**Geos 223** **Introductory Paleontology** **Spring 2006**

# Lab 6: Brachiopods and Bryozoans

Name: ________________________________

Section: ________________________________

## AIMS:

This lab will introduce you to the two skeletonized lophophorate phyla: the Brachiopoda and the Bryozoa. You will become familiar with the basic anatomy of each group and see several important fossil representatives. Emphasis is placed on the various modes of life adopted by different members of each group, and how the form of the organism has been evolutionarily modified to suit each mode. You will also use a computer database to compile plots of diversity through time. By the end of this lab, you should have a good knowledge of the anatomy of brachiopods and bryozoans, an appreciation for how organismal form reflects function, and a good understanding of the process (and problems) of building diversity curves from paleontological data.

## PART A: BRACHIOPODA.

Brachiopods are one of the three lophophorate phyla (along with bryozoans and phoronid worms). All three phyla feed using a lophophore: a row of ciliated hollow tentacles developed around the mouth. The cilia (1) beat to drive a current of water across the tentacles, and (2) filter that current for microscopic suspended food particles. The food particles are then moved down the tentacles to a food groove at their bases, which runs the length of the lophophore to the mouth.

Brachiopods are solitary, marine, sessile, benthic lophophorates, protected by a biomineralized shell of two valves (the pedicle valve and the brachial valve). The valves of linguliform "inarticulate" brachiopods are made of organophosphates and are not articulated together. The valves of the other "inarticulate" subphylum Craniiformea are calcareous. The valves of "articulate" brachiopods (subphylum Rhynchonelliformea), however, are made of calcium carbonate and are articulated by a complex array of skeletal projections (teeth and sockets) and muscles. The Brachiopoda evolved in the

Early Cambrian and is still extant, although its peak abundance was in the Paleozoic as you will see in Part C of this lab.

## RHYNCHONELLIFORM BRACHIOPODS:

### Basic Anatomy:

A1: Recent terebratulid brachiopods.

Specimen A1a is the shell of an extant species of *Terebratula*. IT IS VERY FRAGILE: PLEASE BE EXTREMELY CAREFUL. Terebratulid brachiopods are a long-ranging (Early Devonian to Recent) order of rhynchonelliform brachiopods (i.e., with valves bearing teeth and sockets), and are one of only three rhynchonelliform orders to survive beyond the Jurassic. They are characterized by possession of a looped brachidium. The shell is biconvex, and the hinge line is curved (non-strophic). Most terebratulids have a functional, horny pedicle which raises the shell above the substrate; the pedicle foramen is typically large and open.

Draw and label the two valves. Use figure 7.1 in Clarkson (1998) as a guide.

What was the function of the brachidium?

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What is the white-colored crust on the outside of the pedicle valve?

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Specimens A1b and A1c are of the same species, but still bear the remains of the lophophore feeding structure. Look (very carefully) inside the shell. DO NOT PRISE THE ARTICULATED SPECIMEN OPEN: IT IS VERY FRAGILE!

## A2: Fossil terebratulid brachiopods.

*Kingea* is from the Early Cretaceous, and *Rensellaeria* is one of the earliest terebratulids (Early Devonian). Note the general similarity in form of these fossil terebratulids to the Recent example.

## A3. Rhynchonellid brachiopods.

Like terebratulids, rhynchonellids typically have a biconvex shell with a non-strophic hinge line and a functional pedicle (i.e., are stalked, epifaunal filter-feeders), although the pedicle foramen is often small and located on a beak-like umbo. The Rhynchonellida also persisted beyond the Jurassic and still survives today. However, rhynchonellids develop only short, simple struts (crura) inside the brachial valve to support the lophophores, and most are characterized by development of a deep fold and sulcus and strong ribs on the shell, making the commissure zigzag-shaped. The oldest known rhynchonellids are of Middle Ordovician age.

