11

Fossils and Their Living Relatives: Mollusks, Arthropods, Echinoderms, Graptolites, and Plants

WHAT YOU WILL NEED

1. Study set of fossil bivalves (Class Bivalvia), gastropods, cephalopods, trilobites, cystoids, blastoids, and echinoids.
2. Prepared slide of fossil ostracodes.
3. Rock samples exhibiting graptolites and fossil plants.

THE MOLLUSCA

To many people, mollusks are the most familiar of marine invertebrates. Most members of the phylum possess external calcareous shells, which can be readily collected at coastal areas around the world. The soft fleshy parts of some mollusks are widely used as food by humans. Such familiar animals as snails, slugs, clams, oysters, chitons, squids, and octopuses (Fig. 11.1) are included in the Phylum Mollusca.

Typically, mollusks are unsegmented animals with bilateral symmetry. A fold called the **mantle** has the shell-building function, and a muscular portion of the body (the foot) has a primarily locomotor function. In some forms, like the squid and cuttlefish, the foot is modified into tentacles. Respiration in most forms is accomplished by gills. Well-developed circulatory organs (heart, blood vessels), digestive glands (liver, kidney, intestines), and nervous system are evidence of advanced development. Mollusks vary in size from microscopic to the extraordinary dimensions seen in the giant squid, which may grow to lengths of 15 m.

Bivalvia (Formerly Pelecypoda)

Bivalvia are mollusks with a hatchet-shaped foot, layered gills, right and left **valves,** bilobed mantle, and no definite head. The margins of the mantle are modified to form tubes (siphons) for intake and exhaust of water. Incoming water moves over the gills where food particles are trapped and carried into the digestive system.

The valves in bivalves are held together at the dorsal edge by an elastic ligament. Concentric growth lines originate at a dorsal, slightly swelled area called the **umbo.** The terminal end of the umbo is called the **beak,** and in most forms is directed anteriorly. The inside of an empty valve contains markings that represent places of attachment of organs and muscles. In most shells, large, rounded scars of the adductor muscles can be found dorsally at either end. An exception is seen in oysters and scallops, which have only one adductor muscle. A thin line **(pallial line),** usually paralleling the free margin, marks the place of attachment of the mantle to the inner surface of the shell (Fig. 11.2). A posterior indentation of the pallial line, called the **pallial sinus,** marks the position of the foot retractor muscle and provides information about the size of the siphons. Because siphon size is indicative of habits, the pallial sinus is of particular use in fossil study.

All Bivalvia are aquatic, and the majority are marine. With a few exceptions, they are sedentary organisms that live buried in the mud or sand. Some species can either attach themselves to or burrow into rock or wood. The Bivalvia are typically gregarious and in many localities are enormously abundant over large areas. In general, an abundance of species and individuals of fossil marine bivalves implies shallow-water deposition. The shells of modern deep-water forms are often thin, translucent, and small. Except for mud-dwellers, shallow-water species possess thicker, more robust, ornamented and colored shells.

Bivalves made their first appearance in Cambrian time but did not become notably varied or numerous until the Mesozoic (Fig. 11.3). Many thick-shelled, oysterlike forms like *Gryphaea* (Fig. 11.4) are found in Jurassic and Cretaceous strata. In these bivalves, the lower valve became large and massive, whereas the upper valve was reduced in size to a mere cap. Species of scallops like *Pecten* (Fig. 11.4) are good local guide fossils for Cenozoic rocks.

Study Questions

1. Sketch an external and internal view of the modern clam shell in your study set and label the pallial line, pallial sinus, growth lines, muscle scars, and hinge line.

Figure 11.1 Diversity of living mollusks.

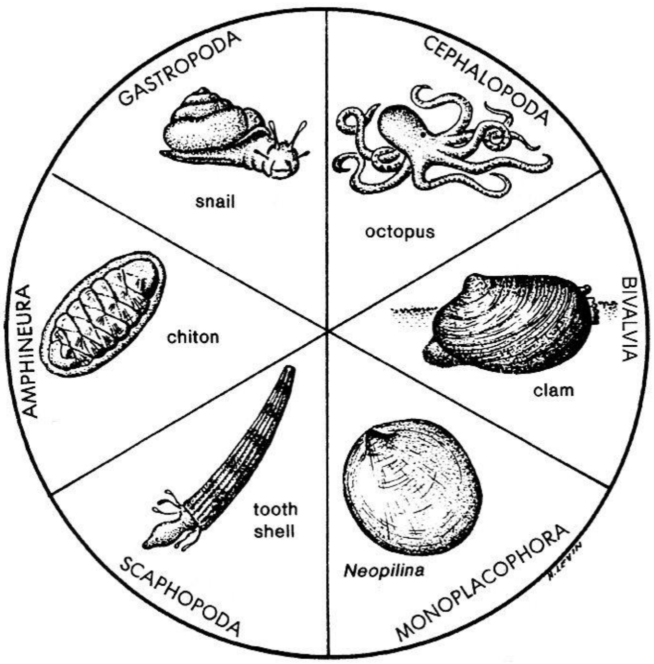


Figure 11.2 Features of the shell of a bivalve.

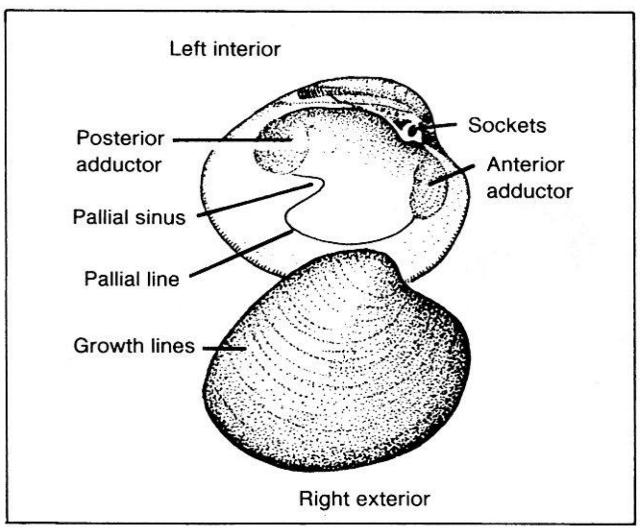


Figure 11.3 Geologic range of gastropods and bivalves.

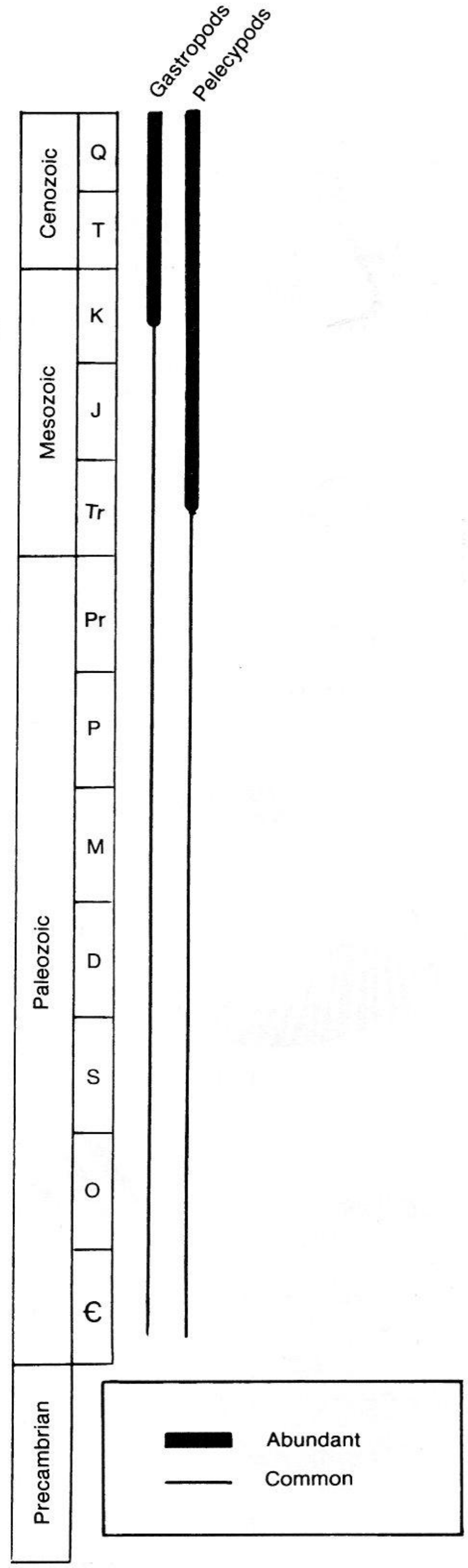
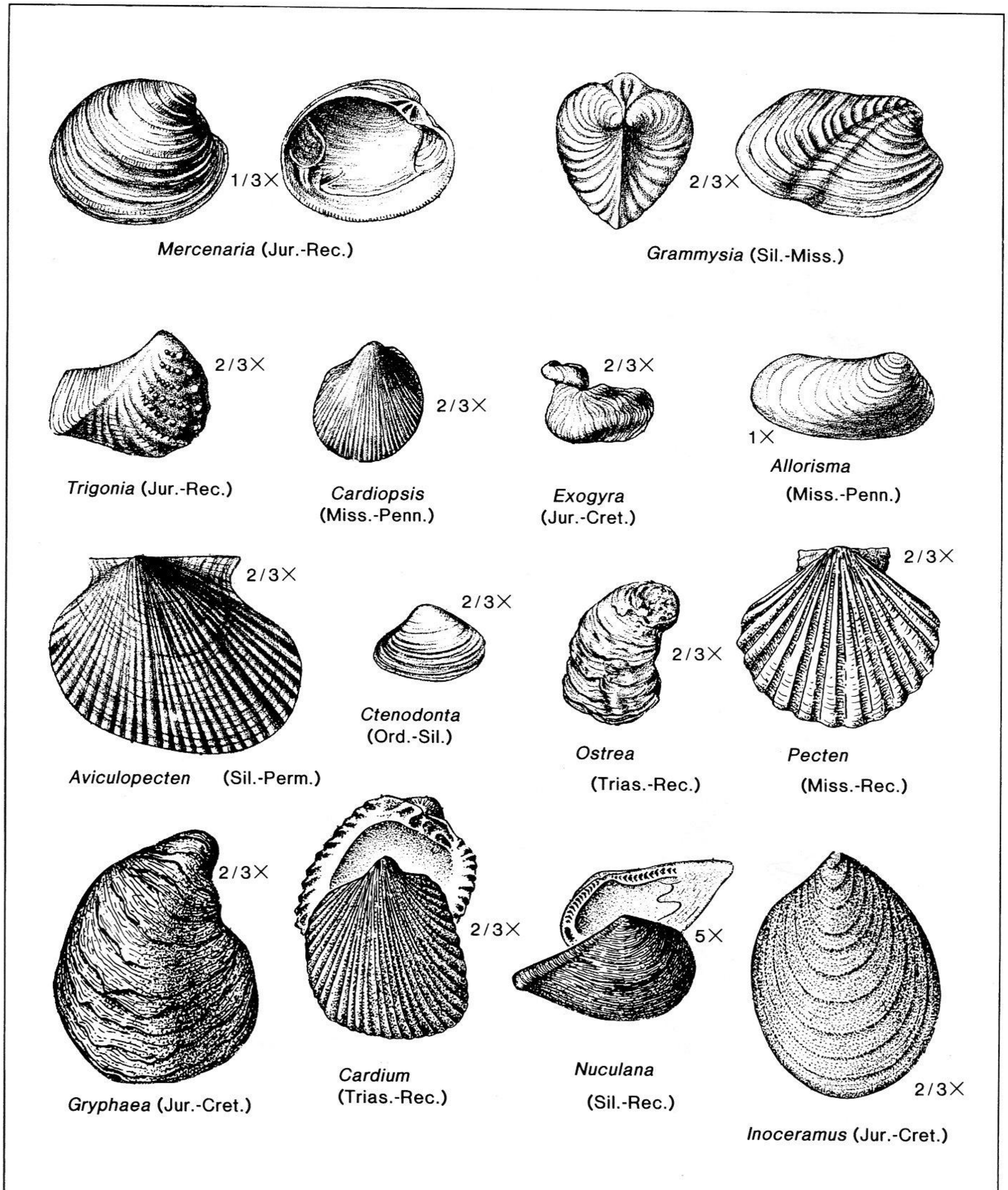


Figure 11.4 Fossil bivalvia.

Partly from Collinson, C. W., 1959, Illinois State Geological Survey, Educational Series 4.



2. By comparing the study specimens with the illustrations, try to identify the bivalves as to generic name.

3. At Pozzuoli, Italy, borings of marine bivalves are found about halfway up the vertical columns of a ruined building that once stood in a Roman marketplace. From this, what do you infer about changes in sea level here during the past two thousand years?

4. What explanation may be offered for the observation that heavy-shelled bivalves are mainly nearshore dwellers?

5. In general, bivalves have equal valves, in contrast to brachiopods, which have unequal valves. Which bivalves depicted in Fig. 11.4 are an exception to this generalization?

   Which bivalve is most like a brachiopod in having valves that are *nearly* bilaterally symmetrical?

6. Bivalves are *filter feeders.* What does this mean?

7. What differences in symmetry of shells exist between a bivalve like *Mercenaria* (Fig. 11.4) and a brachiopod like *Atrypa* (Fig. 10.35)?

   Provide a sketch to illustrate the differences in the space below.

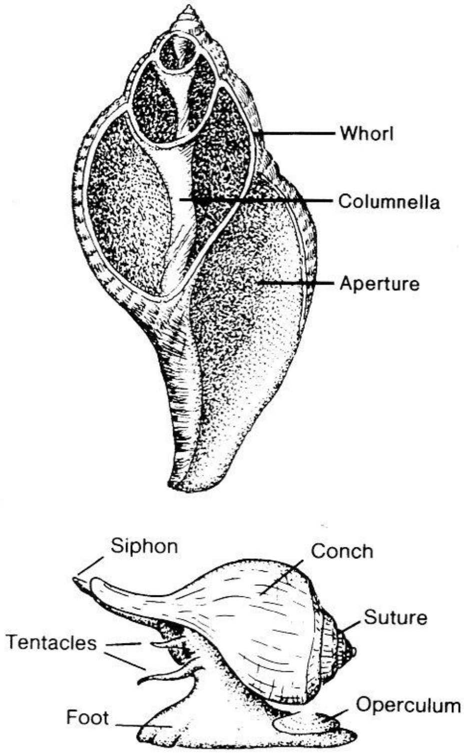
Gastropoda

Over 14,000 species of fossil **gastropods** have been described, and probably an even greater number of species exists today. Members of the class build a one-piece, coiled shell, although some forms do not secrete a shell. The typical gastropod has a distinct head with mouth, eyes, and tentacles, and a ventral flattened foot. Undulatory motion of the foot provides locomotion. The head and foot can be retracted into the shell, and in some forms, the opening (aperture) of the shell can be closed by an **operculum** when the foot is withdrawn. The shell **(conch)** develops as an expanding tube that coils around a hollow axis **(columnella).** That part of the conch representing one revolution is called a **whorl,** and the surface of contact between whorls is expressed by a line called a *suture* (Fig. 11.5). Ornamentation is varied, and may consist of growth lines, ribs, spines, nodes, or combinations of these features.

Since their first appearance in the Cambrian (Fig. 11.3), gastropods have adjusted to a variety of environments. Many live on or burrow into the bottoms of seas or lakes. Others have evolved into air-breathing land dwellers.

In general, an abundance of marine gastropods implies shallow, warm, water. Of living species, the greater number inhabit tropical waters where robust, thick-shelled, highly ornamental species thrive. The number of species decreases in deeper and cooler parts of the sea. Thin-walled conchs with little ornamentation are often characteristic of deeper water forms.

Figure 11.5 Gastropod anatomical features.



Study Questions

1. Examine the gastropods in your study set and identify as many as you can by comparison with the illustrations (Fig. 11.6).
2. Sketch one of the fossil snail specimens and label aperture and growth lines.

3. Does the conch coil in a plane or a spiral?

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4. Most gastropods coil in a spiral. Which of the gastropods depicted in Figure 11.6 coil in a plane (planispiral coiling)?

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Cephalopoda

The **cephalopods** are probably the most advanced and complex of the mollusks. They are oceanic animals and include octopuses, squids, cuttlefish, and nautiluses. The pearly or chambered nautilus is a living form that provides many clues to the habits and soft anatomy of fossil cephalopods. In *Nautilus* (Fig. 11.7 and 11.8), the bilaterally symmetrical body has a prominent head that bears paired, image-forming eyes. Tentacles are present as a modification of the anterior portion of the foot. As in other members of the Mollusca, gills, mantle, and siphon are present. Locomotion is accomplished by expulsion of water from the mantle cavity through a tubular fleshy funnel. In a sense, the animal is jet propelled.

