Chapter 9B
THE FOSSIL IS PART OF THE ROCK

BRACHIOPODS
(Phylum Brachiopoda)

Time span: Early Cambrian to now

Organism
The soft body is enclosed in a shell consisting of two valves (Figure 9B-1; Clarkson, E.N.K., 1979, Invertebrate Palaeontology and Evolution: George Allen & Unwin, 323 p. Figure 7.1 and Figure 7.2). The shell is usually fixed to the sea floor by a stalk (the pedicle) that protrudes through an opening (the pedicle foramen) in one of the valves, called the pedicle valve. The other, smaller, valve is called the brachial valve.

Brachiopods are filter feeders: most of the shell cavity is filled with a long, looped band called the lophophore on which are sticky filaments with cilia that wave to create a current through the shell cavity. Small food particles are caught by the filaments and passed to a simple gut.

Skeleton
The valves are hinged or articulated for a short or long distance along one edge. Unlike mollusks, the valves have a symmetry plane that bisects both valves perpendicular to the hinge line; the two valves are fundamentally different in shape, not just mirror images.

The valves are usually robust, and they have always been of calcite, so they preserve relatively well. Some brachiopods have chitinophosphatic instead of calcareous shells. Size varies from less than a centimeter to several centimeters. Valve shape varies widely. Ribs and growth ridges are of varying prominence.

Classification
Brachiopods are subdivided into two classes, Inarticulata and Articulata. The inarticulates are those with chitinophosphatic shells. They're not very abundant in the fossil record and they're not very useful stratigraphically, but they're interesting because they're so well adapted and evolutionarily conservative: one genus, Lingula, has been around since the Early Cambrian!

The articulates are subdivided into six orders, whose names we won't burden you with. Figure 9B-2 (Clarkson, E.N.K., 1979, Invertebrate Palaeontology and Evolution: George Allen & Unwin, 323 p. Figure 7.13) shows a variety of different forms. These orders have various time spans, and varying degrees of importance during their time spans. Only three have not become extinct.
**Importance**

Brachiopods were a major component of invertebrate faunas in the past, especially in the Paleozoic; their heyday was from the beginning of the Ordovician to the end of the Permian. They are of only minor importance now. The shells are usually well preserved, and they are stratigraphically important, especially in the mid-Paleozoic.

**Habitat**

Brachiopods are attached bottom dwellers, on various sediment types; they are exclusively marine, usually shallow.

**Comments**

Brachiopods are the most common fossil you'll find in many Lower and Middle Paleozoic rocks. Warning: you can see the same brachiopod in various views, because there's an inner and an outer surface to each of the two valves, and you see each of the four surfaces in either positive or negative. Sometimes just the cemented filling (called a steinkern) of the still-articulated shell is preserved; this looks like a shell itself, but it's the negative of both the inner surfaces.
BRYozoANS
(Phylum Bryozoa)

Time span: Late Cambrian to now

Organism

Bryozoans are colonial marine invertebrates. The individual organism, called a zooid, is in the shape of a cylinder with a ring of retractable tentacles coming out of the top (Figure 9B-3; Clarkson, E.N.K., 1979, Invertebrate Paleontology and Evolution: George Allen & Unwin, 323 p. Figure 6.1 and Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 7_41). Cilia on the tentacles wave to create a current toward the base of the tentacles. Plankton brought in by this current are caught by the tentacles and carried down into the gut within the cylindrical body.

The zooid is housed in a skeleton called the cystid, which may or may not be mineralized. The zooids always live in a closely packed colony called a zoarium.

Bryozoans superficially resemble colonial corals, but they are more advanced physiologically. They have some fundamental physiological similarities to brachiopods (but their fossil record looks entirely different).

Skeleton

The calcareous colonies take on a wide variety of forms: they look like cups, leaves, branches, tufts, globs, and even spirals (Figure 9B-4; Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 7_44). Usually you see fragments of colonies rather than whole colonies.

