Lab 5: Mollusks

Name: ______________________________

Section: ______________________________

AIMS:

This lab will introduce you to the eutrochozoan protostome phylum Mollusca. You will become familiar with the basic anatomy of the three mollusk groups which are most abundant in the fossil record: gastropods, bivalves, and cephalopods. 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 identify "mystery fossils". By the end of this lab, you should have a good knowledge of the anatomy of the three most diverse groups of mollusks, an appreciation for how organismal form reflects function, and an understanding of how innovations in ecology and anatomy resulted in the evolutionary radiation of each group.

INTRODUCTION:

Mollusks are unsegmented protostomes with a trochophore larval stage during early development, and are one of the most diverse metazoan phyla. The basic mollusk body plan consists of a muscular foot, a visceral mass (containing the digestive tract and associated organs), a mantle cavity containing gills, a radula for feeding, and a calcareous shell protecting the visceral mass. The shell has a high preservation potential, and mollusks are common in the fossil record.

There may be as many as ten classes of mollusks (depending on which text book you read). Each class has modified the basic body plan to some degree, allowing the group to radiate into different ecological niches. We will here focus on just three classes, which are common as fossils and exemplify the evolutionary diversification of mollusks.

PART A: GASTROPODA.

Broadly characterized as the slugs and snails, the Gastropoda is a mollusk class defined by having a single-chambered shell (often coiled), and undergoing torsion during development so that the mantle cavity lies above the head in the mature organism. A few gastropod lineages have evolved chambered shells (similar at first glance to those of cephalopod mollusks), but all such gastropods lack a siphuncle. Gastropods range from the Cambrian to the Recent, and today include more than half of all mollusk species. There are three subclasses: the Prosobranchiata (marine or freshwater snails), the Opisthobranchiata (sea hares, pteropods, and nudibranchs), and the Pulmonata (land-living snails and slugs, with some secondarily aquatic forms). Of these groups, the prosobranchs have the best fossil record and will be the focus of this lab.

Prosobranchs are aquatic (marine or freshwater) snails with one or two gills in the mantle cavity. The prosobranchs evolved in the Early Cambrian, and are very abundant today. The group is remarkably diverse, including limpets, winkles, topshells, whelks, cone shells, cowries, mudsnails, slipper limpets, and more. The evolutionary radiation of gastropods, particularly through the Mesozoic and Cenozoic, is largely attributable to their diversification into novel feeding habits.

THE EARLIEST GASTROPODS?

A1: Helcionellids and pelagiellids.

These tiny shells occur in the “Small Shelly Fauna”, a diverse assemblage of shelly fossils of equivocal affinities found in Lower Cambrian rocks around the world. Although the shells of helcionellids and pelagiellids resemble gastropod shells it is uncertain as to whether the organisms underwent torsion. Debates rage as to whether these animals represent the earliest gastropods or belong to other mollusk groups such as the Monoplacophora.

PALEOZOIC PROSOBRANCHS:

The diversity and disparity of gastropods during the Paleozoic was relatively low. This is no doubt associated with the relatively limited range of life modes these organisms exploited: grazing, deposit feeding, and parasitic or coprophagous habits had evolved, but suspension feeding and carnivory was rare or absent. Most species were primitive, aspidobranch gill-bearing archaeogastropods, although mesogastropods (with more efficient pectinibranch gills) were present from the Ordovician.

A2: Planispiral forms: *Euomphalus*.

Euomphalids such as *Euomphalus* (see also *Straparollus*) are relatively common Paleozoic archaeogastropods.

A3: Low-spired forms: *Straparollus*, *Turbanopsis*, and *Bembexia*.

A4: Moderately high-spired forms: *Cyclonema*, *Naticopsis*, and *Glabrocingulum*.

The evolution of the pleurotomarian grazer *Glabrocingulum* has been extensively studied (see paper by Schindel, 1982).

A5: High-spired forms: *Murchisonia* and *Soleniscus*.

A6: *Platyceras*.

