomenclature has developed of every little bump and fold on the shell. For our purposes, we can just worry about the dorsal (brachial) and ventral (pediclar) valves and the pedicle foramen.

26. Punctae

Extensions of mantle tissue into channels in articulates. These are the same Gwynia from a previous slide. Punctae are visible as white spots on translucent shell. Punctae end blindly just under the periostracum. Function is unknown. Do not possess nerve cells, so are not “eyes.” May contain repellent chemicals.

27. What’s Inside a Brachiopod?

Thayer calls them “minimal organisms.” The organic tissue forms only about 3% of the live weight of the animal and is crammed into the posterior portion of the shell. The rest (60-75%) of the shell is the mantle cavity, which is filled with the lophophore. Lophophore is an elaborate feeding and respiratory organ. There are two arms (brachia) that bear a ciliated food groove that convey food to the mouth located at the junction of the two brachia. Brachs are filter feeders and feed on small organic particles and dissolved organic matter. A few possibly take small plankters. The digestive system bears a mouth, esophagus, stomach, intestine, and (in inarticulates) an anus. The anus opens to the mantle cavity to the right of the midline and is one of the few breaks in strict left-right symmetry. In articulates, the intestine ends blindly, and waste products are expelled back out the mouth into the mantle cavity. The circulatory system is open. There is a weak heart above the stomach, but most movement of “blood” is by ciliary action of the body cavity. Excretion is by paired nephridia (two pairs in one group). Nervous system is simple, with subesophageal ganglion, circum-esophageal ring, and nerves to mantle, muscles, pedicle, and lophophore. No sensory organs developed, but sensitive to touch at mantle edge and shallow-water species respond to light and shadow, though no eyes are present.

28. Musculature of an Articulate Brachiopod

Mentioned that both opening and closing are under muscular control. Closing accomplished by central adductor muscles, consisting of “quick” portion for rapid closure and “catch” portion for holding valves closed. Equivalent to the two parts of the adductor in a scallop. Unlike bivalved mollusks, diduction is by muscle attached to tip of dorsal valve, so action is to pull valves apart. Pedicle is a solid band of connective tissue. Movements limited to opening, closing, some rotation about pedicle. Opening is generally limited to a small vertical action, leaving a narrow gape.

29. Musculature of an Inarticulate Brachiopod

Inarticulate brachiopods have no hinge and valves are not attached, except by animal tissue. Closing is accomplished by central adductor, again with quick and catch portions. Diduction is accomplished by a “posterior adductor.” Oblique muscles allow some rotation of valves. Pedicle is muscular and contains an extension of the body cavity, so is capable of contraction and limited worm-like movements.

30. The Lophophore

31. The Lophophore

Bears single row of ciliated cirri (or filaments) bordering a food groove.

32. Development of the Lophophore

Coiling of lophophore is not random “packing.” Three main patterns of folding, may represent optimal solutions to the packing. Lophophore can grow only at tip. All species start out with a simple trocholophe. Final stage in Gwynia. Doubles back to form schizolophe. Then can follow one of three paths. 1) Inner arm of schizolophe twists (transient zygolophe) then forms median spiral of plectolophe. 2) Two sides divide into multiple lobes, forming ptycholophe. 3) An ever-growing spiral forms a spirolophe.

33. The Brachidium

Brachidium can be highly elaborate, as in this fossil species. How’d you like to clean that?! One shell in show and tell opened to expose simple brachidium .

34. Brachiopod Reproduction

* Most have separate sexes, a few are hermaphrodites.
* There is one (rarely two) pairs of dorsal and ventral gonads.
* Gametes are shed into the body cavity, then released through the nephridia.
* Fertilization is external in some and larvae are planktonic.
* In others, fertilization occurs in the mantle cavity, and larvae are brooded.
* Larvae are the only motile phase, can settle in as little as a few hours in some articulates, hence the large numbers and patchy distribution of individuals.

35. Comparison of the Three Main Groups

Developmental and other studies show that division into inarticulate and articulate is too simplistic. Inarticulates actually two distinct groups.

36. Classification of Living Brachiopods: Inarticulates

Two groups of inarticulates, three families, few genera and species. Lingulids are “typical” inarticulates we’ve discussed. Depending on who you read, disciniscids may belong to either group (but not both). Attach by short pedicle to substrate, through foramen, looking like Anomia. See show-and-tell. Craniids cement directly by ventral (dorsal? lower) valve to substrate. Opening consists of simple raising of limpet-like upper valve, opening may be simple elastic response of muscles.

37. Classification of Living Brachiopods: Articulates

Articulates more diverse than inarticulates, ca. 25 families.

38. Brachiopods of the Gulf of Mexico

39. Brachiopod Trivia

* Said to have a “distinctive bitter smell and extremely noxious taste,” though eaten by some peoples. Maybe like the leaves of an artichoke?
* Occur in all latitudes and depths (to 6000 m).
* Live 5-10 years, sexually mature at 2-3.
* Not many predators. Punctae may contain noxious chemicals.
* Largest (living) is Magellania venosa, at 3+ inches; see show-and-tell. Fossils to a little over 4 inches.
* One of lowest metabolic rates of any animal.
* Pearl has been reported in Terebratulina.