Superficially, conchs of cephalopods resemble conchs of some gastropods. However, most cephalopods coil in a plane, whereas the majority of gastropods are helicoid. An even more important distinction is that the cephalopod conch (Fig. 11.8) is divided into chambers **(camerae)** by transverse partitions called **septa.** The soft parts reside in the final chamber (living chamber), and new septa are added behind the visceral mass as it grows forward in the conch.

A thin, porous, calcareous tube termed the **siphuncle** (Fig. 11.9) extends through the septa. The siphuncle secretes gas through its porous wall into the camerae, thus regulating the animal's buoyancy. The juncture of the septa with the inner surface of the conch is marked by lines called *sutures.* The configuration of a suture is determined by the shape of the periphery of a septum. If the edge of the septum is smooth, like that of a saucer, then the suture will be similarly smooth. If the septum is fluted, like the margin of a pie shell, this will be reflected in the zigzag pattern of the suture.

The folds of the sutures that are convex toward the aperture of the conch are called *saddles.* Lobes are folds that are convex toward the first-formed part of the conch. The pattern of sutures provides the means for identifying genera and species of cephalopods and is also the basis for distinguishing between two great orders of externally shelled cephalopods, the Nautiloidea (Fig. 11.10) and the Ammonoidea (Fig. 11.11). The Nautiloidea have smooth or broadly undulating sutures and central siphuncle location. They were abundant and widely distributed during the Paleozoic. Nautiloids declined after that time, and today the chambered nautilus is the only survivor.

Figure 11.6 Fossil gastropods.

Partly from Collinson, C. W., 1959, Illinois State Geological Survey, Educational Series 4.

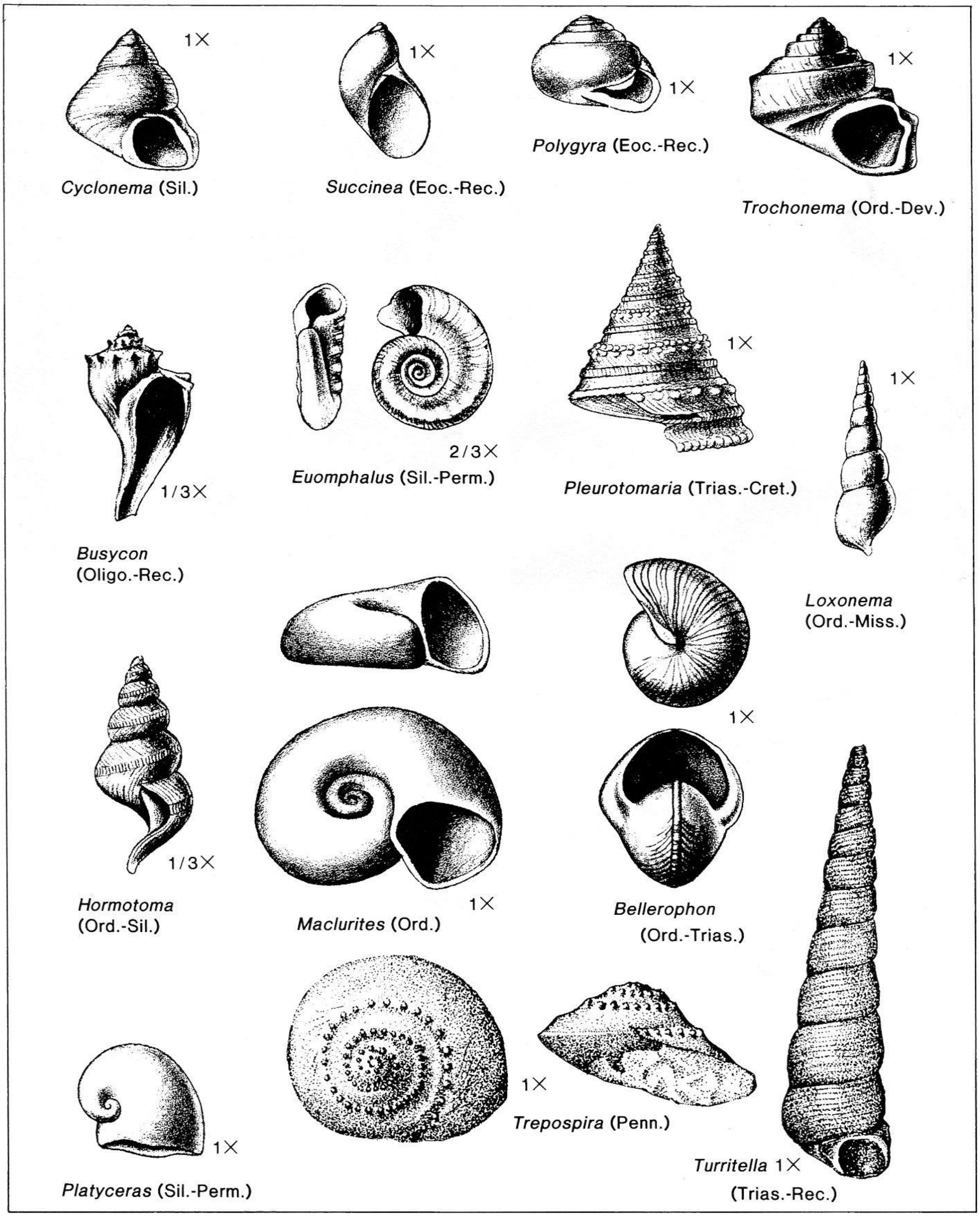


Figure 11.7 The living nautiloid cephalopod *Nautilus belauensis.* Note the prominent eye (which has no lens and functions much like a pin-hole camera), the many tentacles, and the protective hood that blocks the opening of the shell when the animal withdraws inside.

Courtesy of W. Bruce Saunders.

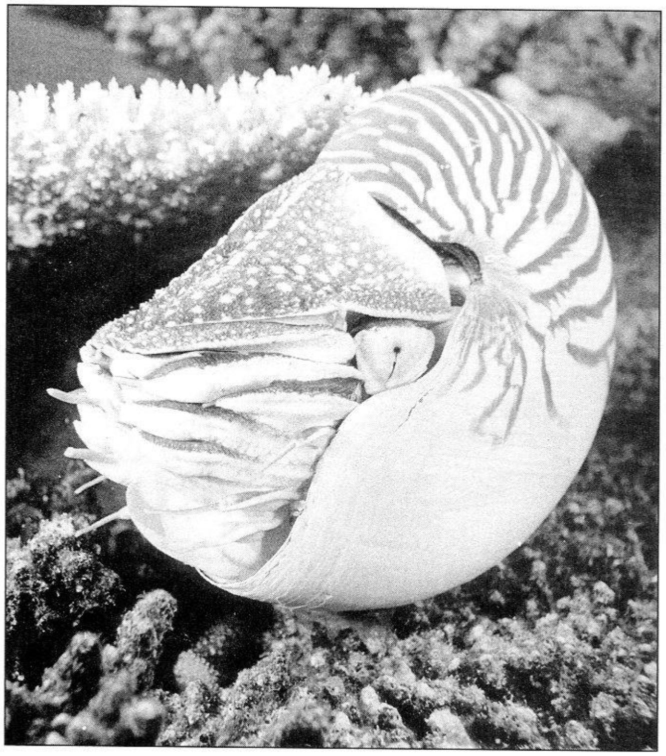
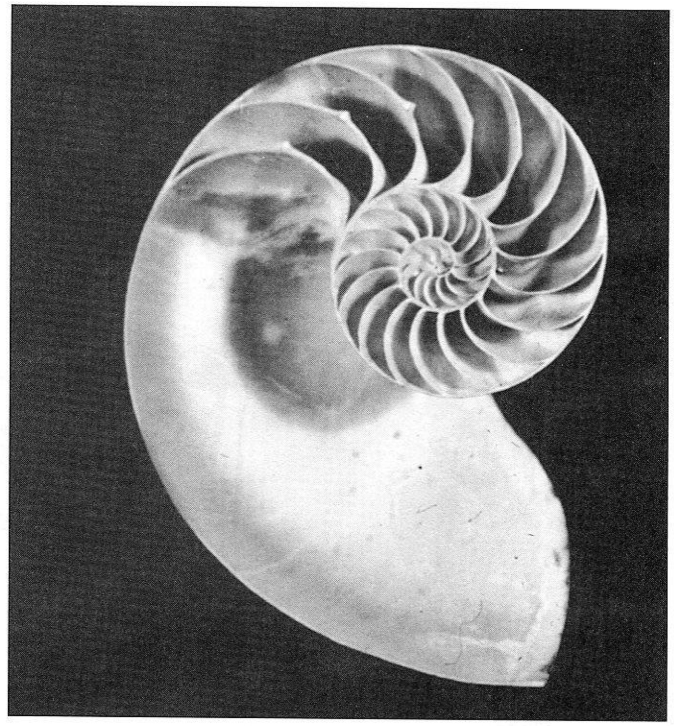


Figure 11.8 Conch of *Nautilus,* sawed in half to reveal the large living chamber, septa, and septal necks through which the siphuncle passed. The siphon is soft tissue, and thus not present in this specimen. (Maximum diameter of conch is 19 cm.)



Ammonoids differ from nautiloids in their more complex sutures (Fig. 11.12) and their smaller, more ventrally located siphuncle. Paleozoic ammonoids have sutures with smooth lobes and saddles. Such sutures are called *goniatitic.* Most of the Triassic ammonoids have sutures with smooth saddles and denticulated lobes *(ceratitic).* A few Triassic ammonoids and most Jurassic and Cretaceous forms have *ammonitic* sutures, with complex wrinkling on both saddles and lobes. The geologic range of each of the major cephalopod groups is depicted on Figure 11.13.

Some members of the Class Cephalopoda have internal rather than external shells. An example is the cuttlefish, whose internal cuttlebone is placed in bird cages as a source of calcium for pet birds. Only one order of internal-shelled cephalopods, the Belemnoidea, is important geologically. (Fig. 11.14). The unchambered guard portion of fossil **belemnite** shells are often bullet-shaped and take on a brown coloration. Belemnites are useful guide fossils in rocks of Jurassic and Cretaceous age.

Figure 11.9 Section of *Nautilus* in plane of coiling.

From Levin, H. L., *Ancient Invertebrates and Their Living Relatives,* Upper Saddle River, NJ: Prentice Hall, 1999.

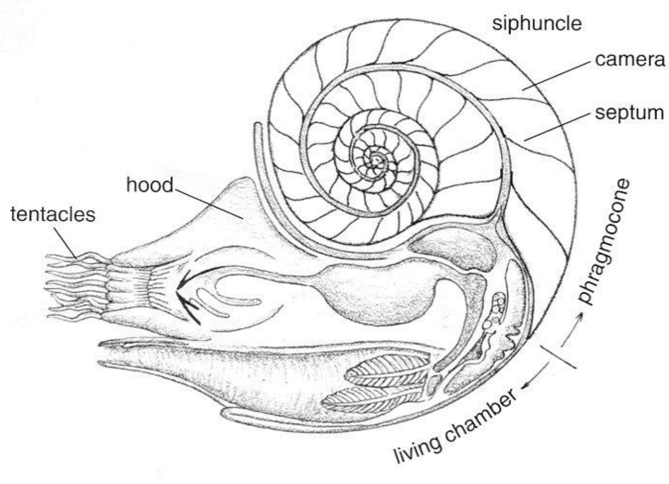
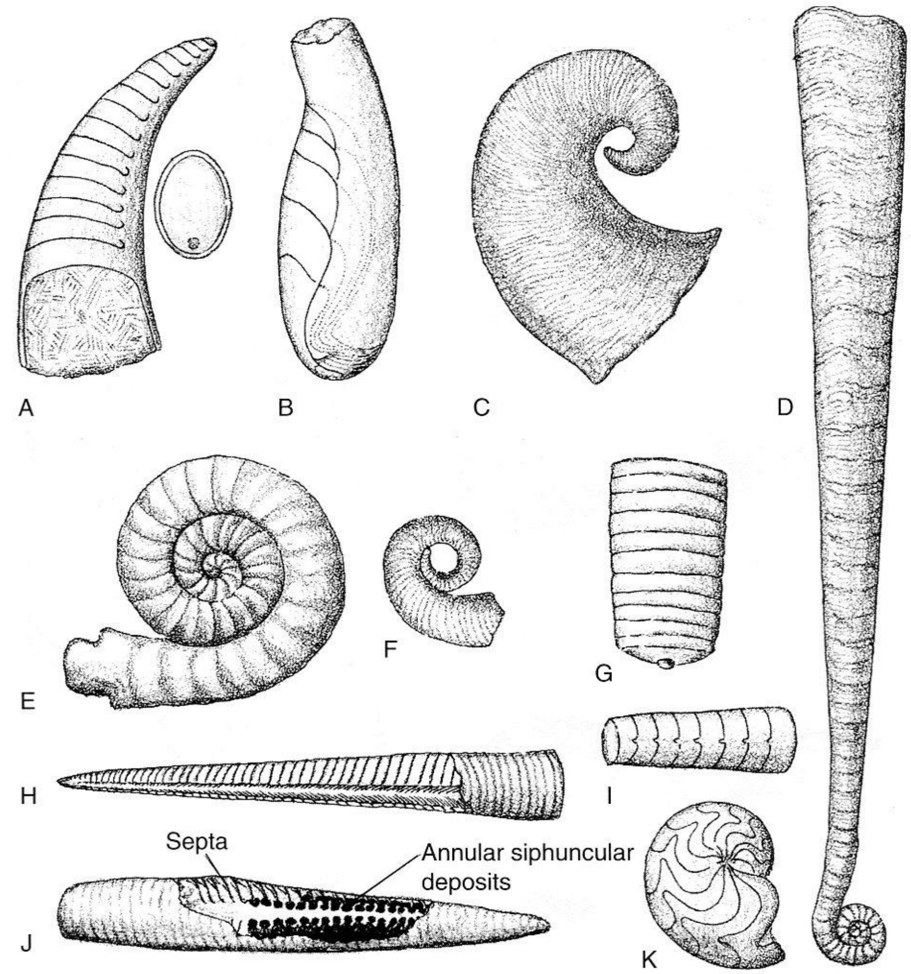


Figure 11.10 Some nautiloid cephalopods. (A) *Plectronoceras,* ×2 (Cambrian). (B) *Ascoceras,* ×0.5 (Silurian). (C) *Phragmoceras,* ×0.5 (Silurian). (D) *Lituites,* ×0.5 (Ordovician). (E) *Ophioceras,* ×2.7. (F) *Trochoceras,* ×0.2 (Devonian). (G) *Michelinoceras,* ×0.7 (Ord.-Trias.). (H) *Endoceras,* ×0.2 (Ordovician). (I) *Bactrites,* ×1 (Sil.-Perm). (J) *Actinoceras,* ×3.0 (Ord.-Sil.) (K) *Aturia,* ×03.0 (Paleocene-Miocene).

From Levin, H. L., *Ancient Invertebrates and Their Living Relatives,* Upper Saddle River, NJ: Prentice Hall, 1999.