Classification

Bryozoans are divided into three classes, two of which appeared in the Ordovician and one in the Mesozoic. One of the orders of the class Stenolaemata were the dominant bryozoans in the Paleozoic, and another order of that class were the dominant bryozoans in the Mesozoic.

Importance

Bryozoans are fairly abundant throughout the fossil record, and you'll see some rocks that contain mostly fragments of bryozoan colonies, but they're not as common as some other kinds of fossils. The species are mostly wide-ranging in time and therefore not very useful stratigraphically.

Habitat

Today, bryozoans are found at all depths from the shoreline down to trenches, but they're most abundant in shallow water. They need a fairly firm substrate on which to anchor and grow colonies, so they're not common on muddy bottoms. Strong currents and waves are destructive of the relatively fragile
colonies. Bryozoans are contributors to reefs, but they have never formed reefs themselves.
CEPHALOPODS
(Phylum Mollusca)

Time span: Late Cambrian to now

Organism
Cephalopods are mollusks that live in a single chambered shell. As with all the mollusks, the soft body has a mouth, an anus, and gills (Figure 9B-5; Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 10_55 and Clarkson, E.N.K., 1979, Invertebrate Palaeontology and Evolution: George Allen & Unwin, 323 p. Figure 8.20).

Cephalopods are the most advanced of mollusks: their brains are more highly developed and their sense organs are more specialized than in pelecypods or gastropods. They are predatory carnivores with a highly developed ability to swim.

Cephalopods have an effective means of maintaining buoyancy: the chambers, each containing both gas and water, are connected by a long tube, the siphuncle, though which water can be added or removed from the chambers to adjust the bulk density of the animal. The danger of implosion restricts cephalopods to the uppermost several hundred meters of the ocean.

Skeleton
Some cephalopods are coiled (usually tightly, and almost always planispirally; Figures 9B-5, 9B-6; Clarkson, E.N.K., 1979, Invertebrate Palaeontology and Evolution: George Allen & Unwin, 323 p. Figure 8.18) and others are straight (Figure 9B-7; Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 10_58) to somewhat curved, but the common element of all the shells is that they are made up of many chambers. New chambers are added at the outer end as the animal grows, and the animal lives in the outermost chamber.

The outer surface of the shell shows closely spaced growth lines, and the inner surface of the shell (which is often seen in fossils that are internal molds) is marked by sutures where the septa between adjacent chambers meets the shell wall.

Classification
A large number of different kinds of cephalopods, divided into three subclasses, developed during the Paleozoic. Most of these had straight or curved shells, although some were coiled. These are usually called nautiloids (one kind was the forerunner of the modern Nautilus), but it would be better to call them non-ammonoid cephalopods. All of these except the coiled forms that led to Nautilus became extinct by the end of the Paleozoic.

Cephalopods of another subclass, called ammonoids (often also called ammonites), became abundant in the Mesozoic. Ammonoids have beautiful planispirally coiled shells.
The only other geologically important group, the belemnites, with straight shells, belong to still another subclass; they evolved in the Late Paleozoic and became extinct in the Early Cenozoic.

**Habitat**

Cephalopods swim freely in the shallow waters of the open ocean, and the shell settles to the bottom after the organism dies. Since they do not live on the bottom, they can be geographically wide-ranging, and can be found in a variety of sediments, although fine sediment is the rule.

**Importance**

Cephalopods, especially nautiloids in the Paleozoic and ammonoids in the Mesozoic, are of enormous stratigraphic importance. They are among the very best index fossils, because the species tend to be short-ranging in time and long-ranging in space (See especially Figure 9B-7A).

**Comments**

Cephalopods are common enough in certain rock types to be useful, but they are not common as fossils. You're not nearly as likely to see a cephalopod as a brachiopod, a crinoid, or a pelecypod.
CORALS
(Phylum Cnidaria)

Time span: Early Cambrian to now

Organism
Cnidarians are the simplest of all true metazoans, although they're better organized than sponges, because their cells are organized into definite tissues. The sedentary organism, called the polyp, of the order of a centimeter across, has cells organized into just two layers, an outer ectoderm and an inner endoderm, with a jellylike structureless layer, the mesogloea, between them (Figure 9B-8; Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 4_11 and Figure 4_26). The body cavity, surrounded by a ring of tentacles, has only one opening, which serves as mouth and anus.