The typical rhynchonellid morphology is demonstrated by *Anastrophia* and *Hypothyridina* (A3a and A3b; both Devonian). Draw and label one of these fossils.

The “*Camarotoechia*” specimen (A3c) is one of the oldest (Ordovician) rhynchonellids. This genus name was widely used in the past, being applied to species ranging from Ordovician to Permian age. However, following recent taxonomic treatment, the genus *Camarotoechia* (in the strict sense) is restricted to the Upper Devonian. *Pugnoides* (A3d) and its relative *Pugnax* are mid- to late Paleozoic rhynchonellids famous for development of an enormously exaggerated fold and sulcus.

What was the functional purpose of the fold and sulcus, and of the ribs, in brachiopod shells?

## A4: “Spiriferid” brachiopods.

“Spiriferid” brachiopods (orders Spiriferida and Spiriferinida) were common in Paleozoic marine sediments, but became extinct during the Jurassic. The shells are generally rhynchonellid-like: both valves were convex, often with strong ribbing and a prominent fold and sulcus. However, the hinge line of spiriferids was long and straight (strophic), commonly giving the shell an alate outline.

Spiriferids were characterized by possessing brachidia which were coiled into a laterally directed spiral (A4a; see also Clarkson, 1998, fig. 7.7).

Which direction did the water current flow across the brachidium?

The alate shell outline is well demonstrated by *Mucrospirifer* (Devonian; A4b) and *Spirifer* (Lower Carboniferous; A4c). The *Mucrospirifer* specimens show subtle variation in shell shape.

Draw one of the specimens.

In some spiriferids (e.g., *Cyrtospirifer*, A4d) the alate form was taken to an exteme, with the hinge being very long. The shell of such brachiopods is “winged”. In others (e.g., *Spirifer fornaculus,* A4e; *Cyrtina*, A4f, also *Cyrtia*) the interarea was huge.

What mode of life did these spiriferids have?

What was the functional purpose of the elongate “wings” and the enlarged interarea to the spiriferid shell?

On which valve is the interarea well developed?

*Eospirifer* (A4g) is a Silurian spiriferid. Note the broad ribs on the shell. Spiriferids range back to the Middle Ordovician.

### A5: Atrypid brachiopods.

These common Middle Ordovician to Late Devonian brachiopods also possessed spiral brachidia. Their shells are biconvex with a short hinge line.

### A6: Athyridid brachiopods.

These Late Ordovician to Jurassic brachiopods also possessed spiral brachidia, but the shells are smooth, with a narrow, non-strophic hinge line.

To which other brachiopod group are the shells of athyridids most similar?

What mode of life do you think athyridids had?

What evidence supports your answer?

### A7: Pentamerid brachiopods.

Pentamerids ranged from the Middle Cambrian to Late Devonian, and were particularly abundant in the Silurian.

Describe the exterior morphology of the shell of the pentamerid *Gypidula* (A7a).

What mode of life did *Gypidula* exhibit? What supports your conclusion?

Internal molds of pentamerids (A7b, c) exhibit several “slits” around the hinge line on both the brachial and pedicle valves, which represent what would have been calcareous ridges and walls on the inside of the valves.

Draw and label these structures. Use Clarkson (1998, fig. 7.8) to help.

What was the purpose of these structures?

### A8: Orthid brachiopods.

Orthids are the rhynchonelliforms with biconvex shells (usually unequally so) and strophic hinges. They lack brachidia. Orthids ranged from the Cambrian to the Late Permian. The orthid morphology is typified by the Silurian genus *Dalmanella* (A8a). *Rhipidomella* (A8b) shows a somewhat more planoconvex shape.

*Dinorthis* (A8c) was abundant in shallow-water marine environments of the Ordovician.

How did *Dinorthis* live? (Use the morphology of the fossil plus Paleobase 1.0 to help you).

The external morphologies of the Ordovician orthids *Hebertella* (A8d) and particularly *Platystrophia* (A8e) resemble that of a spiriferid, and are classic examples of convergent evolution.