Study Questions

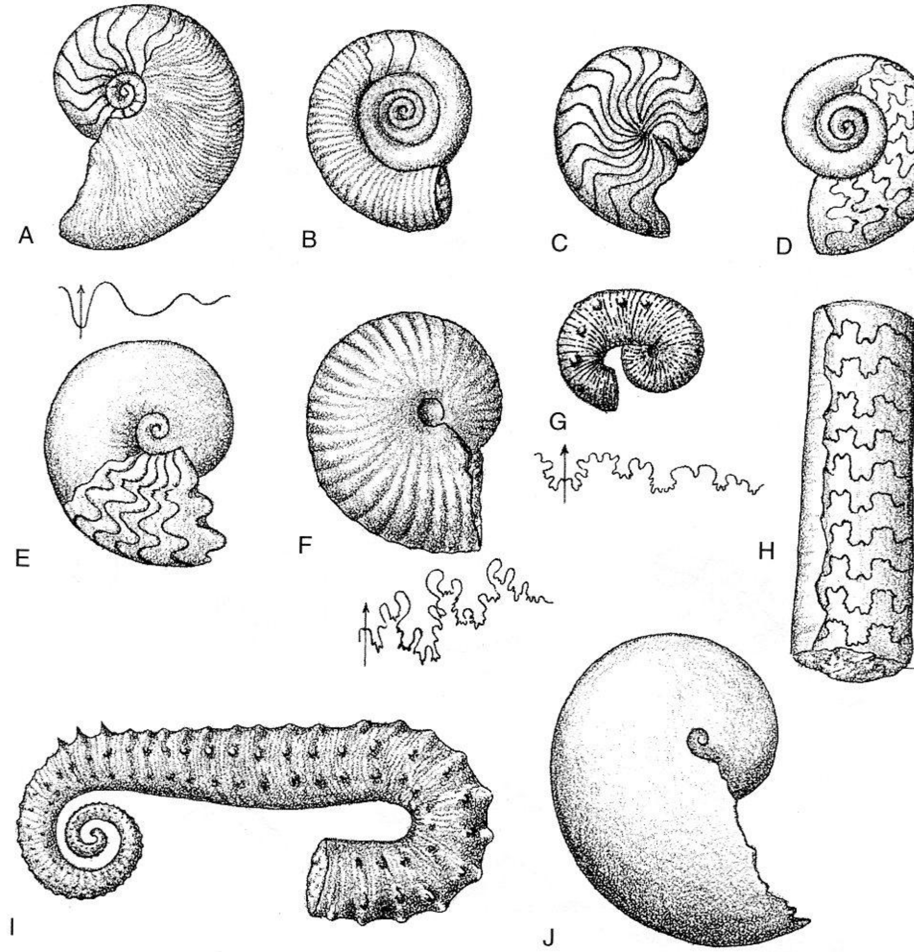
1. By comparison with the illustrations (Figs. 11.10 and 11.11), identify as many of the cephalopods in your study set as you can. Prepare a sketch of one specimen and label suture type.

2. How do cephalopods differ from gastropods with regard to shell structure and portion of conch occupied by soft parts?

3. Examine Figure 11.8 or an actual conch of *Nautilus* that has been sawed in half. Note the holes in the septa that provide for the siphon. Does *Nautilus* have a continuous siphuncle?

Figure 11.11 Ammonoids. (A) *Agoniatites* (with suture pattern), ×0.35 (Devonian). (B) *Clymenia*, ×0.35 (Devonian). (C) *Tornoceras*, ×0.7 (Devonian). (D) *Prolecanites*, ×1.2 (Mississippian). (E) *Meekoceras*, ×0.7 (Triassic). (F) *Phylloceras* (with suture pattern), ×0.7 (Trias.-Cret.). (G) *Scaphites* (with suture pattern), ×0.8 (Cretaceous). (H) *Baculites*, ×0.4 (Cretaceous). (I) *Ancyloceras*, ×0.12 (Cretaceous). (J) *Placenticeras*, ×0.7 (Cretaceous).

From Levin, H. L., *Ancient Invertebrates and Their Living Relatives*, Upper Saddle River, NJ: Prentice Hall, 1999.



4. Figure 11.15 represents a straight conch of a nautiloid similar to *Michelinoceras* (see Fig. 11.10). The areas shown in black represent soft parts or shell material. If the chambers contain only gas, what would be the orientation of the conch when passively suspended in water? Would this orientation seem advantageous for swimming? If the assumption is made that a horizontal position is preferred, how might this be accomplished in evolving generations of cephalopods? (Hint: Consider adding "balast" or changing the pattern of coiling as ways to achieve horizontality.)

5. Figure 11.16 depicts changes in the number of genera of cephalopods and fishes through a segment of geologic time. From the graph, suggest a possible hypothesis for the extinction of ammonites and reduction of nautiloids at the end of the Cretaceous.

6. Cephalopods have been more useful than gastropods in stratigraphic correlation and as index fossils. Suggest a reason (or several reasons) why they are more useful.

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Figure 11.12 Cephalopod suture patterns.*

*By convention, illustrations of fossil coiled cephalopods have living chamber placed uppermost, inverted from the normal living position.

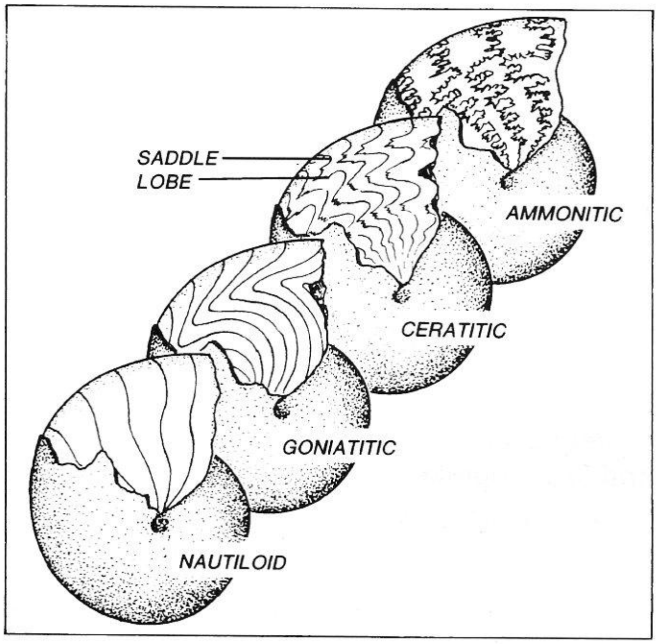


Figure 11.13 Geologic ranges of major groups of cephalopods.

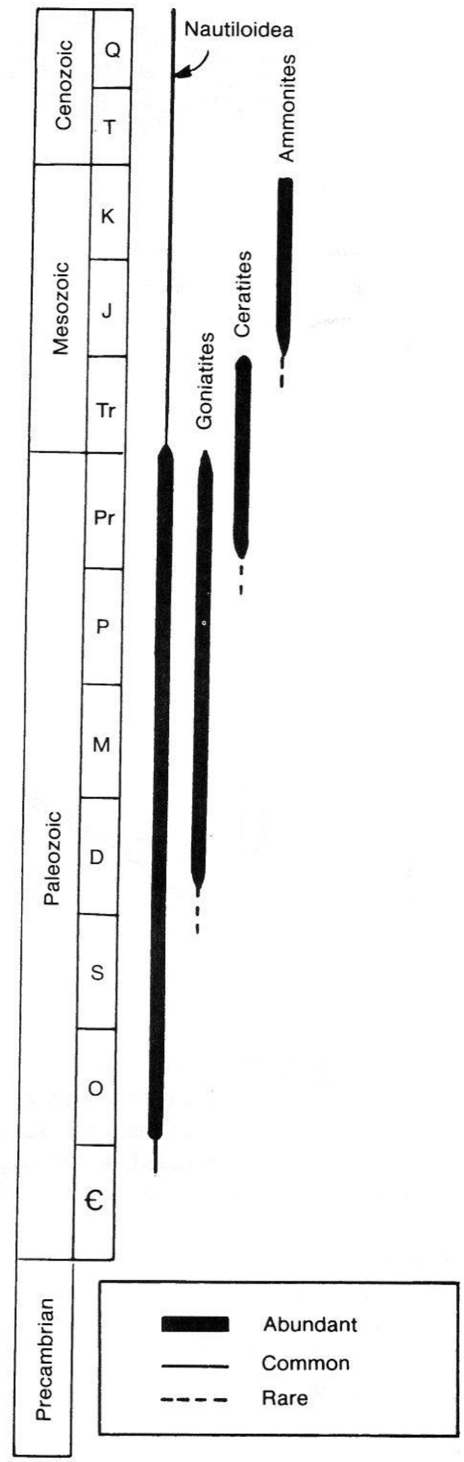


Figure 11.14 Restoration of a belemnite.

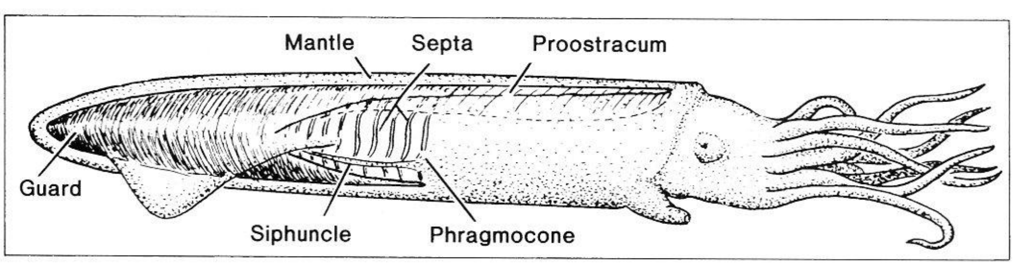


Figure 11.15 Problem of buoyancy in orthocone cephalopods.

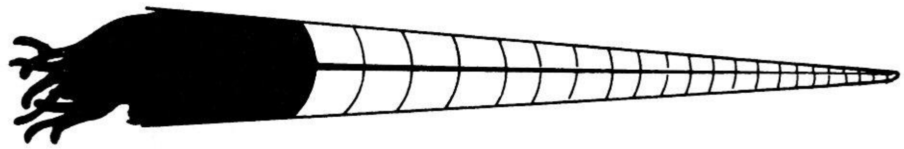
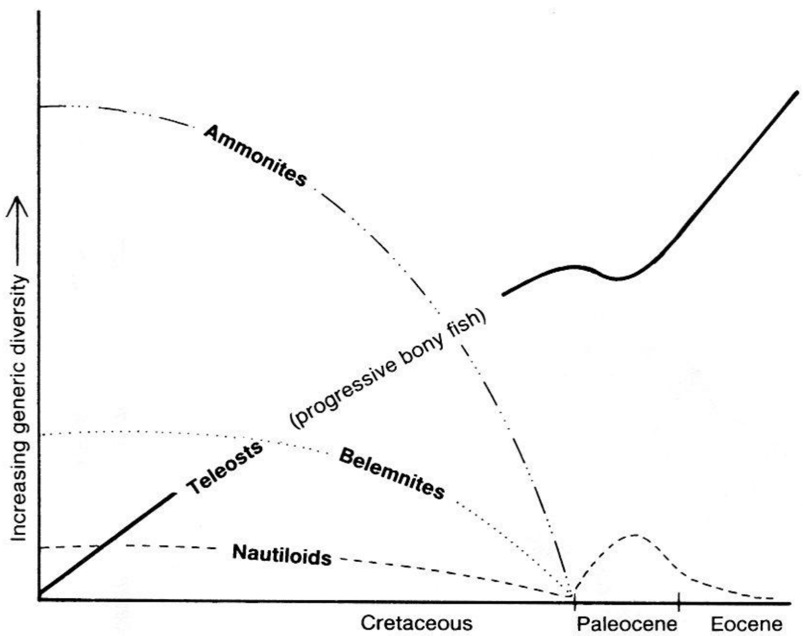


Figure 11.16 Change through time in number of fish genera and number of cephalopod genera.
From Newell (1962), *J. Paleontology,* **36:** 605.



7. The diagram (Fig. 11.17) illustrates an inclined coal seam. Miners working the seam find that it ends abruptly at point A. The abrupt truncation suggests that a fault plane has been encountered. A company geologist examines the hanging wall at A and finds belemnites of the same species as those that had been discovered earlier in a formation exposed west of the milling plant. What are the prospects for additional coal recovery east of the fault? What type of fault is represented? (Refer to Chapter 14 for a summary of fault nomenclature.)

Monoplacophora, Amphineura, and Scaphopoda

Three classes of the Phylum Mollusca are of lesser importance to geologists. These are the Class **Monoplacophora** (Cambrian to Recent), **Amphineura** (Upper Cambrian to Recent), and **Scaphopoda** (Ordovician to Recent). Monoplacophorans (Fig. 11.18) have small, conical shells usually less than one inch in diameter. Amphineurans (Fig. 11.19) include the chitons or "sea mice." Their shell is composed of eight transverse plates that cover and protect the dorsal surface of the animal. Scaphopods or "tooth shells" are small mollusks characterized by a tubular shell open at both ends and shaped like a miniature tusk (Fig. 11.20).

THE ARTHROPODA

The number of species in the arthropod phylum is truly immense. Over 80 % of living animal species are arthropods, and the numbers of individuals represented is astronomical.

Figure 11.17 Coal mine.

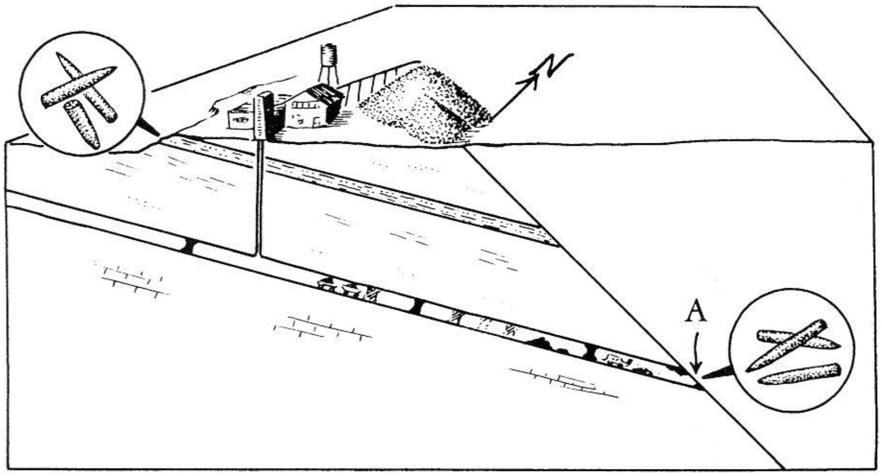


Figure 11.18 Monoplacophorans.

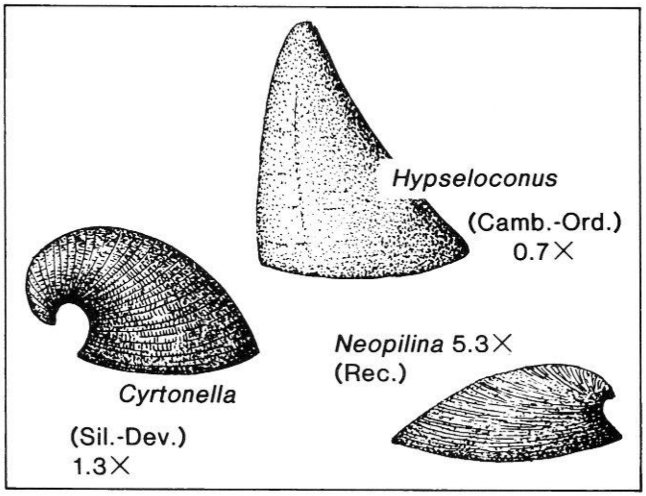


Figure 11.19 A modern amphineuran.

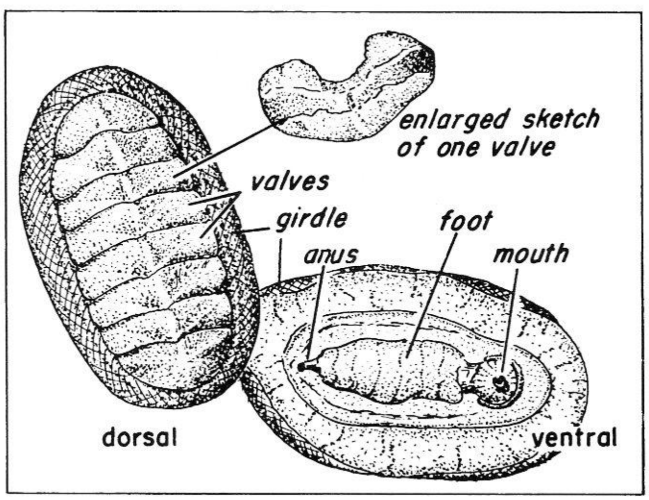
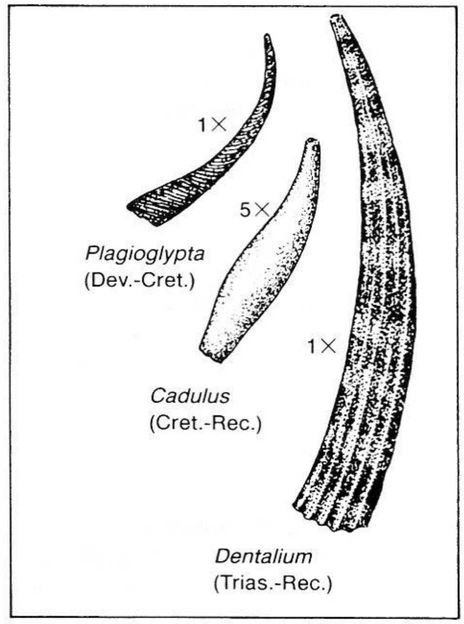


Figure 11.20 Scaphopods.



Included here are the lobsters, spiders, insects, centipedes, and a host of other animals too numerous to mention.