Some corals are solitary, others colonial. It's the colonial corals that are of greatest sedimentological importance.

Skeleton
The polyp sits in a basal skeleton called the corallum, generally cup-shaped or columnar. The lowermost cells of the organism secrete aragonite or calcite to build the corallum upward as time goes on. The corallum has an outer wall, the epitheca, within which are numerous septa parallel to the axis of the corallum and radiating outward.

The solitary corals are often shaped like horns or columns; the colonial corals take on a great variety of fanlike, branching, or tabular shapes.

Classification
Corals are one subclass, Zoantharia, of the class Anthozoa (including also sea anemones and sea pens), which is itself one of three classes of cnidarians, the others being Hydrozoa (hydroids and millepores) and Scyphozoa (jellyfish).

Corals are classified into four orders, three of which are very important in the fossil record: Rugosa (rugose corals), Cambrian to Triassic; Tabulata (tabulate corals), Cambrian to Permian; and Scleractinia (scleractinian corals), Triassic to now (Figure 9B-9; Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 4_39 and Figure 4_41).

θ Rugose corals: solitary (usually a curved horn, sometimes cylindrical) and colonial (many styles, but mostly branching, parallel-columnar, and massively packed).
θ Tabulate corals: always colonial; cylindrical, branching, massive.
θ Scleractinian corals: solitary (conical, cylindrical, horn-shaped) and colonial (columnar, massive, branching, and brain-shaped)

Habitat
The rugose corals lived unattached on the bottom. They seem to have preferred soft muddy bottoms. The colonies never grew to be very large, and these
corals were not reef-builders. The tabulate corals seem to have liked generally similar environments; they had no good means of attachment, so they didn't build large frameworks either. Paleozoic corals are commonly found in fine-grained limestones and calcareous mudstones. As you've already seen, the colonial kinds of scleractinians have built great reefs by attachment of the colonies to a hard substrate.

Importance
Corals are generally not very useful in correlation, but they tell us a lot about paleoecology. And, of course, the scleractinians have been the great reef-builders.

Comments
Corals, along with other members of this phylum (sea anemones, jellyfish, hydroids) used to be included in the phylum Coelenterata but are now thought to be a separate but related phylum.

Certain solitary rugose corals show fine growth ridges, a couple of hundred per centimeter, on the epithecal surface. These growth ridges are grouped into bands or annuli. The growth ridges reflect daily growth cycles, and the broader bands represent monthly and yearly cycles. Certain Devonian corals show that the year had just about 400 days then. Assuming that the year was of the same length, there must have been more and shorter days in the year during the Devonian! This is consistent with the idea that the Earth's rate of rotation has been slowing by tidal friction.
CRINOIDS
(Phylum Echinodermata)

Time span: Early Ordovician to now

Organism and Skeleton
Echinoderms, entirely marine, are a phylum of invertebrates that are very different from all other invertebrate groups. They all have internal skeletons consisting of porous single-crystal calcite plates, articulated in various ways and covered by a thin skin of protoplasm. Most echinoderms have a five-rayed or pentameral symmetry.

The crinoid body consists of a globular plated cup, the theca, which has a lower part, the calyx, with thick rigid plates and an upper part, a kind of domed flexible roof, the tegmen, with a central mouth and a lateral anus (Figure 9B-10; Clarkson, E.N.K., 1979, Invertebrate Palaeontology and Evolution: George Allen & Unwin, 323 p. Figure 9.35). Inside the theca is a spiral gut. Extending from the theca are long, flexible, plated arms, called brachia. The brachia have sticky pinnules that catch floating food, which is passed along food grooves to the gut. When feeding, the organism orients its arms to form a fan facing upcurrent.