Platyceras is a long-ranging archaeogastropod genus, spanning from the Silurian to Carboniferous. It is often found attached to a host organism (such as the calyx of a crinoid or blastoid).

Examine the literature with the specimens. How is *Platyceras* thought to have fed?

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A7: Bellerophontids: *Euphemites* and *Bellerophon*.

The evolutionary affinities of this common and diverse (over 70 genera, ranging from the Cambrian to the Triassic) group of extinct marine snails are highly controversial, and again center on the question of whether or not they underwent torsion. Some workers consider them to be true prosobranch gastropods, while others consider them to be more closely related to monoplacophoran mollusks.

A8: *Maclurites.*

Macluritid archaeogastropods resemble euomphalids, and are only known from Paleozoic rocks. It has been argued that macluritids were sedentary suspension-feeders which, if true, would mean that they were perhaps the earliest gastropods to invade this particular feeding niche.

What suggests that *Maclurites* was a sedentary rather than mobile feeder?

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POST-PALEOZOIC PROSOBRANCHS:

The establishment of suspension feeding and carnivory among gastropods in the Mesozoic resulted in a sustained evolutionary radiation which persists to the present day. Carnivory in particular was a key factor in this diversification, initiating an arms race between the carnivores and their gastropod prey. In the Cretaceous the carnivorous neogastropod clade evolved from a mesogastropod ancestor, and have radiated at a remarkable rate ever since. Other predatory animal groups such as fish, malacostracan crustaceans, and asteroid echinoderms (starfish) were diversifying at this time, and also applied strong selection pressure for defensive morphological and behavioral adaptations among gastropods. The shells of post-Paleozoic prosobranchs are often highly ornamented and spiny.

How would spines deter carnivorous gastropods?

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Specimens A9 to A17 highlight the range of feeding modes among post-Paleozoic gastropods, and introduce you to some of the most important gastropod groups.

A9: Grazing gastropods: limpets, keyhole limpets, ormers, and topshells.

Limpets (A9a), keyhole limpets (A9b), ormers (also called abalones, A9c), and the spire-shelled topshells (A9d-g) are archaeogastropods which graze algae. Algal grazing is an ancient habit, exploited throughout gastropod history. Gastropods bearing patelliform shells are restricted to feeding from firm substrate surfaces (e.g., rocks).

What is the function of the holes in the shells of keyhole limpets and ormers?

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What is the internal layer of the ormer shell made of?

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A10: Grazing gastropods: Cowries.

Cowries are post-Paleozoic mesogastropods which graze on sessile animals such as cnidarians, an ancient habit which is shared by the helically-coiled pleurotomarian archaeogastropods (Cambrian to Recent; e.g., *Glabrocingulum*, A4).

A11: Deposit-feeding gastropods: Mudsnails.

Another ancient feeding habit, established during the Paleozoic.

A12: Suspension-feeding gastropods: Slipper limpets.

Slipper limpets (A12a-c) are post-Paleozoic suspension-feeding mesogastropods which stack into piles during reproduction. Suspension-feeding was rare or absent among Paleozoic gastropods (although see A8). Neritids (A12d) are archaeogastropods which have converged upon a morphology strikingly similar to slipper limpets.

A13: Suspension-feeding gastropods: Vermetids.

Vermetiform gastropods are extremely unusual gastropods: they are sessile, and their shells are only loosely coiled. Indeed, in shape vermetid shells closely resemble the tubes of sessile serpulid worms (hence the name of the gastropods): a classic case of convergent evolution between very different animal groups.

What is the advantage of the vermetid shell morphology to such a mode of life?

A14: Carnivorous mesogastropods: Naticids.

Naticids are carnivorous mesogastropods which have drilled holes through the shells of their unfortunate gastropod prey since the Mesozoic. Their paleobiology, evolutionary history, and evolutionary impact on prey have been well studied (see the literature).

A15: Carnivorous neogastropods: Stenoglossans.

The Neogastropoda is a clade of carnivorous gastropods which evolved in the Cretaceous and has undergone a rapid diversification ever since. They retain the derived pectinibranch gill of their mesogastropod ancestors, and are characterized by development of tube-like extensions (siphons) sprouting from the shell near the aperture.