The arthropods possess **chitinous** exterior skeletons, segmented bodies, paired and jointed appendages, and highly specialized nerve and sensory organs. Among the arthropods are creatures well adapted for life in and on the surface of the land, for flight, and for existence in all types of natural water bodies. Their success in populating diverse environments is extraordinary, and yet only a relatively few groups have left a significant fossil record. Even the insects, so numerous and diverse today, left a scant fossil record. Preservation is difficult for animals that die in terrestrial environments. Some fossilized insects have been recovered at a few exceptional localities, but the vast majority of sedimentary rocks do not contain insect remains. In terms of their use in stratigraphic studies, the most important arthropods are the trilobites and ostracods. Both of these groups have left an impressive fossil record.

Trilobites (Figs. 11.21 and 11.22)

The skeleton of a trilobite consisted of a dorsal shield, thin ventral membrane, and external covering of the appendages. The **chitin** composing the skeleton was thickened and hardened by calcium carbonate in areas not requiring flexibility. The name *trilobite* means "three lobes" and refers to the division of the dorsal shield into three longitudinal portions, the axial lobe and two lateral or pleural lobes. Three major body regions can be identified as the **cephalon,** the segmented *thorax,* and a posterior portion, the **pygidium.** The pygidium is believed to have evolved by the welding together of posterior thoracic segments. The appendages of the trilobite were located on the ventral surface but are rarely preserved. Sediment would tend to cling readily to this irregular ventral surface, and it is usually impossible to free the fragile appendages from the rock. The smoother dorsal surface can be more easily broken from the sedimentary matrix.

Growth was accomplished in trilobites, as in many arthropods, by molting. Thin places in the exoskeleton called sutures (Fig. 11.21) not only imparted flexibility but also made the molting process easier. Although many trilobites apparently were blind, the majority developed either eyes of the simple, single-lens type or compound eyes composed of a large number of separate visual bodies. In some forms, the separate facets were covered by a continuous protective cornealike layer, whereas in others, each tiny facet had its own equally small cornea. For the latter, the eyes have a reticulated or sievelike appearance.

Trilobites were entirely marine, for their remains are found in association with corals, crinoids, brachiopods, and cephalopods. Most forms appear to have been bottom dwellers, and many evidently burrowed or crawled over the bottom mud or sand of ancient seas. A smaller number show adaptations, suggesting a pelagic existence as either floaters or swimmers.

If biological success can be measured in terms of complexity of structure, variability of form, and numbers of individuals, then trilobites must be considered enormously successful. They first appeared about 600 million years ago, and wherever shallow-water marine Cambrian rocks are found, trilobites are likely to be the most abundant fossils. New species of trilobites appeared at a rapid rate during the Cambrian and Ordovician, but soon thereafter they began to decline, finally becoming extinct in the Permian (Fig. 11.23).

Study Questions

1. By comparison with the illustrations (Figs. 11.21 and 11.22), identify as many of the trilobites in the study set as you can. What types of preservation are represented?

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2. Figure 11.24 shows the molted cephalon of the Ordovician trilobite *Calliops.* What kind of eyes did this trilobite possess?

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3. Sketch the most perfectly preserved trilobite specimen and label the pygidium, thorax, axial lobe, pleural lobes, and cephalon.

4. How do trilobites grow? Is it possible to have several fossil trilobites from a single individual?

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5. The eyes of trilobites can be used to make inferences about their living habits. How would you match the eye adaptations with the living habits?

a. Dwellers on surface of sea floor

b. Active swimmers

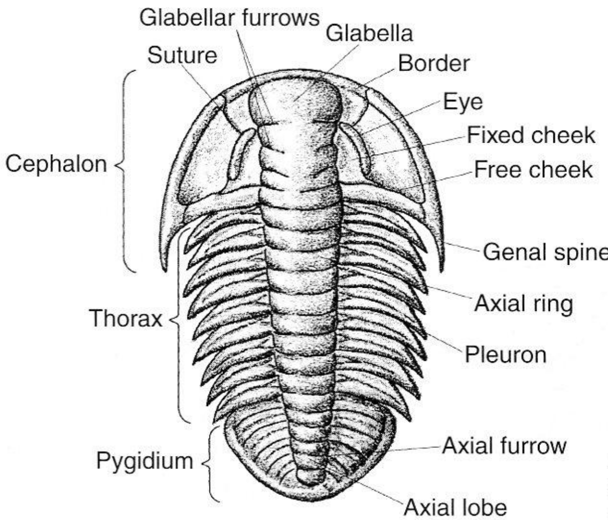
c. Ooze dwellers

d. Burrowers

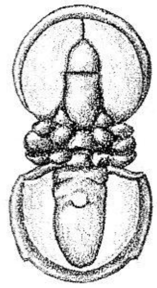
_____ Eyes on the dorsal surface of cephalon
_____ Eyes on ventral side of cephalon
_____ Eyes on end of long stalks on dorsal side of cephalon
_____ Eyes lacking or functionless

Figure 11.21 Trilobites, plate A.

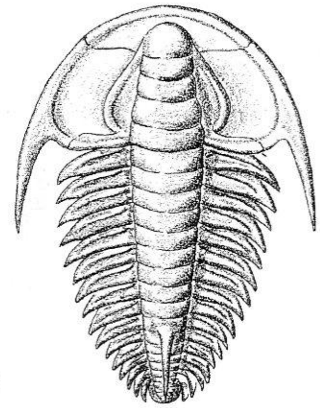
From Levin, H. L., *Ancient Invertebrates and Their Living Relatives*, Upper Saddle River, NJ: Prentice Hall, 1999.



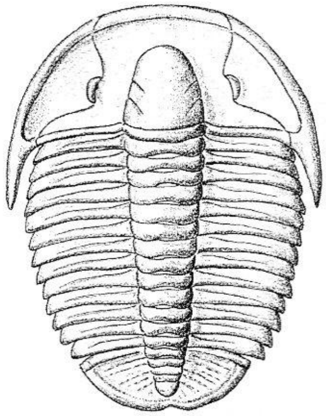
Bathyuriscus. Length 4 cm. (Cambriam)



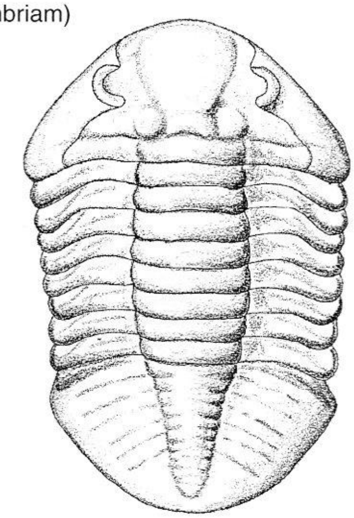
Agnostus. Length of specimen 0.7 mm. (Cambrian)



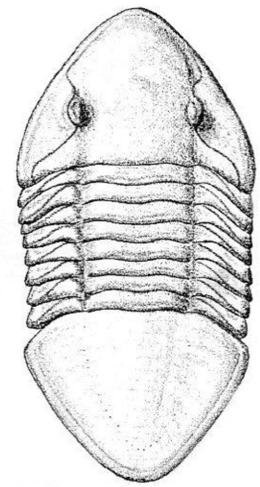
Redlichia. Length about 10 cm. (Cambrian)



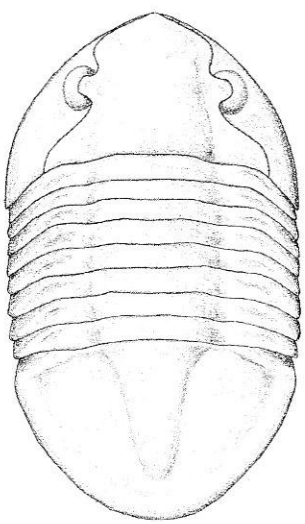
Elrathia. Length 2.3 cm. (Cambrian)



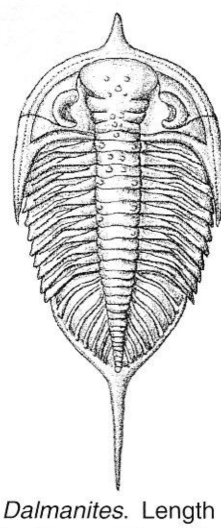
Asaphus. Length up to 8 cm. (Ord.)



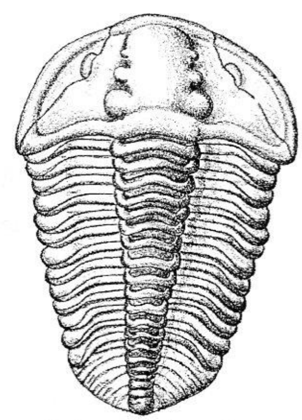
Isotelus. Length 3 to 15 cm. (Ordovician)



Homotelus. Maximum length about 15 cm. (Ordovician)



Dalmanites. Length up to 10 cm. (Silurian)



Calymene. Length up to 10 cm. (Sil.–Dev.)

Figure 11.22 Trilobites, plate B.

From Levin, H. L., *Ancient Invertebrates and Their Living Relatives*, Upper Saddle River, NJ: Prentice Hall, 1999.

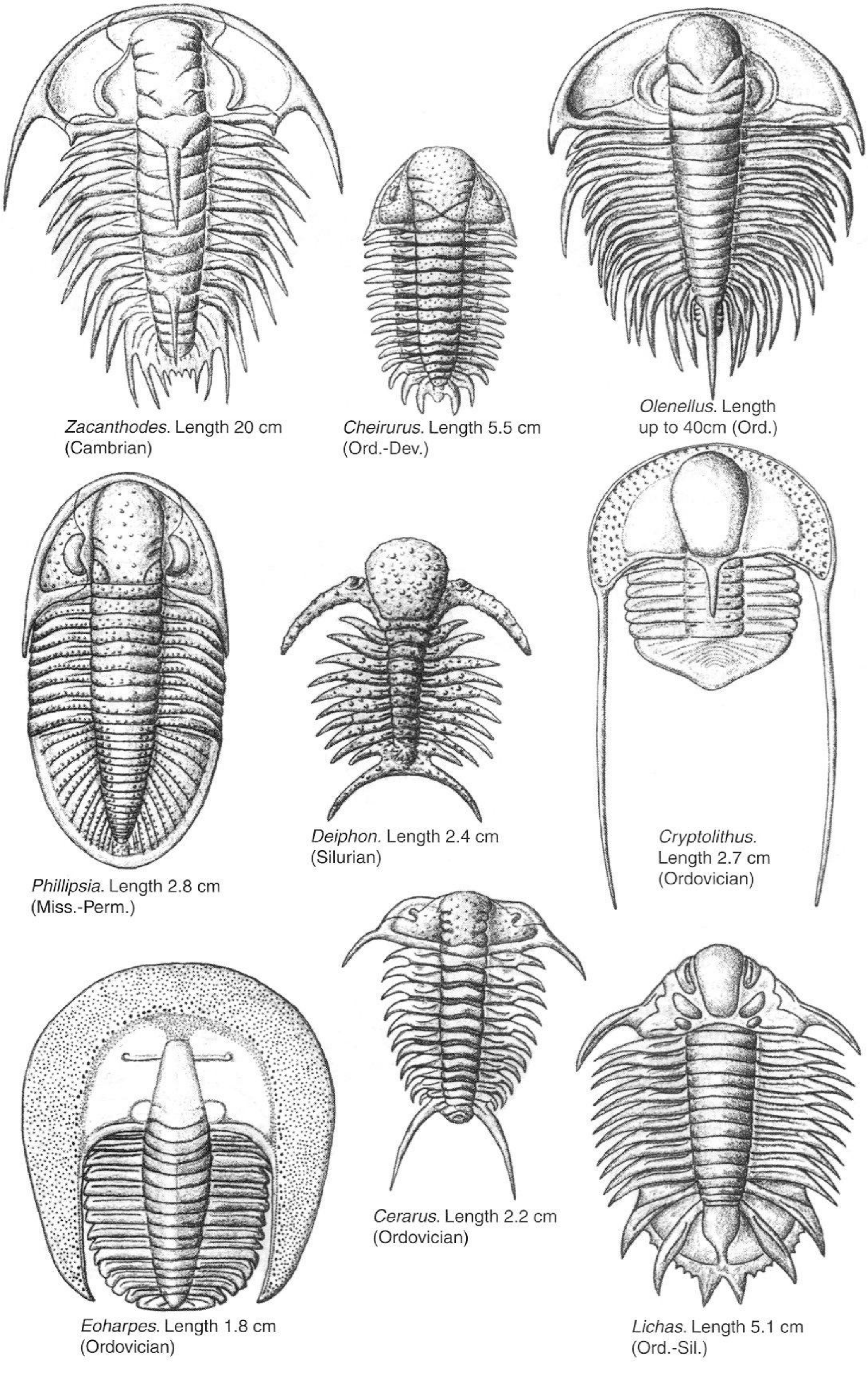


Figure 11.23 Geologic range of trilobites.

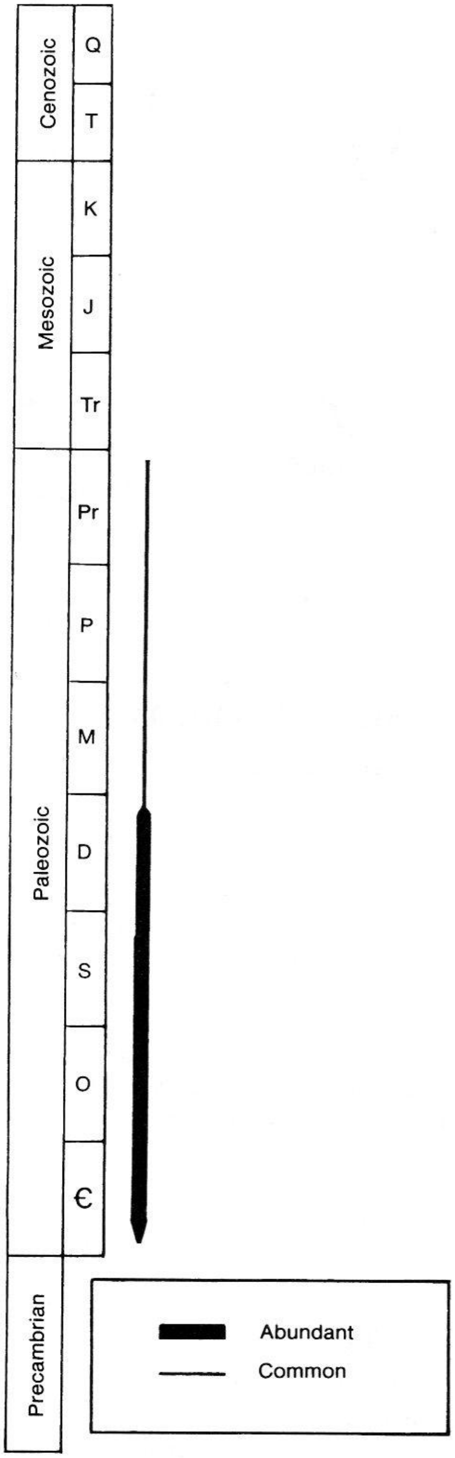


Figure 11.24 Cephalon of *Calliops callicephala* (Ordovician).

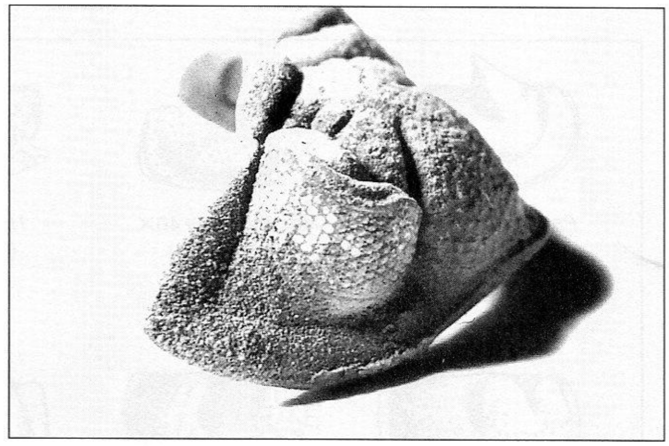
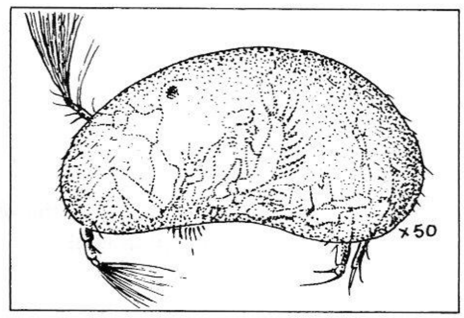


Figure 11.25 A living species of ostracode.