Most modern crinoids are attached directly to the bottom without a stalk, but most ancient crinoids had long, flexible stalks consisting of stacks of doughnut-shaped disks, like vertebrae, called ossicles, held in a flexible skin (Figure 9B-11; Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 14.17). A central canal runs the length of the stalk, passing through the hole in the middle of each ossicle. The organism is attached to the bottom by a rootlike holdfast.

Classification
Crinoids, a subphylum of echinoderms, are divided into four orders. Two of these became extinct in the Permian and one in the Triassic. Another echinoderm subphylum, Blastozoa, is quite similar to crinoids; as nonspecialists, you and we would have a hard time telling them apart. The taxonomically unofficial term pelmatozoans is used for all these echinoderms with plated calices mounted on stems and with pinnulate arms for food gathering.

Habitat
Modern crinoids live at all depths, although most live below a hundred meters. Ancient crinoids must have lived more commonly in waters of shelf depth. Most crinoids today live in flowing water, orienting themselves upcurrent for efficient filtration-feeding, and many ancient crinoids must have too. But other ancient crinoids seem to have lived in quiet water in muddy environments, facing straight upward. So in the ancient you find crinoids in well sorted coarse sediments as well as poorly sorted fine sediments.
Importance

Crinoids are not especially useful in correlation, but they provide interesting paleoecological insights. Crinoids were very abundant in the Paleozoic, and since then they have declined. They have been forced mainly into the deep ocean, where they sometimes form enormous "gardens" of sea lillies.

Comments

Crinoids are rarely found preserved whole, but disarticulated or partly disarticulated crinoid debris, especially ossicles but also calyx plates, are extremely common. Many coarse, well sorted limestones (biosparite; grainstone) consist of mostly crinoid plates and ossicles.
GASTROPODS  
(Phylum Mollusca)  
*Time span: Early Cambrian to now*

**Organism**

The body of a gastropod is in three parts: a *head*, a *foot*, and *viscera* (Figure 9B-12; Clarkson, E.N.K., 1979, *Invertebrate Palaeontology and Evolution*: George Allen & Unwin, 323 p. Figure 8.15). The head has a mouth, a pair of stalked eyes, and tentacles that act as sensory organs. The mouth opens into a cavity, the *pharynx*, containing a chitinous band, the *radula*, with transverse teeth. The radula acts as a rasp or file for boring and for cutting up vegetation (gastropods are herbivorous). The foot is a flat creeping organ behind the head underneath the body. Gastropods have a heart, a liver, kidneys, and a well-developed nervous system. Aquatic forms have gills, and terrestrial forms have lungs. There are male and female gastropods.

**Skeleton**

Most gastropod shells have the form of a helicoid spiral in which the cone is coiled loosely or tightly around an imaginary axis (Figure 9B-13; Clarkson, E.N.K., 1979, *Invertebrate Palaeontology and Evolution*: George Allen & Unwin, 323 p. Figure 8.16). The tightness of the coiling varies considerably, as does overall shape and also external ornamentation. The shells of modern gastropods are *calcitic*, but judging by the poorness of preservation, those of Paleozoic gastropods were probably *aragonitic*.

Many gastropods have a horny or calcareous plate, the *operculum*, carried on the back part of the foot, to close the shell opening after the animal retreats entirely within its shell. You don't often find fossil opercula.

**Classification**

Gastropods are subdivided into three subclasses: Prosobranchiata, which includes most of the fossil gastropods as well as modern marine shelled gastropods; Opisthobranchiata, which includes marine gastropods that have lost their shells; and Pulmonata, which have developed lungs and become adapted to life on land.

**Habitat**

Gastropods have an amazingly wide range of adaptation, from abyssal ocean depths to high mountains. The marine shelled gastropods of interest to paleontologists must have mostly crawled upon mud and sand bottoms. Some modern gastropods also cling tenaciously to rocks.