What is the function of the neogastropod siphon?

Stenoglossans, such as olive shells (A15a-b), and whelks and dog-whelks (A15c-d), and the high-spired, burrowing terebrids (A15e) are carnivores which do not utilize the toxins of their toxoglossan neogastropod relatives. Muricid stenoglossans (A15f) are the notorious “killer drillers” of the post-Paleozoic. Muricids make characteristic bore-holes in the shells of their gastropod or bivalve prey, which provides evidence of the presence of muricids in paleocommunities even when their body fossils are not found. It may take several hours or even days for the muricid to drill through the shell, before it can inject a muscle relaxant into the victim and thus access the flesh more easily.

Draw a muricid shell.

A16: Carnivorous neogastropods: Toxoglossans.

Toxoglossan neogastropods (cone shells) have evolved potent poisons which are injected into their prey, sometimes by means of extensible "harpoons". Toxoglossans originated and radiated in the Cenozoic.

A17: Turritellids.

Turritellids are deposit-feeding and suspension-feeding mesogastropods which originated in the Cretaceous. They are very diverse, with approximately 500 extant species and 1000 fossil species described. They are found in a wide range of environments, from shoreline (littoral) to deep-water (continental slope) settings, and are often very abundant (indeed, some Tertiary limestones are made almost exclusively of turritellid shells). Their abundance has made them targets for carnivores, and specimens bearing drill-holes are common.

Draw a turritellid.

PART B: BIVALVIA.

Bivalves (also called clams, pelecypods, or lamellibranchs) are a diverse group of mollusks which have evolved a filter-feeding mode of life. Their gills have become hugely enlarged, and serve in both respiration and filtering the inhalent water in the mantle cavity. With the evolution of a filter-feeding mode of life, bivalves have lost the radula and bear no real head. The muscular foot is often huge and inflatable, aiding the infaunal bivalves in digging burrows. The calcareous shell of bivalves consists of two symmetrical valves, articulated along a hinge line and closed by adductor muscles. A rubbery ligament opens the valves when the adductors relax, and bivalves have no diductor muscles.

The evolutionary history of bivalves is very similar to that of gastropods: the earliest bivalves are found in Lower Cambrian rocks, and although their Paleozoic diversity is respectable they underwent a major and sustained radiation in the Mesozoic and Cenozoic. However, bivalves achieved this diversification in a very different way than gastropods. Whereas gastropods evolved many different feeding habits (see above), bivalves remain primarily filter-feeders (although deposit-feeding and even predatory habits have evolved in some lineages) and have radiated by exploiting many ecological niches from which they could filter-feed.

B1: Basic bivalve shell morphology.

Examine these shells to familiarize yourself with basic bivalve shell morphology. You should be able to see the umbo, teeth (both taxodont and heterodont tooth types are represented), ligament pit, muscle scars, and pallial line. Can you identify left from right valves?

Draw and label one of the valves.

What does the pallial line represent?

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B2: Shallow burrowers.

Shallow burrowers are characterized by having only small or no siphons, and therefore only a tiny or no pallial sinus. This is an ancient mode of life, ranging back at least as far as the Ordovician.

B2a: *Eucrassatella* (Recent).

B2b: Arcoid (Pliocene).

Modern *Arca* is a byssally attached epifaunal bivalve, but other arcoids are shallow burrowers.

B2c: *Venericardia* (Eocene).

B2d: *Trigonia* (Cretaceous).

Trigoniids were highly successful non-siphonate shallow burrowers until their almost total extinction at the end of the Cretaceous. They are represented by only one extant genus, *Neotrigonia*. They are characteristically sub-trigonal and prominently ornamented.

B3: Deep burrowers.

With the evolution of siphons (from folded mantle tissue) in the late Paleozoic, bivalves were able to filter-feed from well below the sediment surface. Deep burrowing became very common in the Mesozoic.

B3a: *Mercenaria* (Recent).

A moderately deep burrower with a respectably sized pallial sinus.