## A9: Strophomenate brachiopods.

Strophomenate brachiopods range from the Cambrian to the Triassic. They typically have plano-convex or concavoconvex shells with strophic hinges. Although they are rhynchonelliforms, the teeth are simple and often lost. There are two main groups of strophomenates: the Order Strophomenida (Cambrian to Triassic) and the Order Productida (Devonian to Triassic). Most strophomenates lack brachidia.

The inside of the valve of a productid (A9a) shows well-preserved muscle scars and a lobate cardinal process.

Which valve is represented?

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What was the function of the cardinal process?

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Which muscles left the scars on this specimen? What was the function of these muscles?

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Most productid and strophomenid brachiopods abandoned the pedicle as a means of attachment to the substrate and instead developed a “recumbent” habit, resting freely in the sediment. Many had a concavo-convex morphology, with the concave brachial valve “cupped” within the highly convex pedicle valve, although some were very flat (e.g., A9b). Many evolved very long spines which speared the pedicle valve into the sediment. In this orientation (with the pedicle valve below the brachial valve), productids were “upside-down” relative to stalked brachiopods. *Strophomena* (A9c) and *Leptaena* (A9d) are classic examples. Some Carboniferous productids could attain relatively large sizes (e.g., A9e).

<u>Draw</u> *Leptaena* (A9d). Note the long, parallel ribs, the straight hinge, the lack of a pedicle foramen in the tightly curved umbo of the pedicle valve, and the coarse “crinkles” on the pedicle valve near the umbo which characterize this abundant genus.

## LINGULIFORM BRACHIOPODS:

<u>A10: *Lingula.*</u>

These specimens represent the famous *Lingula* (Order Lingulida), a burrowing brachiopod inhabiting brackish and intertidal sandy environments. In contrast to “articulate” (rhynchonelliform) brachiopods, *Lingula* has valves of almost identical morphology, lacks teeth and sockets and a hinge line (and so is an “inarticulate” brachiopod), and has no diductor muscles. Its shell is organophosphatic rather than calcareous. The pedicle is very long and is used to anchor the organism into its burrow. *Lingula* represents one of very brachiopods to have colonized the infaunal habitat; a niche more widely occupied by bivalves.

The lingulid morphology has been remarkably conservative, being found even as far back as the Cambrian. What do we call extant members of such a long-lived and conservative taxon?

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### A11: *Orbiculoidea*.

Several “inarticulate” brachiopod groups, including the linguliform *Orbiculoidea* (A11) seen here, evolved a mode of life by which they cemented themselves to a hard substrate by their pedicle valve. *Orbiculoidea* ranged from the Ordovician to the Permian, although the encrusting habit for “inarticulates” ranges from the Cambrian to the Recent. However, the brachiopod groups utilizing this habit have always been of relatively low diversity.

Which other groups of animals might you expect cementing brachiopods to compete most closely with (for ecological space and food)?

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## PART B: BRYOZOA.

At first glance bryozoans are similar to corals: many small individuals (all related through asexual budding) form a colony, each inhabiting a single “box” (calcareous or membranous) within a communal skeleton. However, soft-tissue anatomy reveals that the resemblance is superficial: bryozoan zooids are triploblastic protostomes and filter-feed using a lophophore structure; while cnidarian polyps are diploblastic organisms and use stinging cells to catch prey. In the absence of soft-tissue details (as is the case in the fossil record), the most obvious difference is size: bryozoan zooecia are tiny, while coral calices are often much larger. Bryozoan zooecia are sometimes covered by a mineralized “roof” with a small hole or operculum serving as an access hatch to the surrounding seawater, while the corallites of colonial corals are “open-topped”, with septa, dissepiments, etc., often visible.