6. What are the three longitudinal primary divisions of the trilobite carapace?

____

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What are the three primary divisions occurring transverse to the longitudinal divisions?

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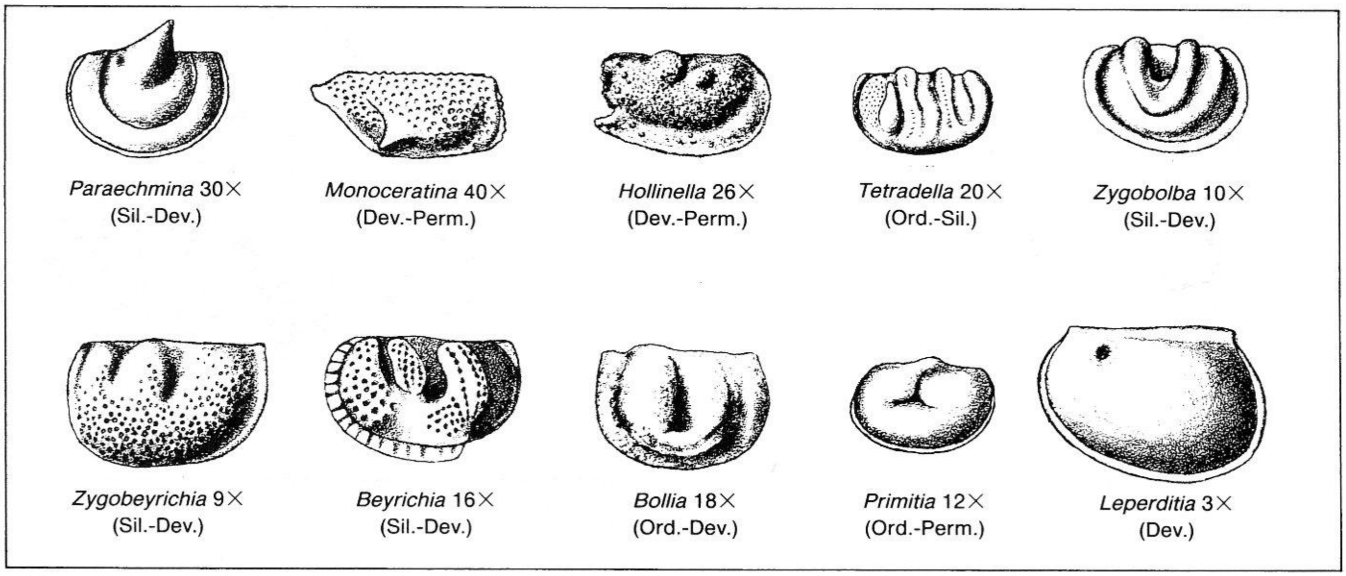
Ostracoda

The **ostracodes** are small, lentil-shaped **crustaceans** with a bivalved shell **(carapace)** enclosing an indistinctly segmented body, from which extend seven pairs of appendages (Fig. 11.25). Adult carapaces are mostly between 0.5 and 4.0 mm in length, are composed of chitin and calcium carbonate, and are articulated along the dorsal margin. Ornamentation and sculpture of the carapace are often intricate and always useful in identification of species.

Ostracodes appeared in the Early Ordovician and are still common today in both marine and freshwater bodies. Like trilobites, they grow by molting. They commonly are found crawling, swimming, and generally swarming about near the bottom of the sea or lake.

Figure 11.26 Paleozoic Ostracoda.

Partly from Collinson, C. W., 1959, Illinois State Geological Survey, Educational Series 4.



Fossil ostracodes (Fig. 11.26) are valuable aids in stratigraphic correlation. Because of their small size, they can be obtained from samples of well cuttings. In Paleozoic strata where small fossils are not so plentiful, the ostracodes are used in correlating strata from well to well.

Study Questions

1. Examine the prepared slide of ostracodes and sketch one of the specimens.

2. What other fossil invertebrates have you studied that are bivalved? How might you distinguish the bivalve carapace of ostracodes from the valves of other invertebrates that have two valves?

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The Echinodermata

The Phylum Echinodermata (Fig. 11.27) contains highly developed animals with typically pentamerous (five-fold) symmetry and a skeleton often knobby or studded with spines. Another unique characteristic of the phylum is the presence of fluid-filled **tube feet** (Fig. 11.28), which aid in locomotion and obtaining food. The tube feet are only a part of the water vascular system that characterizes members of the phylum.

The Phylum Echinodermata can be subdivided into seven to twelve classes, some of which were short-lived echinoderm classes in the Lower Paleozoic. Although they were clearly echinoderms, their characteristics were so different from other known echinoderms that separate classes were assigned, and controversy in assignment of these classes has caused the variety of number. In this examination of the fossil record, only the more familiar echinoderms are included.

Class Asteroidea

Members of the Class Asteroidea typically have five arms that radiate outward from an ill-defined central disc. There are two to four rows of tube feet in each arm. The body (Fig. 11.28) is encased in a leathery "skin" studded with small calcareous plates. Upon death and decay, the leathery covering is often lost and the plates swept away. As a result, fossil remains of starfish are not common. Asteroids are predators of worms, crustaceans, and mollusks. Although some species inhabit the deeper parts of the oceans, the majority live within the littoral zone. The asteroids range from Ordovician to the present (Fig. 11.29).

Figure 11.27 Diversity of living echinoderms.

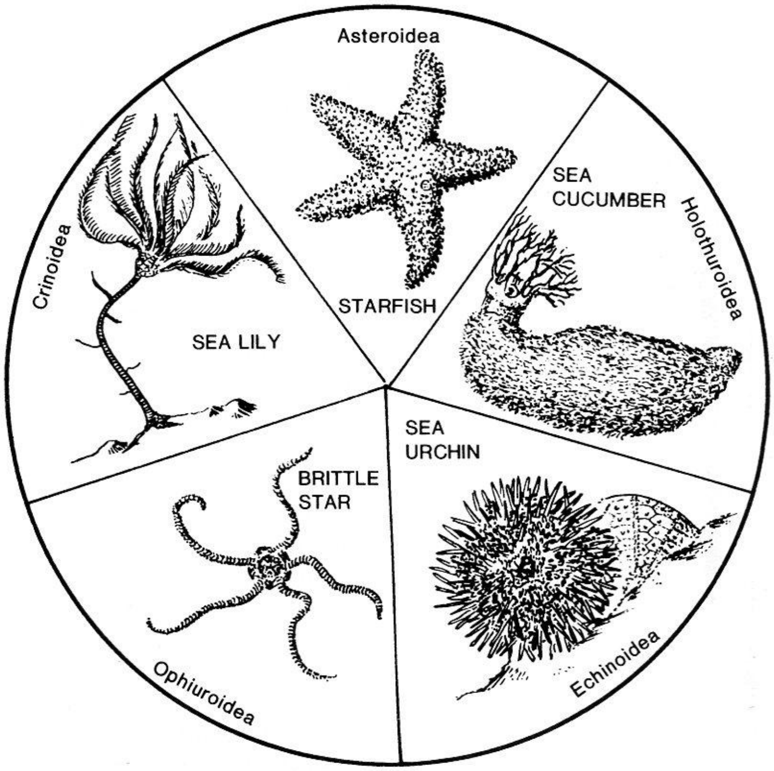
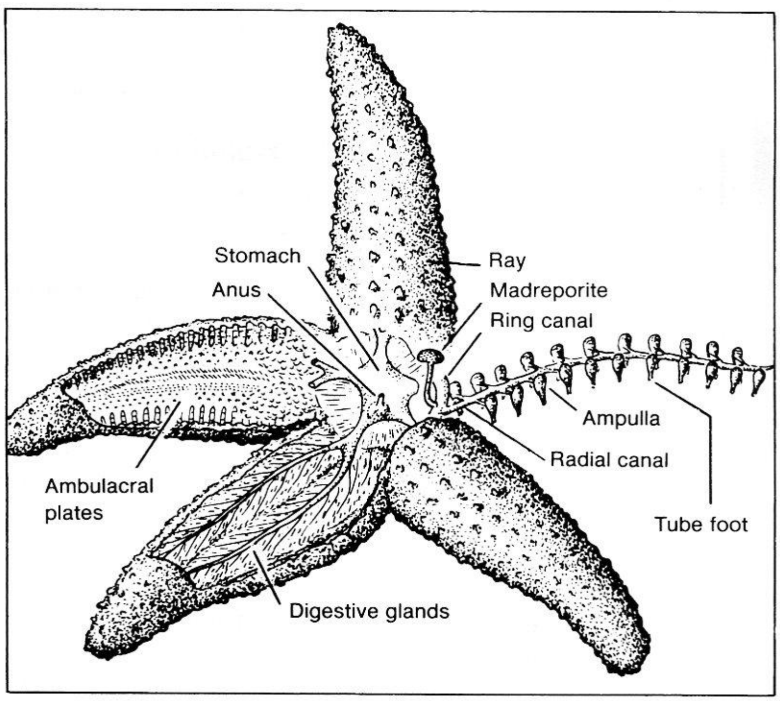


Figure 11.28 Diagram of starfish organs.



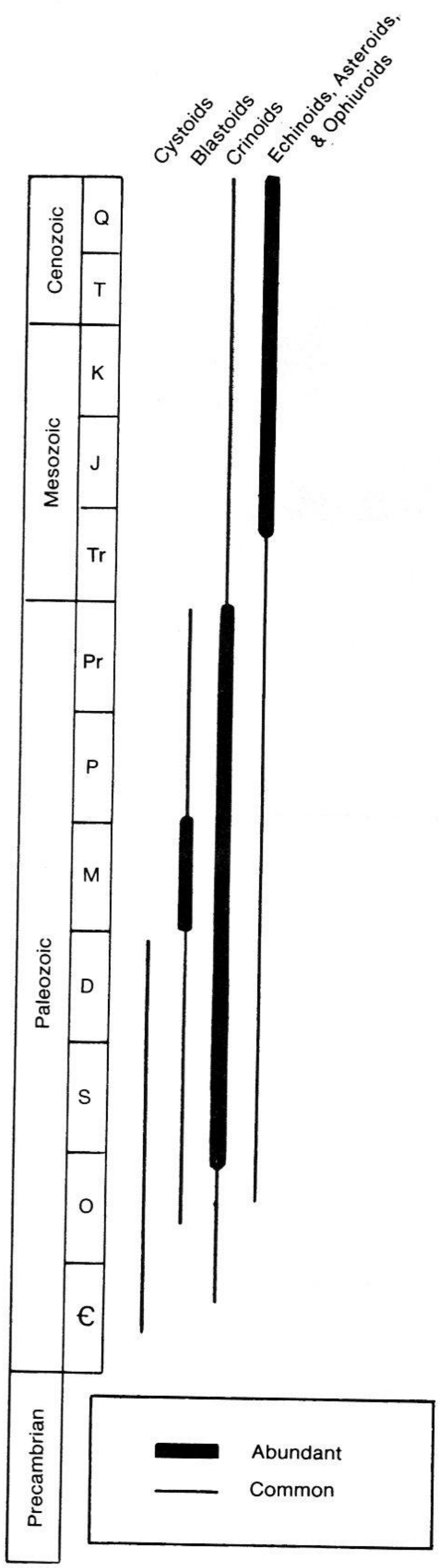


Figure 11.29 Geologic ranges of some important groups within the phylum of Echinodermata.

Class Ophiuroidea

The ophiuroids (brittle stars) differ from the common starfish in their small, sharply delimited central disc and long serpentlike slender arms. Another difference is that the arms lack grooves (**ambulacral** [grooves]) for transporting food particles toward the mouth, and food is taken in only at the mouth on the ventral side of the oral or central disc. The tube feet have sensory and locomotor functions and occur on the ventral sides of the arms. Ophiuroids are known from rocks as old as Ordovician, but they are not common fossils.

Class Echinoidea

The **echinoids** (Fig. 11.30) vary in shape from spheroidal (Fig. 11.31) to flattened discoidal. An echinoid can be compared to a starfish with its arms pulled up over its aboral surface. Five grooves with tube feet, called ambulacral areas, radiate from the mouth up to the opposite (aboral) surface. In flattened forms, the mouth and anus appear on the anterior and posterior periphery. In a typical spheroidal form, the mouth is on the lower surface and may be armed with five sharp teeth as part of a masticatory apparatus called the **"Aristotle's lantern."** Typically, the shell consists of twenty rows of plates. Five of these correspond to the arms of the starfish and are perforated by holes for the tube feet. Regularly arranged tubercles occur on the plates and mark the position at which spines were articulated. Locomotion is accomplished by movement of tube feet and spines.

Echinoids occur at all depths in the sea but prefer warm, shallow waters. They feed largely on seaweed but are known to eat dead animal matter that they come upon. Although echinoids have been found in rocks as old as Ordovician, they did not become abundant as fossils until the Jurassic. Cretaceous and Cenozoic echinoids are common and are widely used as index fossils.

Class Holothuroidea

Perhaps the most bizarre of the echinoderms are the Holothuroidea, exemplified by the "sea cucumber" (Fig. 11.32). The body is sausage-shaped, there are no arms or spines, and the skeleton is composed of numerous microscopic, oddly shaped calcareous ossicles called holothurian sclerites (Fig. 11.32B). Its echinoderm characteristics can be observed most readily in the five longitudinal rows of tube feet. Fossil holothurian sclerites are known from rocks as old as Mississippian. They are sometimes found in rocks being prepared for studies of microfossils such as foraminifers and ostracodes.

Class Crinoidea

The name "sea lily" is descriptively appropriate, though biologically incorrect, for this group of animals. In a way, the **crinoid** (Fig. 11.33) can be regarded as an inverted starfish with a stalk or stem attached to the underside. The crinoid is composed of three main parts: the calyx, the arms, and the stem (Fig. 11.34). Most of the vital organs are encased in the cuplike **calyx** or head of calcareous plates. The mouth is on the upper surface, and the anus is located to one side of

Figure 11.30 Echinoderms.

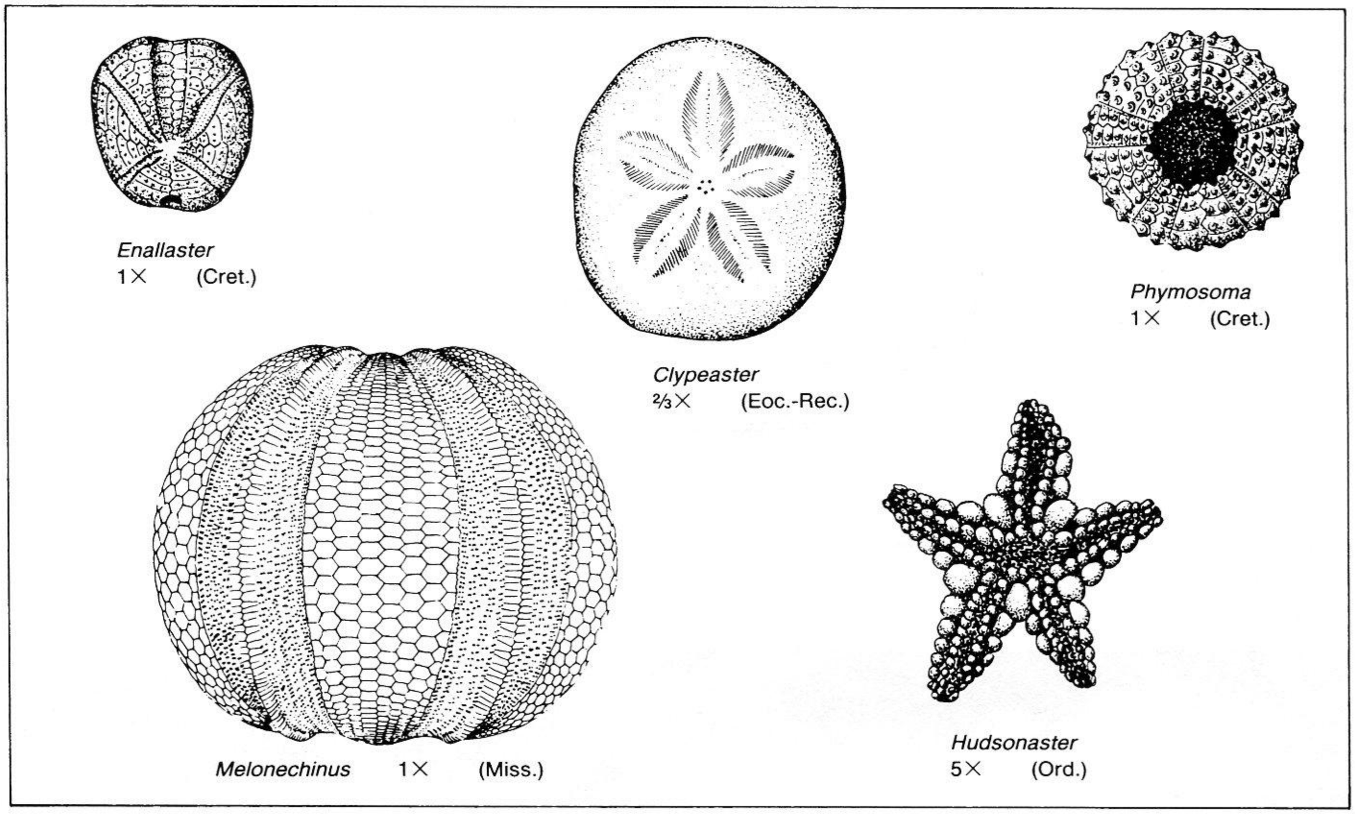


Figure 11.31 (A) Aboral view of a sea urchin with spines removed. (B) Aristotle's lantern. Redrawn from R. T. Jackson, Phylogeny of the Echini, with revision of Paleozoic species.