B3b: Tellinacean.

A deep burrower with a large pallial sinus.

What kind of teeth does this bivalve possess?

B3c: *Panopea* (Miocene/Pliocene).

This huge bivalve can filter-feed from up to a meter or so below the sediment surface. It has a permanent gape between the valves on account of its huge siphons. Modern *Panopea* bivalves are given the common name “geoduck” in the Pacific Northwest.

B3d,e: Razor shells (*Tegula* and *Solen*).

These bivalves with streamlined, blade-shaped shells can burrow rapidly. Like *Panopea*, they have a permanent gape.

B4: Boring bivalves.

These bivalves can excavate a permanent burrow in a hard substrate such as rock or wood. The habit has evolved at least nine times since the early Paleozoic.

What is the adaptive significance of the thin shell of this pholid?

B5: Semi-infaunal bivalves.

Semi-infaunal bivalves filter-feed while partially buried in the sediment.

What suggests that this *Pinna* specimen was semi-infaunal?

B6: Byssally attached bivalves.

Mussels (*Mytilus*, B6a) and some scallops (e.g., *Pteria*, B6b) are epifaunal, attaching themselves to a substrate by means of collagenous byssal threads.

What is the function of the extended "ears" of the *Pteria* shell?

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B7: Cemented bivalves.

Oysters (*Ostrea*, B7a-b) are epifaunal bivalves which cement their left valve to a hard substrate by means of a calcareous "glue". Note the irregular external surface of the shell, resulting from the need to follow the contours of the rock to which they are attached.

Rudists (Order Hippuritoidea; B7c-e) are an extinct group of heterodont bivalves which were important members of Jurassic and Cretaceous marine ecosystems. Like oysters, they cemented themselves to firm substrates, and were able to form bioherms (thickets and reefs) in the Cretaceous. Their bizarre morphology, with highly asymmetrical valves, can be confusing: it is hard to tell they are bivalves!

Draw a rudist bivalve.

B8: Free-lying (reclining) bivalves.

Spondylus (B8a) is a Cretaceous to Recent genus characterized by its spines. Some *Spondylus* species cement themselves to firm substrates (e.g, in coral reefs), and the spines are defensive. But other species are free-lying (reclining) on soft sediments, and the spines are used as “snowshoes” to avoid sinking in to the sediment, or as “spears” to anchor the shell into the sediment.

The “Devil’s Toenail” bivalves *Gryphaea* (B8b; Triassic to Jurassic) and *Exogyra* (B8c-e; Cretaceous) are fossil oysters which evolved a reclining mode of life, resting in the sediment. The thick left valve was heavy enough to prevent overturning of the organism, which would have been fatal. The evolutionary history of the *Gryphaea* lineage has been studied in great detail.

Draw *Gryphaea* or *Exogyra*.

B9: Swimming bivalves.

Some scallops (e.g., *Pecten*, B9a; *Lyropecten*, B9b; *Aviculopecten*, B9c) are able to flap their valves open and closed with sufficient rigor to swim. This activity is very energetic, and is typically only used to escape predators. When not swimming, such scallops rest free on the sediment surface.

How many adductor muscles does *Pecten* have?

What is this condition called?

Posidonians (e.g., *Dunbarella*, B9d) are an extinct group of bivalves (Devonian to Cretaceous) which are commonly found in black shales typical of low-oxygen depositional conditions. This distribution, plus their paper-thin valves, has led to speculation that they were permanently nektonic (swimming), and settled to the inhospitable deep ocean basins upon death. However, some workers consider that posidonians were adapted to life on the seafloor in low-oxygen conditions, and were only facultative swimmers.

How are these *Dunbarella* specimens preserved?

B10: Deposit-feeding bivalves.

Nuculoids bivalves evolved a deposit-feeding mode of life. They use their labial palps to extract organic detritus from the sediment. The habit is ancient, ranging back to the Ordovician, and such deposit-feeders can be locally abundant in some communities.

What kind of dentition do nuculoids possess?

B11: *Tridacna*.