**Importance**

Gastropods generally evolved slowly and are long-ranging in time, so they are not of major importance for correlation. Their abundance has generally increased through time.
Comments

Gastropods are not abundant in many rocks, but if you hunt around you're likely to find one. Preservation of Paleozoic gastropods is usually as external impressions.
GRAPTOLEITES
(Phylum Hemichordata)

Time span: Middle Cambrian to Early Mississippian

Organism and Skeleton
Graptolites were free-floating colonial marine animals. The skeleton consists of a series of hollow interlinked tubes constructed of a thin sheetlike material called periderm (Figure 9B-14; Clarkson, E.N.K., 1979, Invertebrate Palaeontology and Evolution: George Allen & Unwin, 323 p. Figure 10.1). The first-formed part of the graptolite is a conical tube called the sicula. Upward from the sicula grew a number of cuplike thecae. The thecae show prominent growth lines. All the thecae are connected by a common canal, so presumably food caught by the individual animals was ingested and shared by the whole colony. The colonies had various numbers of branches, or stipes. The entire colony is known as a rhabdosome. Nothing is known about the the soft-bodied animals that occupied the thecae.

Classification
Graptolites (officially, class Graptolithina) are divided into several orders, only two really important: Dendroidea (dendroids), Cambrian to Mississippian, and Graptoloidea (graptoloids), Early Ordovician to Early Devonian. The dendroids were many-branched colonies; the graptoloids had rhabdosomes with only a few stipes (eight, four, two, or just one).

Habitat
Dendroids appear to have been sessile benthonic organisms (Figure 9B-15; Clarkson, E.N.K., 1979, Invertebrate Palaeontology and Evolution: George Allen & Unwin, 323 p. Figure 10.3 and Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 15_25). They probably grew upright, with a holdfast below the sicula and with the stipes extending upward like a shrub. Graptoloids, on the other hand, seem to have been planktonic.

Importance
Graptolites are very important for dating Ordovician and Silurian rocks. But there are problems: graptolite species are fairly long-ranging in time, and preservation is not really good, and graptolites are found mainly in deep-water shales, not coarser shallow-marine rocks.

Comments
Graptolites are almost always preserved as carbonaceous films on bedding planes, because of compression and diagenesis after the colony came to rest on a mud bottom and was buried. So unless the shale tends to split along bedding planes, which is a lot less common than along the cleavage, you don't have much chance of finding graptolites.
PELECYPODS  
(Phylum Mollusca)  

Time span: Early Ordovician to now

Organism

Pelecypods are mollusks with a soft body enclosed between paired, hinged shells. The body, fairly highly organized, consists of a visceral mass, a foot, and gills. The visceral mass, attached to the inner surface of the two valves, consists of mouth, an esophagus, a stomach, a coiled intestine, and an anus (Figure 9B-16; Clarkson, E.N.K., 1979, Invertebrate Palaeontology and Evolution: George Allen & Unwin, 323 p. Figure 8.7. and Figure 9B-17; Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 10_13). In many pelecypods the mouth and the anus are a pair of tubes in a retractable siphon that sticks out from the shell. A circulatory system with a heart, a nervous system, and kidneys are well developed. The muscular foot is used for moving and burrowing.

Skeleton

The two valves of the shell are almost exactly mirror images of each other (Fig. 9B-18; Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 10_18), the way your right and left hands are. The only difference is that the details of teeth and sockets for articulation at the hinge are different in the two valves. When pulled closed by adductor muscles attached within the shell, the two valves meet tightly along a curved line that usually lies nearly in a plane. The valves show closely spaced growth lines that are records of the former positions of the edge of the shell; new shell material is added only at the margins of the shell. Some pelecypods also show prominent ribs radiating from the point of juncture of the shells.

The shells in some species are calcite, in others aragonite, and in many are alternating layers of calcite and aragonite. Because of recrystallization of the aragonite to calcite, most fossil pelecypod shells no longer show fine structural detail.

Classification

It's fairly easy to classify pelecypods at the level of species and genera, but it's difficult to classify them at high taxonomic levels. They've been divided into six subclasses. All of these but one (which evolved in the Triassic) appeared at the beginning of the Ordovician, when pelecypods underwent a spectacular burst of adaptive radiation. There was another great expansion of pelecypods in the Mesozoic and early Cenozoic.