Bryozoans are very common in the fossil record from as long ago as the Ordovician, and are still abundant today. They exhibit a variety of colonial growth forms: encrusting, massive, erect (plate-like or arborescent), and free-living. Each of these growth forms dates back to the Ordovician (although free-living forms have undergone a major radiation since the Cretaceous), and each has convergently evolved numerous times in independent lineages. Erect bryozoan colonies could form a robust framework and baffle sediment, and so sometimes contributed to bioherm formation.

Stenolaemates, characterized by zooids which continue to grow in size throughout the development of the colony, dominate the fossil record of bryozoans through the Paleozoic (with five diverse orders; B1) and the Mesozoic (with the sole post-Triassic order [Cyclostomata] being very diverse until the end of the Cretaceous). Gymnolaemate bryozoans (particularly the cheilostomes) are the dominant group through the Cenozoic and in the Recent. The size of gymnolaemate zooids is fixed early in colony development. In this lab we will see representatives of several stenolaemate groups, highlighting the colony growth forms which repeatedly evolved across each.

## B2: Cystoporate stenolaemates.

*Fistulipora* exhibits encrusting and massive colony growth forms, and is the commonest cystoporate genus. It ranges from the Silurian to the Permian. It is frequently found encrusting bioclasts such as brachiopods, crinoids, and corals.

## B3: Cryptostome stenolaemates.

This specimen of *Escharopora* exhibits a blade-like morphology, and is an example of an erect colony.

## B4: Trepostome stenolaemates.

Trepostomes are a diverse and important stenolaemate group ranging from the Ordovician to Triassic. They are particularly common in Ordovician and Silurian rocks. Their thick-walled zooecia resulted in sturdy, well-calcified colonies, and have earned the trepostomes the common name of "stony bryozoans". The zooecial walls and growth of the zooids are well seen in the thin-section (B4a; compare to Clarkson, 1998, fig. 6.8).

The *Petigopora* colonies (B4b) are encrusting the brachial valve of brachiopod.
What kind of brachiopod are they encrusting?

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Why might the colonies be restricted to the brachial valve?

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*Spatiopora* (B4c) is another encrusting trepostome, here growing on an orthocone nautiloid. Note the development of prominent parallel ridges (monticules) in the colony.

*Amplexopora* (B4d) is a trepostome which develops a massive colony growth form. The polished surface reveals the growth history of the colony. Note the small mounds (monticules) on the colony surface. The feeding zooids were less densely packed (or even absent) on the summit of the monticules.

What purpose did the monticules serve?

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*Monticulipora* (B4e) and *Heterotrypa* (B4f) are also monticule-bearing trepostomes, but these genera exhibit a plate-like growth form.

*Hallopora* (B4g) is a common Ordovician and Silurian trepostome with an erect, branching growth form (see also B4h).

## B5: Fenestrate stenolaemates.

Fenestrate bryozoans ranged from the Early Ordovician to the Late Permian. Their colonies formed a net-like mesh frame, wrapped into a funnel, half-funnel, or fan shape and standing erect above the sediment surface (see Clarkson, 1998, fig. 6.13). Rows of zooecia formed the vertical branches of the mesh, and narrow cross-bars acted as struts holding the branches apart. Fenestrae ("windows") between the branches and bars permitted movement of water from one surface of the colony to the other. The zooids around the fenestrae filtered the water for food.

Fenestellids such as *Fenestella* (B5a) and *Polypora* (B5b) are abundant in the Late Paleozoic, and typify the fenestrate morphology. Use a hand lens to examine their anatomy, and compare this to Clarkson (1998, fig. 6.13e). Can you see the zooecial apertures from which the zooids fed?

*Archimedes* (B5c, d) is a famous and unmistakable Carboniferous fenestellid in which the mesh-like sheets were coiled into a helical spiral. See Clarkson (1998, p. 151) for a discussion of this amazing bryozoan.

## PART C: BRACHIOPOD AND BIVALVE DIVERSITY THROUGH TIME.

One of the major contributions of paleontology to the evolutionary sciences is the documentation of how the diversity of groups has changed through “deep time”. Indeed, much of this course deals with studying the diversity patterns of particular invertebrate groups through the Phanerozoic, and with investigating potential evolutionary explanations for the dynamic patterns detected.