From *Boston Society of Natural History*, Memoir 7.

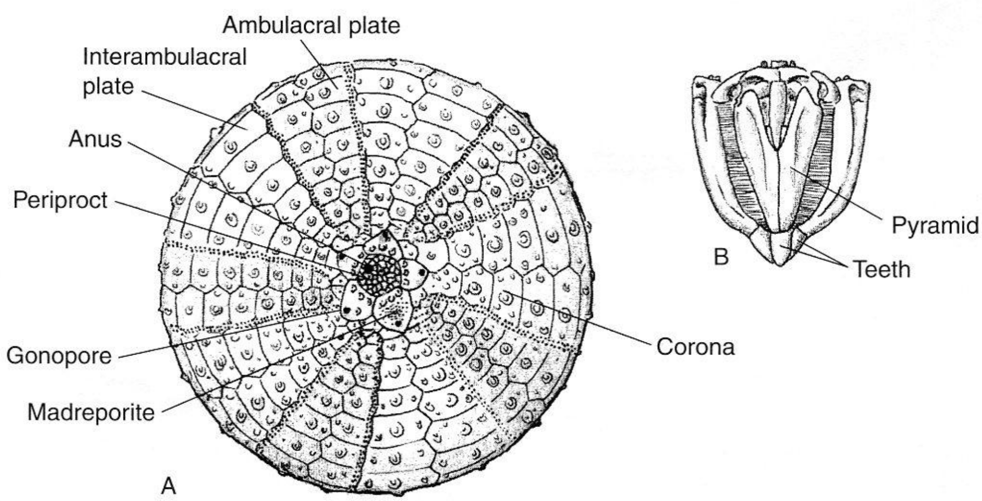


Figure 11.32 (A) External view of a sea cucumber or holothuroid (x0.4).(B) Holothurian sclerites (x30).

From Levin, H. L., *Ancient Invertebrates and Their Living Relatives*, Upper Saddle River, NJ: Prentice Hall, 1999.

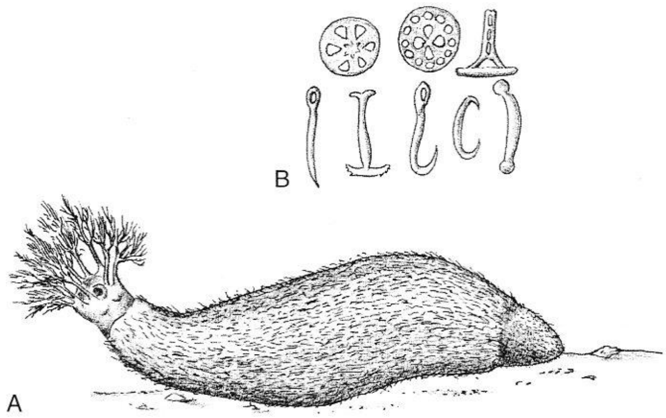


Figure 11.33 Limestone slab containing well-preserved Mississippian crinoids.

Photograph courtesy of Wards Natural Science Establishment, Rochester, New York.

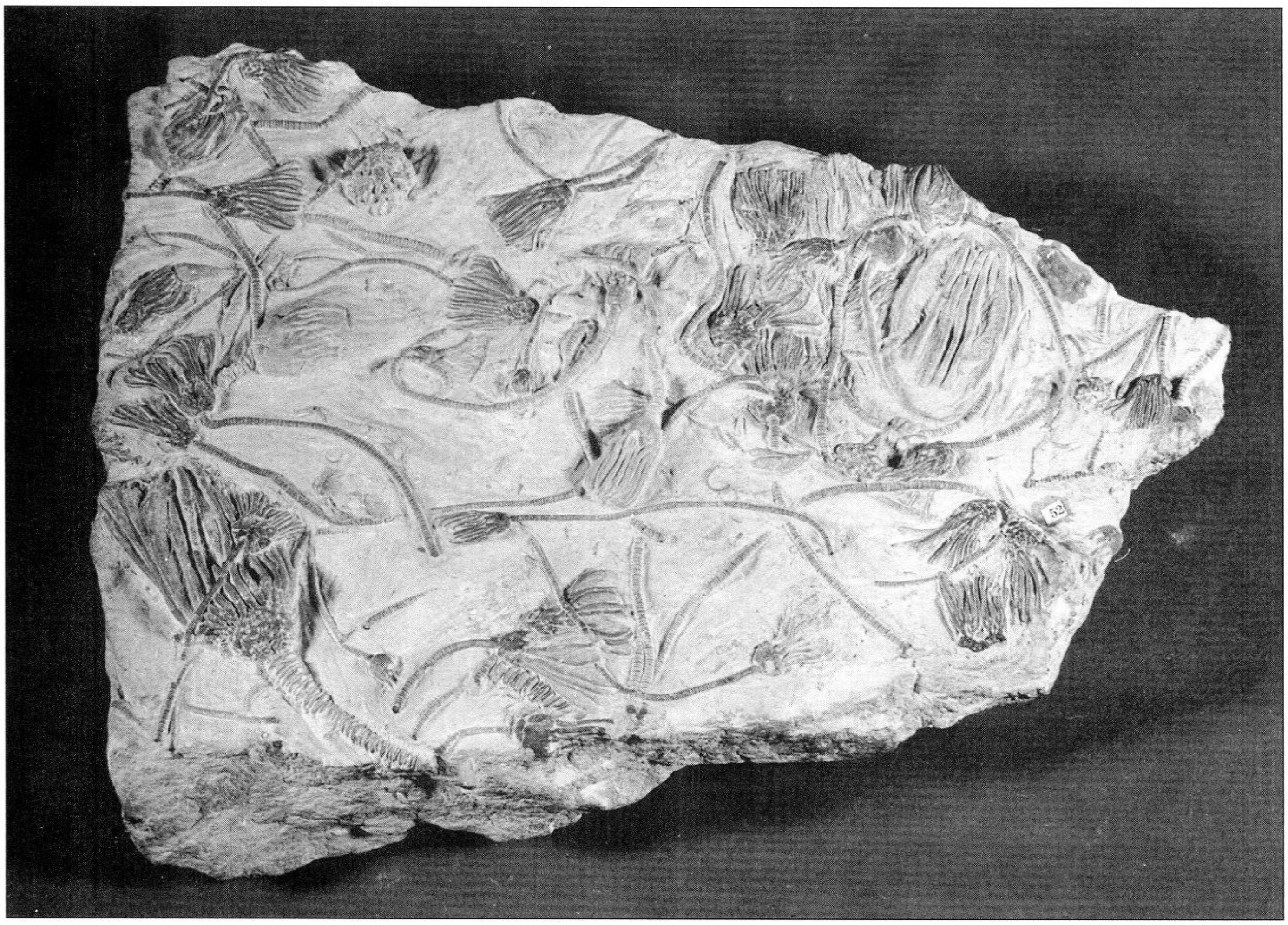
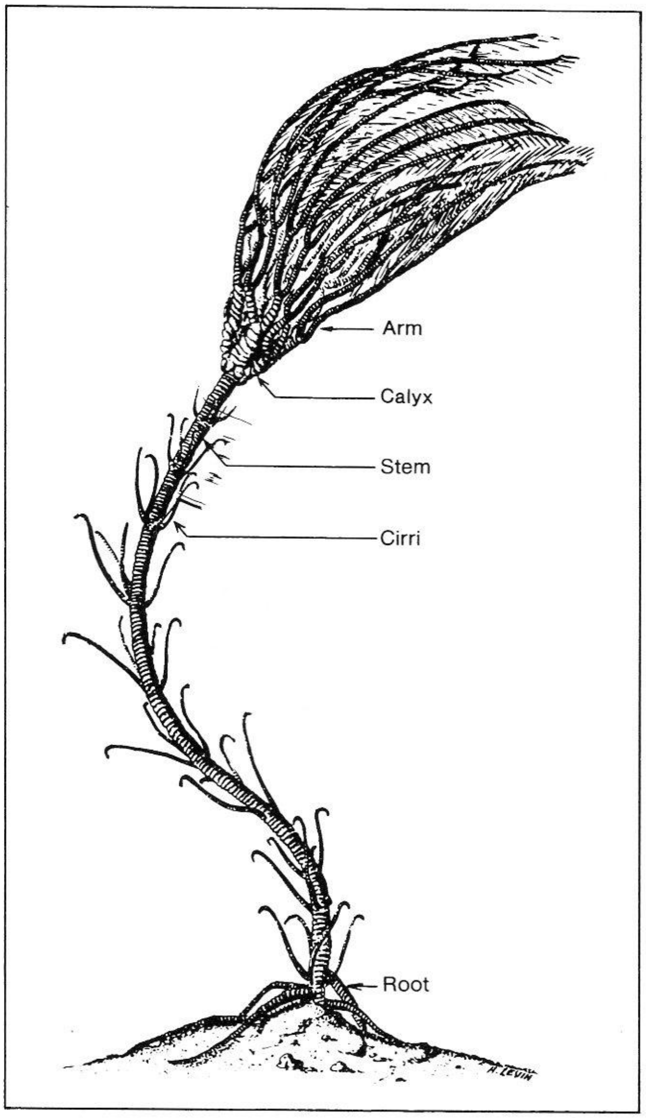


Figure 11.34 Restoration of a crinoid.



the mouth. Five branching arms extend upward from the calyx. They bear food grooves, barblike pinnules, and cilia, which aid in food gathering. In some living and most ancient forms, a long stem composed of calcareous disclike plates extends downward from the bottom of the calyx for attachment to the sea floor. Disaggregated plates of crinoid stems, arms, and calyx are common fossils. Unfortunately, the complete calyx, which is important in species identification, is rarely found.

Although not so numerous and varied as their Paleozoic ancestors (Fig. 11.35), the crinoids of present seas are notably present in both shallow and deep waters between about 50°S and 80°N latitude. The majority of modern forms are free living, are gregarious, and prefer relatively clear, well-aerated water with an abundance of minute planktonic organisms for food.

Crinoids first appeared in Ordovician rocks, but their golden age was the Mississippian (Fig. 11.36). During that period, crinoid skeletal plates littered the sea floor, forming extensive layers of crinoidal limestone. The Mississippian was truly an "Age of Crinoids." These echinoderms have never since been as numerous nor as varied.

Class Blastoidea

The stalked echinoderms known as **blastoids** (Fig. 11.37) exhibit more readily apparent pentaradiate symmetry than the crinoids. Typically, the budlike calyx (Fig. 11.38) is pentagonal, with five ambulacra radiating symmetrically from the mouth. Thirteen plates (three basals, five radials, and five interradials) enclose the space not occupied by the ambulacral areas. Each ambulacrum possesses a centrally located food groove that branches laterally into side food grooves. Threadlike brachioles extend from the lateral margins of the ambulacra and function in food gathering in a fashion similar to that of the arms of crinoids.

The geologic range of blastoids is Ordovician through Permian (see Fig. 11.29). As with the crinoids, they were most numerous during the Mississippian. Because blastoids have been totally extinct since the Permian, their paleoecology is based largely on organisms found associated with them in rock strata. Such evidence suggests that blastoids lived in clear, shallow marine areas. Almost all are found in limestones and limy shales.

Class Cystoidea*

The pentamerous symmetry that characterizes many classes of echinoderms is poorly shown or even absent in the cystoids (see Fig. 11.38). The calyx has a dorsally located mouth, and the anus is situated on the oral side in an eccentric position. The plates of the calyx may be symmetrically or asymmetrically arranged and are pore-bearing. **Cystoids** (see Fig. 11.29) are found chiefly in Ordovician and Silurian rocks, although their complete geologic range is from the Cambrian to the Upper Devonian.

Study Questions

1. Examine a preserved specimen or a dried specimen of the common starfish *Asterias.* Locate the ambulacral grooves, madreporite (see Fig. 11.28), and position of the mouth. Note the tube feet on the preserved specimen. Prepare a sketch and label features visible on oral and aboral *sides.*

* The class Cystoidea has been recently dismantled and its members placed in either the class Rhombifera or Diploporita. The designation Cystoidea is retained here for simplicity.

Figure 11.35 Fossil crinoids.

Partly from Collinson, C. W., 1959, Illinois State Geological Survey, Educational Series 4.

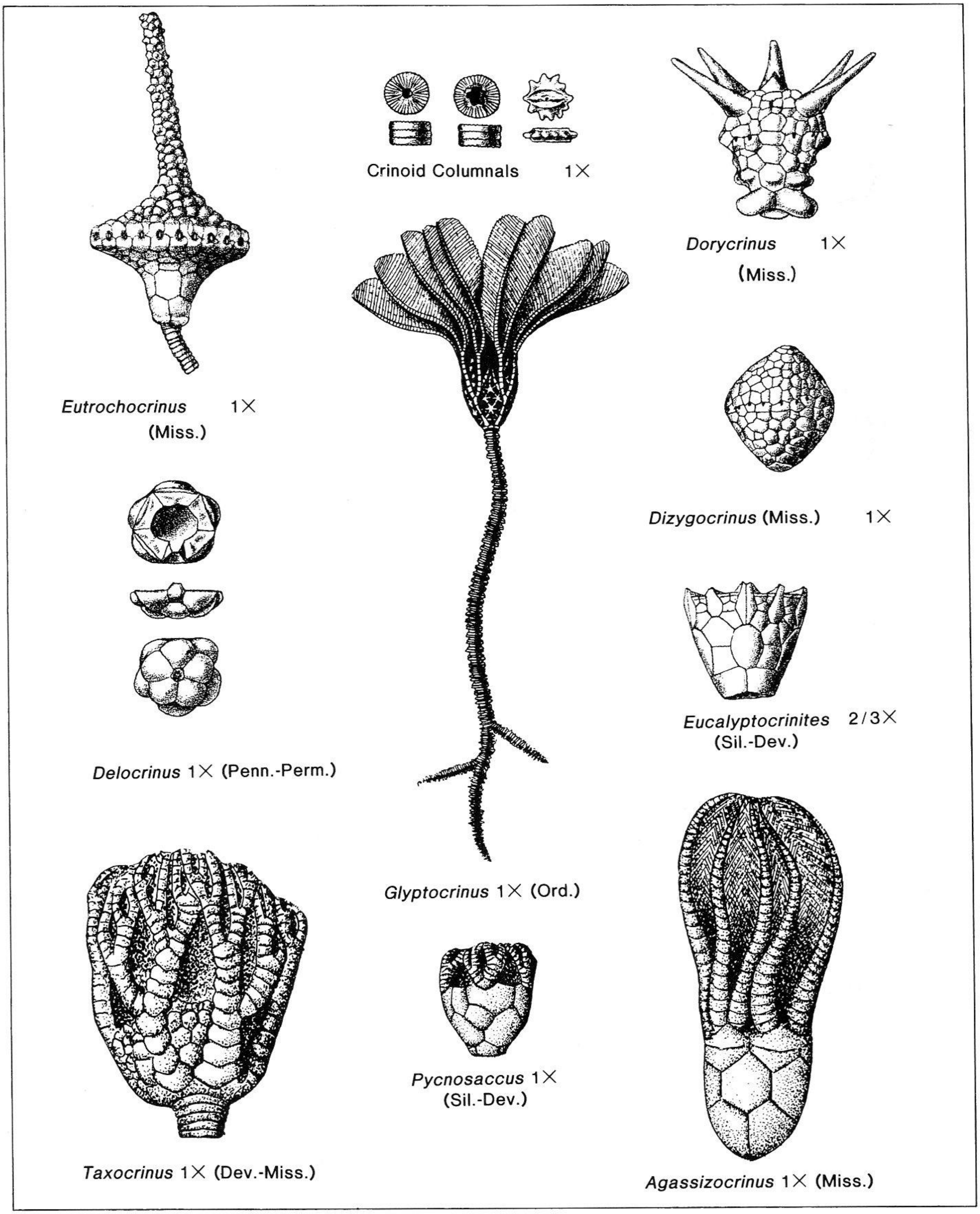
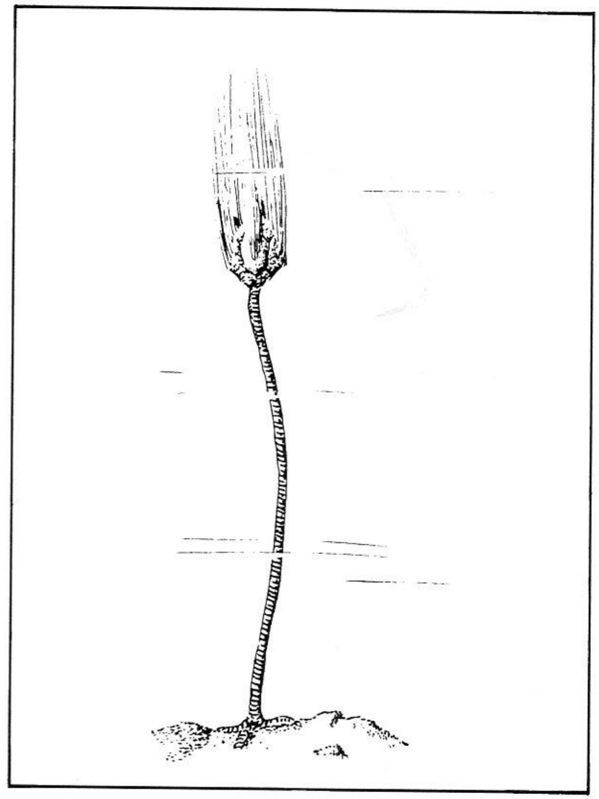


Figure 11.36 Reconstruction of a Mississippian sea floor with abundant crinoids.