Habitat

Pelecypods are bottom-dwellers (mainly marine, but also fresh-water) with a great variety of life modes: infaunal (burrowing, shallow or deep), epifaunal (attached to the substrate by threads or cement, or free-lying), swimming, or
boring. Both infaunal and epifaunal pelecypods have been common. They are much more common in sandstones and mudstones than in limestones.

Pelecypods have been much more successful than their competitors the brachiopods at colonizing difficult environments like the intertidal zone, and are today far more important than brachiopods.

Importance
Pelecypods are mostly too wide-ranging in time to be very useful stratigraphically.

Comments
In the Paleozoic, you're not nearly as likely to see pelecypod fossils as brachiopod fossils, but in the Mesozoic and Cenozoic, it's just the other way around.

Pelecypods are also called lamellibranchs or bivalves.
TRILOBITES

(Phylum Arthropoda)

Time span: Early Cambrian to Permian

Organism
Paleontologists are hampered in their understanding of the soft-body anatomy and physiology of trilobites because trilobites are extinct. Trilobites had chitinous exoskeletons. (Chitin is a kind of nitrogenous polysaccharide that's extremely resistant to solution once it's secreted by the organism). Not much is known about the soft body, but it it's known that trilobites molted.

Skeleton
The chitinous skeleton is always in three parts (Figure 9B-19; Clarkson, E.N.K., 1979, Invertebrate Palaeontology and Evolution: George Allen & Unwin, 323 p. Figure 11.3. and Figure 9B-20; Clarkson, E.N.K., 1979, Invertebrate Palaeontology and Evolution: George Allen & Unwin, 323 p. Figure 11.13): a head or cephalon, in one piece; a thorax, which is segmented; and a tail or pygidium, in one piece. The cephalon usually shows a raised bulbous central area, the glabella, on which are two compound eyes, each facet a single crystal of calcite.

On the underside (the ventral side) of the thorax is a pair of appendages, usually not preserved, on each segment. The segmentation of the thorax allowed some trilobites to roll themselves up, probably for protection.

Classification
Trilobites are classified into about eight orders and sixteen suborders based on morphology of hard parts (Figure 9B-21; Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: McGraw-Hill, 816 p. Figure 13_36). Many characteristics need to be taken into account in classification, and it's hard to know which are the most significant.

Of the six suborders apparently already in existence when trilobites developed hard parts at the beginning of the Cambrian, four became extinct at the end of the Cambrian, but ten appeared near the end of the Cambrian. (Evolutionary lineages are hard to figure out, though.) Of those, only one survived beyond the end of the Devonian.

Habitat
Trilobites must have walked, crawled, plowed, or scooted upon the sediment surface in search of food. The "double-tire-tread" track represented by the trace fossil Cruziana was certainly made by plowing trilobites, and various other scratch-mark trace fossils were probably made by walking or skimming trilobites. Trilobites are most commonly found in siltstones, mudstones, and fine-grained limestones.
**Importance**

Several thousand species have been described. *Trilobites are of great stratigraphic value in the Cambrian (zoned almost entirely on trilobites)* and of somewhat lesser value in the Ordovician. In the Ordovician, trilobites and brachiopods in shallow-water facies are played off against graptolites in deeper-water facies. In Silurian and younger rocks they are much less important than other fossil groups for correlation.

**Comments**

Trilobite fossils are common enough that with some patience you can often find them in the appropriate rock types in the Lower and Middle Paleozoic. You usually find pieces of the cephalon or pygidium. It's almost always the upper (dorsal) surface, not the lower (ventral).

The taxonomic status of trilobites is unclear. It's clear that they should be called arthropods, but it's generally agreed that arthropods are actually polyphyletic. The official view is that trilobites are a questionable subphylum of the artificial phylum Arthropoda, but maybe they should be a separate phylum.