This cardiacean is an epifaunal filter-feeder, but has established a symbiotic relationship with photosynthesizing zooxanthellae. These provide additional nutrients to the bivalve.

B12: *Neithea* (Cretaceous).

What mode of life do you infer for this scallop? Compare to the specimens examined above for ideas!

PART C: CEPHALOPODA.

Cephalopods are certainly the most complex mollusks, and arguably the most complex invertebrates. They have evolved a predatory mode of life, actively chasing down prey. This swimming ability is possible through the complex morphology of the shell, which is multi-chambered. The organism inhabits only the end chamber (anteriormost). Smaller, more posterior chambers previously occupied by the organism (at an earlier stage in its life) are sealed off by septa, and are commonly gas-filled. This gives the shell buoyancy. Counterbalancing cameral fluids or mineral deposits in these chambers can add weight to the shell, thus allowing some control over buoyancy. A fleshy string of tissue (the siphuncle) extends from the organism back through the empty chambers, passing through the septal walls by means of a small hole (the septal neck). The siphuncle can absorb or release gas into the chambers, giving more control over buoyancy. Active swimming is achieved by muscular expulsion of water from the mantle cavity through the hyponome, a muscular tube which can be pointed in any direction: thus the organism can control the direction of locomotion while "jetting". There are three groups of cephalopods: the nautiloids, the ammonoids, and the coleids. All have a good fossil record.

Subclass Nautiloidea:

Nautiloids (Late Cambrian to Recent) possess four gills in the mantle cavity. The shell of nautiloids can be straight (orthocone), bent, or coiled, and the suture line (i.e., the connection between the septa and the outer wall of the shell) is simple. They were relatively diverse in the Paleozoic, but only one order (Nautilida) survived beyond the Triassic.

C1: *Nautilus* (Recent).

This is the famous living nautiloid, and has been intensively studied in terms of its life modes, functional morphology, and anatomy. It is an active predator and scavenger, swimming using its hyponome. Pressure changes in its empty shell chambers (controlled by the siphuncle) are too slow to control the typical daily vertical movement through the water column. A new extant nautiloid genus has recently been recognized.

Draw and label the shell of the Recent *Nautilus*.

C2: Coiled nautiloid (fossil).

Note the simple suture trace.

How can the suture line be visible in fossil cephalopods?

C3: Orthocone nautiloid (Ordovician).

These are examples of straight-shelled nautiloids. Such orthocone nautiloids ranged from the Ordovician to the Triassic, and were the bane of trilobites. Note the tapering shape of the shell and the simple sutures.

Subclass Coleoidea:

Coleoids (?Devonian or Carboniferous to Recent) include the familiar squid, octopuses, and cuttlefish, and the extinct belemnites. Coleoids have an internalized chambered shell, which may be straight or coiled (see the shell of the squid Recent *Spirula*, C4). In many coleoid groups the shell is greatly reduced in size, and may be absent altogether. Two gills are present.

C5: Belemnites.

These cigar-shaped shells are the preserved remains of the internal shell of belemnites, an extinct group of coleoids which ranged from the Devonian to the Cretaceous. The guard, preserved here, surrounded the phragmacone (which was housed in the conical hollow or alveolus of the guard); while the pro-ostracum (not preserved here) was a tongue-like projection from the front of the guard which covered the anterior part of the body. See pages 254-255 of the Clarkson textbook for more details.

Subclass Ammonoidea:

Ammonoids (Early Devonian to Late Cretaceous) are the most familiar fossil cephalopods, and are widely used for biostratigraphic zonation of the Mesozoic. It is unknown how many gills ammonoids possessed, but the shell is coiled, and the suture line is more complex than that of the nautiloids.

C6: Goniatite.

Muensteroceras (Early Carboniferous) shows the typical goniatitic suture, with pointed lobes and rounded saddles.

Draw a goniatitic suture line.

C7: Prolecanitids.

These Upper Paleozoic and basal Triassic ammonoids show a trend towards increasing sutural complexity, demonstrating the phylogenetic link between goniatites and ceratites, as discussed in this literature.

C8: Ceratites.