Courtesy of the United States National Natural History Museum.

2. Examine a dried specimen of an echinoid, or a well-preserved fossil echinoid from your study set. Sketch the oral and aboral surfaces and label ambulacral areas, mouth, anus, and pores for tube feet.

Figure 11.37 Restoration of a blastoid.



3. Lightly shade in the ambulacral areas on the illustrations of *Melonechinus* and *Phymosoma* in Figure 11.29 and of *Pentremites* in Figure 11.38.

4. What skeletal features of crinoids are also present in blastoids?

5. Label the brachioles, calyx, and stem on the illustration of the blastoid in Figure 11.37.

6. Very intricate relationships exist between living animals, but only rarely do fossils indicate to us the complexity of some of these relationships as they existed long ago. Two basic types of relationships are **antagonism,** in which one species suffers through the action of another, and **symbiosis,** in which one or both species benefit, but neither is really harmed. Figure 11.39 shows two views of a relationship in which a snail shell is in position over the anal opening of a blastoid.

Figure 11.38 Cystoids (top row) and blastoids.

Partly from Collinson, C. W., 1959, Illinois State Geological Survey, Educational Series 4.

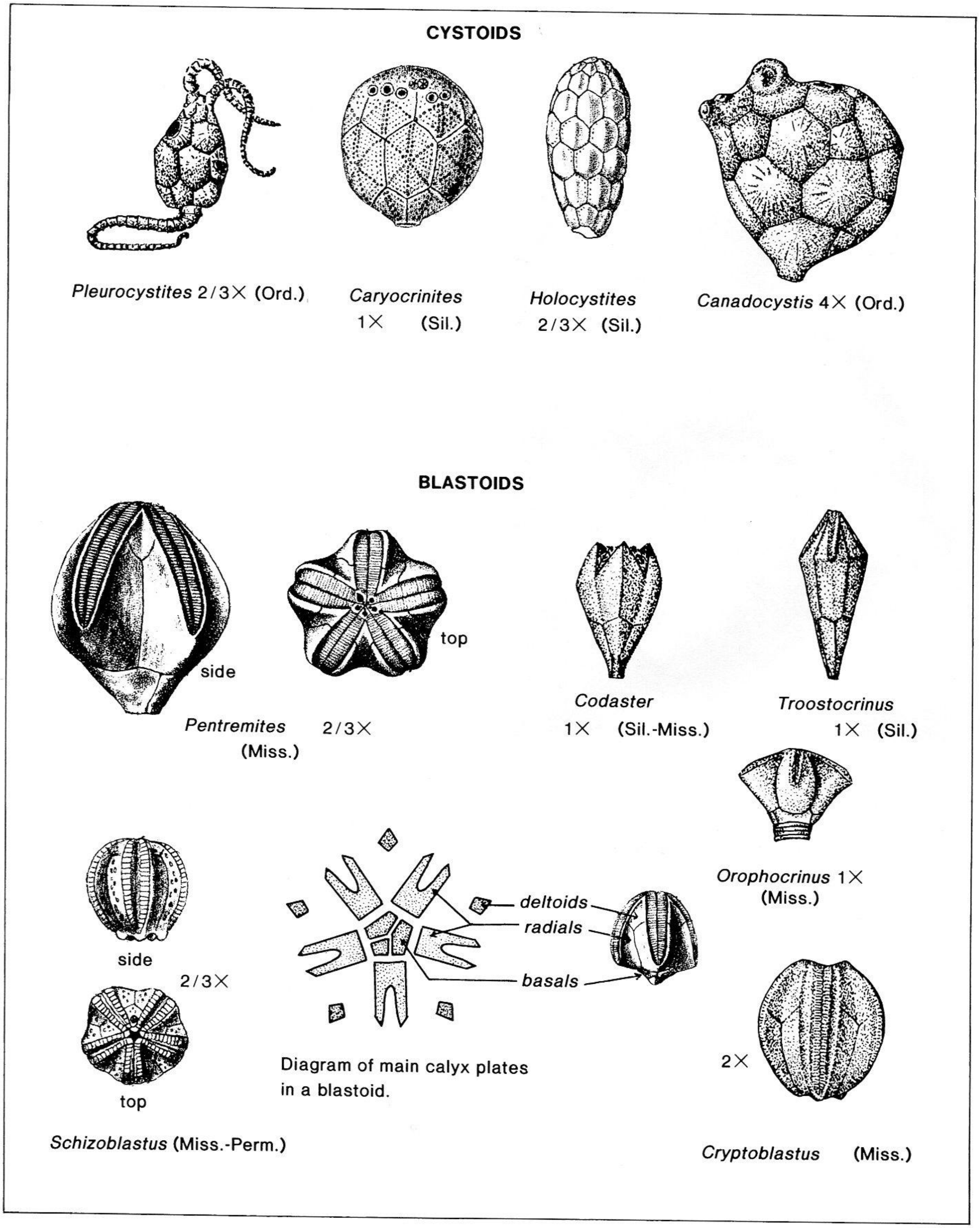
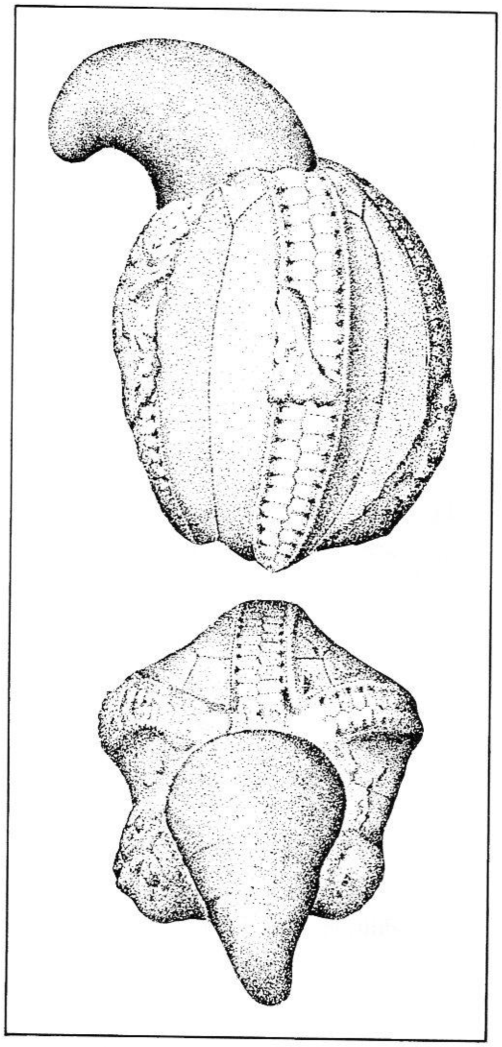


Figure 11.39 Coprophagous relationship between blastoid and snail.



The fossils were collected from Mississippian strata near St. Louis, Missouri. Is this an example of symbiosis or antagonism? If this is symbiosis, is it possible that both organisms benefited, and if so, how?

7. On Figure 11.39, label a central food groove, a side food groove, a radial plate, and a deltoid plate.

Graptolites

Graptolites (Fig. 11.40) are a group of extinct organisms once thought to be plants and later considered coelenterates, then bryozoans; most recently they have been classified by some paleontologists as primitive members of the Phylum Chordata. They, like the bryozoa, were microscopic, suspension-feeding individuals grouped together into colonies. Their skeletons were of a chitinous rather than calcareous material.

Graptolites are typically preserved as carbon films in black shales. They resemble pencil marks that have a saw-tooth appearance; hence the name *graptos* (written) *lithos* (rock). The preserved colonies are termed rhabdosomes and consist of one or more narrow branches called **stipes.** The stipe results from the uniserial or biserial arrangement of cup-like **theca** composed of a type of chitin.

Most graptolites can be identified as belonging to one of two major categories. The first comprises the *dendroid graptolites,* which built complex, branching, fan-shaped rhabdosomes. Some dendroid graptolites may have attached their bases to the sea floor. Others are believed to have suspended themselves from some floating object by a threadlike tube known as the nema.

The second category of graptolites are termed *graptoloid.* They were planktonic forms with distinctive patterns of thecae. The graptoloid rhabdosome generally was composed of far fewer stipes than the rhabdosome of dendroids. In their evolution, they underwent a progressive reduction in the number of stipes. In general, Lower Ordovician beds contain graptolites with more stipes than Middle and Upper Ordovician strata. Silurian graptolites characteristically are constructed of only one stipe.

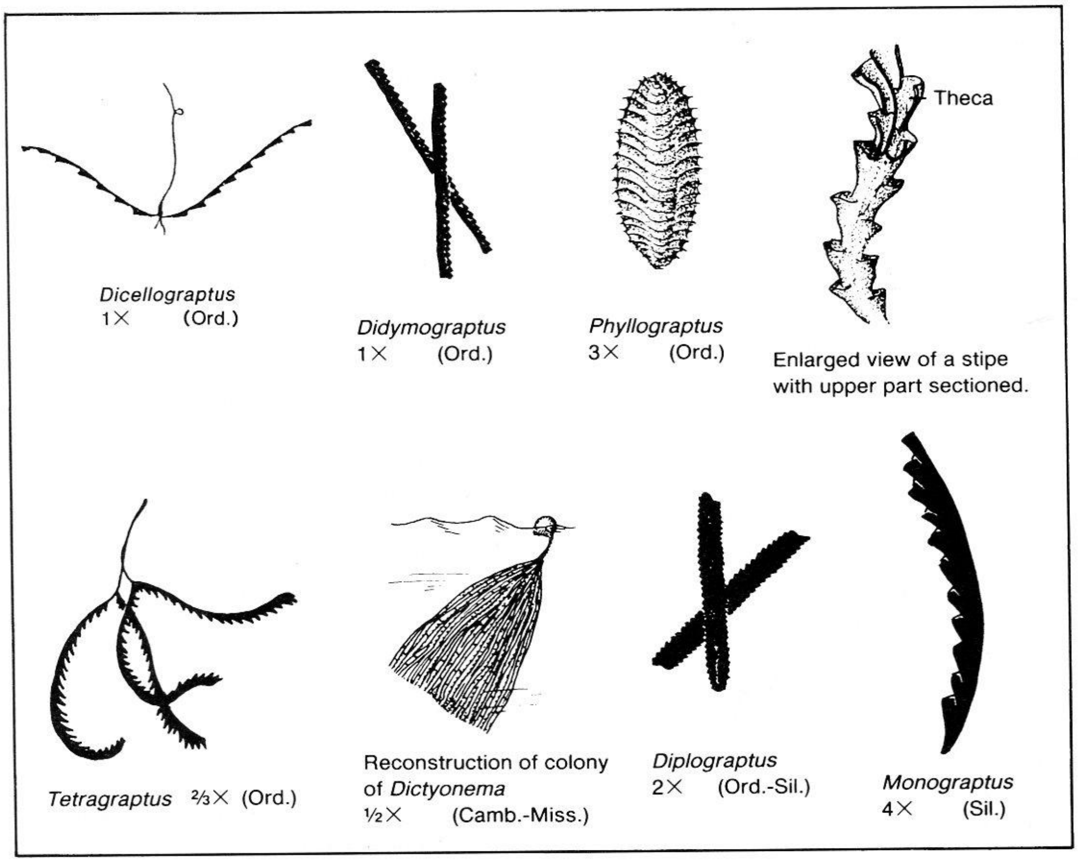
Graptolites are known from rocks of Cambrian through Mississippian age, but they are of greatest importance during the Ordovician and Silurian. Their worldwide distribution and rapid evolution have made them ideal index fossils of special importance in studies of Early Paleozoic strata.

Study Questions

1. Where on the graptolite colony did the individual animals live?

2. How do graptolites differ from corals in living habit and skeleton?

Figure 11.40 Graptolites.



3. How did the living habits of graptolites contribute to their being good index fossils?

Fossil Plants

Plants are multicellular organisms that typically live on land and carry out photosynthesis. They possess photosynthetic pigments, such as chlorophyll, located in cell organelles called chloroplasts. All plants can be placed in one of two groups: the *nonvascular plants* and the **vascular plants.** Nonvascular plants include liverworts, mosses, and hornworts. Such plants have a scant fossil record. The fossil record for vascular plants, however, is noteworthy and warrants examination.

Vascular plants have special tissues and canals to transport moisture and nutrients from beneath the ground to the chlorophyll-bearing leaves where photosynthesis is accomplished. In addition to a vascular transport system, most vascular plants also have features to prevent desiccation, to support the weight of the plant, and to facilitate reproduction on land. There are three major groups of vascular plants: plants that do not bear seeds and utilize spores in reproduction (such as true ferns), plants that bear naked seeds (such as pine trees), and plants with protected seeds and flowers.

Our knowledge of the evolution of plants is vastly improved by the study of **spores** and **pollen** grains (called **palynology**). Produced in vast numbers, these reproductive cells can be transported far and wide by wind and water. Eventually, many are deposited on the floors of lakes, seas, and oceans where they are preserved and become valuable as paleoclimatic indicators and for biostratigraphic correlation.