In this portion of the lab, you will utilize an important electronic paleontological database (the Paleobiology Database) to generate, analyze, and interpret the Phanerozoic diversity pattern for brachiopods. You will also contrast this pattern with that for bivalves, and attempt to interpret the differences.

### 1. BACKGROUND TO THE PALEOBIOLOGY DATABASE (PBDB)

The PBDB represents an effort among the paleontological community to create a permanent digital repository of paleontological data and to provide tools for analyzing these data. The data are collections-based, which means that each record consists of a number of co-occurring taxa and various information on the geologic context in which the fossil taxa occur. To learn more about the structure of the PBDB, go to the URL (http://www.paleodb.org) and select “Frequently Asked Questions”.

To see an example of a collection, select “Collections” near the top of the home page; this will take you to a search form. Fill in the following fields:

*Taxon name: Brachiopoda
*Country: Morocco
*Oldest time interval: Devonian

Press the “Search collections” button near the bottom of the page. A list of collections will be generated. Click on the number of one or more of the collections. Survey the kinds of information included in the geologic context, and scan the taxonomic list. Note that when data are entered, only the genus (and optionally species) name needs to be entered. The higher taxonomic classification is generated dynamically via a series of look-up tables.

## 2. DATA DOWNLOAD

Here you will practice downloading data from the PBDB. From the PBDB home page click “Download data” under “Search our data”. This will take you to the “Download request form”. Use the defaults except for the following:

*VERY IMPORTANT: Enter your name (or a pseudonym) under “Your name”; this will ensure that a file is created on the server that you can later analyze with database tools. Note that if you are going to do more than one download (which you will do for this lab) you should select a different pseudonym for each download, so that each one will be uniquely identified with a particular download.

*Under “Research group or project” select “Marine Invertebrate”.

*Under “Name of taxon” type in “Brachiopoda”.

*Where the form reads “Lump occurrences of the same genus from the same collection?” select “yes, lump them”. This means that a genus is scored as occurring once in a collection regardless of how many species of that genus may be present.

*Scroll to the bottom of the form and click “Create data set”.

What are the pros and cons of the choice regarding lumping genus occurrences?

A dataset will be saved on the server that contains a list of records with the collection number, genus name, and time interval. The time intervals represent an operational subdivision of the Phanerozoic. See the accompanying table for approximate equivalents in terms of international standard stages.

## 3. TRACKING BRACHIOPOD DIVERSITY THROUGH TIME

We will now use this data file to plot a raw diversity curve for brachiopods through time. The first step of this analysis will be to tabulate the number of genera sampled in each time interval.

Go to the PBDB home page and select “Generate diversity curve data” under “Analyze our data”. This will take you to the “Diversity curve request form”. Be sure to enter the same name (pseudonym) from the data download so that the appropriate file will be processed. For “Diversity measure to report” select “sampled-in-bin”. This is a simple measure that tabulates the number of taxa actually recorded in a time interval (not including those whose presence is inferred because they are known before and after that time interval).

What are the pros and cons of using this measure of diversity?

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Scroll to the bottom of the page and click “Submit”. Soon a “diversity curve report” will be generated. Ignore most of the columns except the <u>Interval</u> name, the <u>Sampled genera</u> (i.e., the total number of genera sampled within that time interval), and the <u>Occurrences</u> (i.e., the total number of occurrences of those genera in all fossiliferous collections sampled within that time interval). To access these data in a machine-readable form, scroll to the bottom of the page and click “curvedata.csv”. This will load the table data in comma-separated format, which can be saved into Excel and other spreadsheet programs. Save a copy of this file on the lab computer, with a name you can remember, as it will be used later.

Plot a graph of brachiopod diversity (Sampled genera, y-axis) against time (Interval, x-axis). Describe the plot.