These Late Permian and Triassic ammonoids evolved from a prolecanitid ancestor and ultimately gave rise to the true ammonites in the Triassic.
Draw a ceratitic suture line.

C9: Ammonites.

Ammonites (Triassic to end Cretaceous), such as *Placenticeras* (C9a, mid Cretaceous) have highly complex suture lines as a result of their convoluted septal walls (see *Cardioceras*, C9b). As with all ammonoids, the outside of the shell may be variously ornamented with ribs, tubercles, growth lines, knobs, spines, and keels (e.g., *Cosmoceras*, C9c). Shell shape is determined by factors such as the rate of whorl expansion, whorl outline, and width of the umbilicus.
Draw an ammonitic suture line.

C10: Heteromorph ammonites.

Some ammonites evolutionarily “uncoiled” into bizarre shapes. *Turrilites* is a form which evolved a high-spired coiled shell similar to some gastropods (e.g., the turritellids; A17).

PART D: IDENTIFYING MYSTERY FOSSILS.

One of the challenges of paleontology is to identify specimens accurately, particularly when you may not be too familiar with the group. Thankfully, identification is made easier by extensive databases with “reference specimens”, against which a mystery fossil can be compared. Museum collections have traditionally been the most widely used databases: experts frequently visit museums to make use of their systematic collections. However, these days many museums are publishing systematic databases on CD-ROM for mass distribution: the museum collections now come to the worker! PaleoBase 2.0 is one such systematic database, produced by the British Museum of Natural History in London. We will use this database to identify four “mystery specimens” (all fossil ammonoids).

First, open PaleoBase 2.0 by double-clicking on its icon on the desktop (labeled “PBMacro2.data”). Two green windows appear, one stacked on top of the other. Move the smaller window to the corner of the screen, and click on “Glossary”. Another window appears with glossary files for several mollusk groups. Double click on the “Ammonoid Glossary” option, and a dictionary of morphological terms applied to ammonoids appears. You will use this dictionary, along with pages 238-242 in the Clarkson textbook, to describe features of each of the four fossil ammonoids.

Next, activate the main “PaleoBase” window by clicking on it. Under the “File” pull-down menu, highlight the “Groups” option. A list of 318 mollusk genera appears. You now need to search this database to help you identify the mystery specimens. Under the “Search” pull-down menu, highlight “Search Step by Step”. A search window opens. Click on the green box (top right) which says “318”, then click on the words “All Fossil Groups” to the left. Specify “Molluscs” then “Ammonoids” in the submenus which appear. The green box now says “82”: this means there are 82 ammonoid genera in the database. Somewhere in those 82 names is the correct name for each of the mystery fossils!

You must now refine the search to help you put a name to each of the four mystery ammonoid species. Under the “Morphological Characters 1” part of the window, you will see a range of morphological features such as “Conch Shape”, “Suture Type”, etc. Clicking on any of these pulls up a submenu with a list of descriptive terms (described in the glossary file). Thus, if you think that the mystery fossil has an ammonitic suture pattern, highlight “Ammonitic” under the “Suture Type” feature. Examine each fossil carefully, and specify two or three of the morphological features in the search window. Then click on the magnifying glass icon (top left) to search the database for ammonoid genera which exhibit these morphological attributes. Another list appears, this time (hopefully) much sorter than the 318 genera you saw before. Listed next to each name is the stratigraphic range of the genus. You can use this to narrow your search options even more.

If more than one genus name is listed, you can double click on the genus name to see pictures of the genus (these can be enlarged by clicking on the thumbnail images and selecting “Detail” from the pop-up menu: as always, clicking on the box with the red arrow will send you back to the previous page). Beneath the thumbnail images is a “Description and Remarks” window with written comments on the genus.

Remember that to find a satisfactory identification for a mystery fossil you must find a genus in the database which matches the morphology AND stratigraphic range of the mystery fossil.

D1: Early Jurassic ammonoid.

D2: Late Cretaceous ammonoid.

D3: Early Jurassic ammonoid.

D4: Late Cretaceous ammonoid.