## 4. DATA ANALYSIS

There are many biases involved in tabulating the raw diversity plots such as the one just generated. Here you will use a few simple tools to explore how the amount of paleontological data available may influence perceived biodiversity.

Using the data file just created, plot a graph comparing the number of occurrences to sampled genera (with occurrences on the x-axis and sampled genera on the y-axis, where each point is a time interval). What pattern emerges?

What could this pattern suggest in terms of the relationships between true diversity, number of fossiliferous collections, and sampled diversity?

Next perform subsampling (rarefaction) analysis. This is a statistical procedure that allows prediction of how many genera would probably have been found if fewer occurrences had been sampled. Suppose there are S taxa with $N_1$, $N_2$, ..., $N_S$ occurrences, and that the total number of occurrences is given by N. Then the expected number of taxa found in a sample of n occurrences (n<N) is given by (Raup, 1975):

$$E(S_n)= \sum_{i=1}^{S} \left[1-\left(\left(N-N_i/n\right)/\left(N/n\right)\right)\right]$$

To compute the rarefaction, return to the Diversity curve request form. Again enter your name or pseudonym and select sampled-in-bin for the diversity measure. For "Subsampling method" select "classical rarefaction". This assumes that the total number of occurrences within a given time interval is a reasonable measure of sampling effort (each occurrence represents the presence of a genus in a collection).

Discuss the merits of this assumption, in general and in light of your previous comparison between occurrences and sampled genera.

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*For "Exact number of items" choose 3000. This means that subsampling can be performed only for those time intervals that have 3000 or more occurrences. This number is arbitrary, but is chosen to allow you to compare just a few intervals that meet this quota.

*For "Number of subsampling trials" choose 100. (This may take some time to compute, but the larger the number the more stable the estimate of rarefied diversity.)

*For "Intermediate number of items to report" select "1,1.4,2,2.8...". This will give you a larger number of points than the default and will produce a smoother curve.

Scroll to the bottom and click “Submit”. This will return another diversity curve report. The top half will show the raw data and the bottom half the mean rarefied diversity. Only those intervals that meet the quota (number of items chosen) will show a non-zero value.

Near the bottom of the page will be a link to the subsampling results (“subcurve.tab”). Click this to produce a table of $E(S_n)$ for those intervals that meet the quota. (This is a tab-delimited file that can also be saved as a spreadsheet-readable table.) A rarefaction curve can be constructed by plotting n (the number of occurrences) against $E(S_n)$.

Plot a rarefaction curve for each of the time intervals in the data file. Interpretation is easier if data for all intervals are drawn to the same scale (e.g., on the same plot). Compare the slopes of the rarefaction curves for each time interval.

What can you conclude about relative diversity among these time intervals from the shapes of the rarefaction curves for the intervals that meet the quota?

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## **5. BRACHIOPOD VERSUS BIVALVE DIVERSITY**

In this exercise you will compare the diversity history of two major groups of shelly marine invertebrates: brachiopods and bivalves.

You have already downloaded the brachiopod diversity history and have saved it. Now go to the download request page and repeat everything you did for brachiopods, but this time specify “Bivalvia” for the taxon name. Be sure to use a different pseudonym so that your previous files do not get overwritten on the server.

Go to the diversity curve request form and generate a history of sampled-in-bin diversity for bivalves. Ignore the parts of the request form that deal with subsampling. Click “Submit” to generate the diversity curve report. Click on the “curvedata.csv” link to load the data from this report. Save these data on the lab computer, being sure to use a different file name from the one you used for the brachiopod data.

Compare the Phanerozoic diversity history of bivalves and brachiopods. Discuss the similarities and differences.

It has been suggested that these two groups are sufficiently similar ecologically that they may be regarded as competitors, and moreover that bivalves may have diversified "at the expense of" brachiopods. Discuss the plausibility of this idea, both in principle and with respect to the diversity data you have generated.