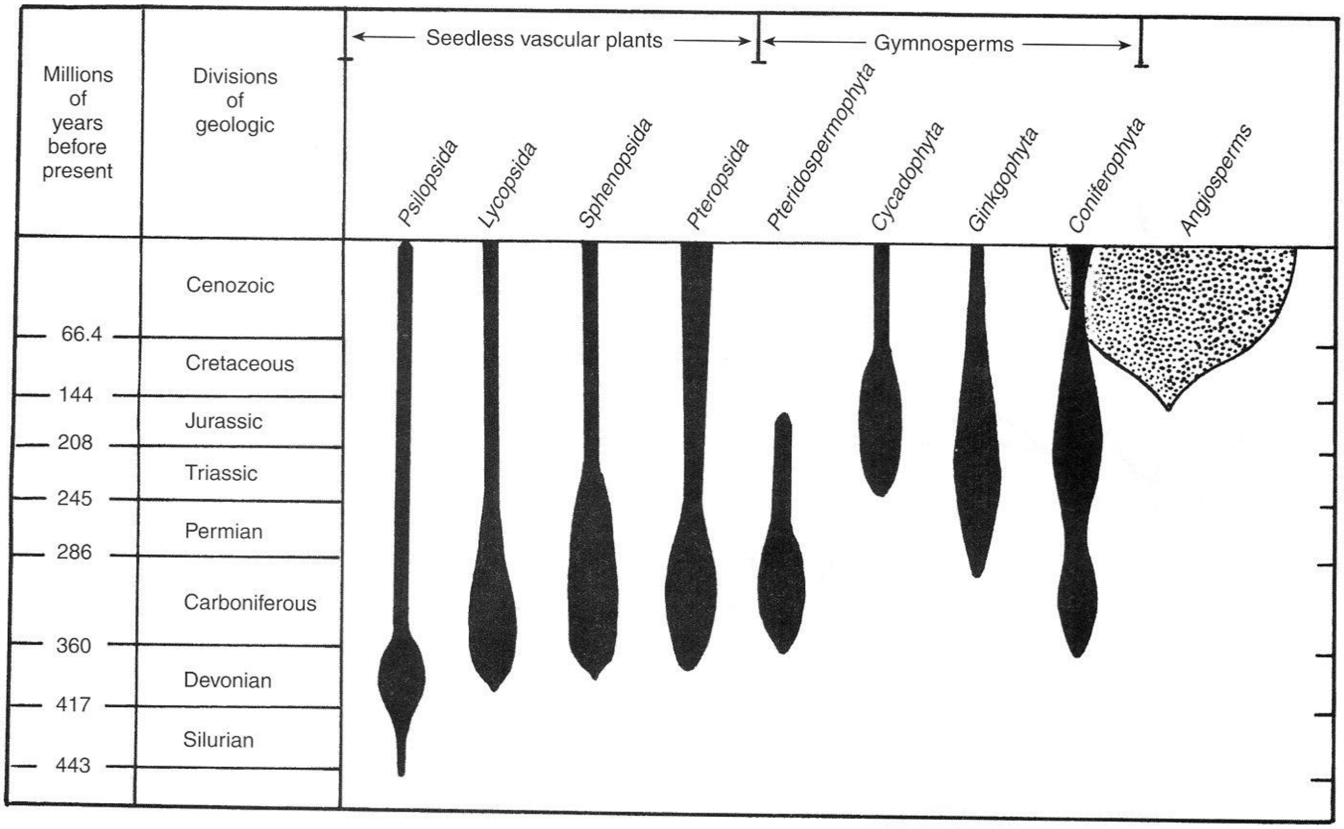
Although a detailed study of plant evolution and palynology is beyond the scope of this introductory manual, some recognition of the more common plant fossils is desirable. The following descriptions will be useful in identifying the more frequently encountered plant fossils.

Seedless Vascular Plants

The first plants to invade the land were spore-bearing, seedless, vascular plants. Precisely when this plant invasion occurred is somewhat uncertain (Fig. 11.41). The first scraps of vascular tissue containing strands of wood are Early Silurian

Figure 11.41 Geologic ranges, relative abundances, and evolutionary relationships of vascular land plants.

From Levin, H. L., *The Earth Through Time*, Philadelphia: Saunders College Publishing, 1992.



in age. However, spores having three radiating scars (so-called trilete spores), resembling those of seedless vascular plants, become relatively abundant in rocks of Late Ordovician age, strongly suggesting the presence of these land plants at that time.

Among spore-bearing plants, the adult plant *(sporophyte)* produces the reproductive cells called spores. The spores do not require fertilization. When spores are dropped to the moist ground, they develop into small, leafless plants called *gametophytes.* A gametophyte, in turn, produces egg and sperm. When the egg is fertilized by contact with sperm, it develops into a new sporophyte. Such reproduction requires a moist environment to prevent dehydration of the egg or sperm.

The **psilophytes** are a group of Early Paleozoic spore-bearers that represent the vanguard of the land invasion. Psilophytes were small plants (rarely more than 30 cm in height) characterized by horizontal stalks **(rhizomes)** that grew just under the surface of the ground in moist soil. Short, slender stems bearing spore sacks **(sporangia)** grew upward above the soil (Fig. 11.42). The plant had neither true leaves nor roots. From these relatively unimpressive plants, however, huge trees developed during the Late Paleozoic. In swampy regions, the accumulation of dead vegetation from these trees provided the material that was eventually converted to coal. Among the principal plants of these "coal forests" were *lycopsids, sphenopsids, true ferns,* and *progymnosperms.*

Today, lycopsids are represented by relatively small plants like the "ground pine" and club mosses. In the late Paleozoic, however, lycopsids with robust trunks and extensive root systems towered 40 m above the ground. Most had long, slender leaves attached directly to the limbs in a spiral arrangement. When these leaves were released, they left diamond-shaped leaf scars (Fig. 11.43). For this reason, lycopsids are dubbed "scale trees."

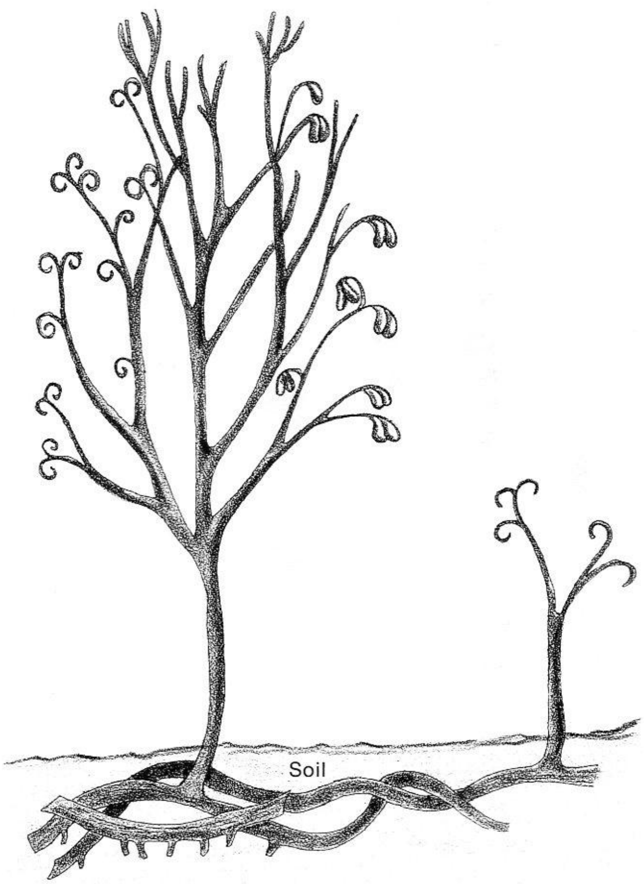
Growing side by side with the scale trees in late Paleozoic forests were the joint-stemmed *sphenopsids.* Scouring rushes and horsetails are living sphenopsids. Extinct forms such as *Calamites* and *Annularia* had unbranched, longitudinally ribbed stems (Fig. 11.43). Circlets of slender leaves grew at each transverse joint of the stems.

True ferns (*pteridophytes*), like *Pecopteris,* were also present among the lycopsids and sphenopsids. Unlike modern ferns, which are generally small, the ferns of the late Paleozoic grew to lofty heights. Spores often were carried in sporangia located on the undersides of leaves.

The final group of seedless plants with a significant fossil record are the *progymnosperms.* As one might surmise from their name, this group of seedless vascular plants are the probable ancestors of the early seed-bearing plants. Indeed, both groups have similar wood tissue.

Figure 11.42 A psilophyte from the Lower Devonian. These primitive small plants rarely exceeded 30 cm in height.

From Levin, H. L., *The Earth Through Time,* Philadelphia: Saunders College Publishing, 1992.



Vascular Plants with Naked Seeds

Vascular plants with naked seeds are informally called **gymnosperms** (from the Greek meaning "naked seed"). The seeds of this group are considered "naked" because they are not completely enclosed by the tissues of the parent at the time of pollination. The divisions of these plants with naked seeds that have a good fossil record are the *pteridospermophytes, glossopterids, coniferophytes, cycadophytes,* and *ginkgoes.*

Pteridospermophytes are the seed ferns. They had fernlike foliage but bore naked seeds on their leaves. The earliest remains of pteridospermophytes are found in Devonian rocks. They were abundant during the late Paleozoic, declined somewhat during the Triassic and Jurassic, and became extinct during the Cretaceous.

During the Carboniferous, gymnospermal plants called *glossopterids* grew luxuriantly across the southern supercontinent of Gondwana. The group takes its name from *Glossopteris* (Fig. 11.44), fossils of which typically consist of thick, tongue-shaped leaves. *Glossopteris* and associated plants of the glossopteris flora were adapted to more temperate climates, as compared to the more tropical conditions that prevailed in the coal forests of North America and Europe.

Conifers, which include pines, spruces, firs, redwoods, and cedars, are the most familiar of the gymnosperms. In conifers, distinctive male and female cones develop. The smaller male cones produce pollen grains containing sperm. Eggs develop in the protective ovules located within the scales of the larger female cones. After pollen has been transported by wind to the female cone, fertilization is completed by movement of sperm (in relative safety) through a moist tube that grows from the pollen grain to the embryonic seed. Under suitable conditions, the fertilized seed may then grow into an adult conifer. Conifers made their appearance during the late Carboniferous (Mississippian and Pennsylvanian). Perhaps the most famous fossil conifers are those preserved as silicified logs in Petrified Forest National Park, Arizona.

The conifers are members of a larger group of conifer-like plants designated as the *coniferophytes.* Coniferophytes include a group of plants called *cordaites* that flourished during the Pennsylvanian and Permian. Cordaites were cone-bearing trees with long straplike leaves. They were particularly abundant in moist, swampy terrains.

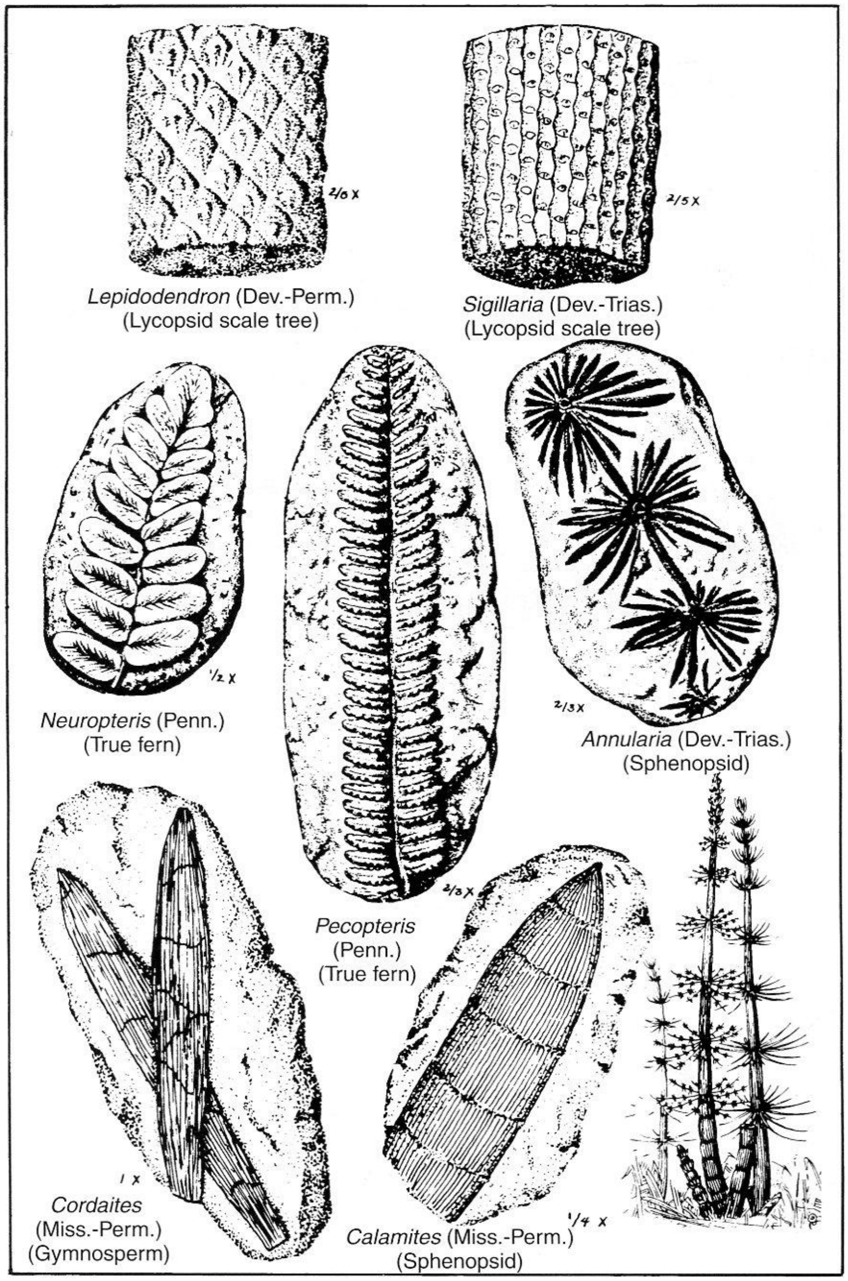
During the Mesozoic, a group of plants known as *cycadophytes* achieved global distribution. Among the cycadophytes, the group known as cycadeoids are extinct, but those called **cycads** are still living and commonly known as sago palms. Many of the Mesozoic cycads were lofty trees surmounted by palmlike foliage. Others grew close to the ground. Whether large or small, they had rough trunks and limbs resulting from bark covered by spirally arranged leaf scars.

The *ginkgoes* are a group of gymnosperms readily recognized by their distinctive bilobed fan-shaped leaves. Ginkgoes made their appearance during the Permian. They spread widely during the Triassic and Jurassic but began to decline in the Cretaceous and Tertiary. Today, only a single species, *Ginkgo biloba,* survives.

Vascular Plants with Protected Seeds and Flowers

The explosive proliferation of vascular plants with protected seeds and flowers was one of the most dramatic events in plant evolution. These plants are called **angiosperms** (Fig. 11.45), and most of the plants we see about us today are angiosperms. In angiosperms, seeds develop in a chamber of the flower called the ovule. Organs on the flower called stamens produce pollen. Pollen is transferred from the stamens to another organ on the flower known as the pistil. As in gymnosperms, a pollen tube is produced by the pollen grain after it has come to rest on the pistil. The pollen tube penetrates to the ovule, and sperm moves through the tube to the seed where fertilization takes place. Colored leaves on the flower are useful in attracting insect pollinators, and the proliferation of plants with flowers was accompanied by a striking parallel evolution of insects. In addition, the enclosed seed permitted the growth of edible coverings, enhancing dispersal by animals that feed on seeds and fruit.

Figure 11.43 Plants of the coal swamps.



The earliest evidence of angiosperms is found in Cretaceous rocks. The group diversified rapidly, and by the end of the Cretaceous, all of the major groups had appeared. Many of these plants were very similar to those observed today. By the mid-Cenozoic, the appearance of prairie grasses supplied the stimulus for the dramatic increase in the numbers of plains-dwelling herbivorous mammals and their predators.

Study Questions

1. Refer to the figures in this section on plants and identify the fossil plants in your study set. Beside each, indicate if the plant is a seedless plant, a gymnosperm, or an angiosperm.
2. What types of fossilization are seen in the fossil plants provided in your study set?

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Figure 11.44 *Glossopteris* leaf, associated with coal deposits formed from the glossopterid forests of the Permian. This fossil was found on Polestar Peak, Ellsworth Land, Antarctica.

Courtesy of J. M. Schopf, C. J. Craddock, and the U.S. Geological Survey.

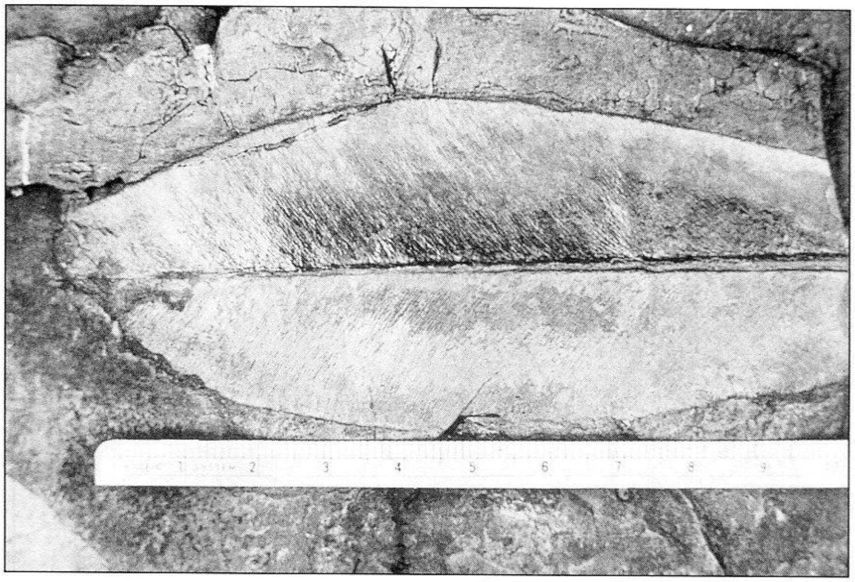
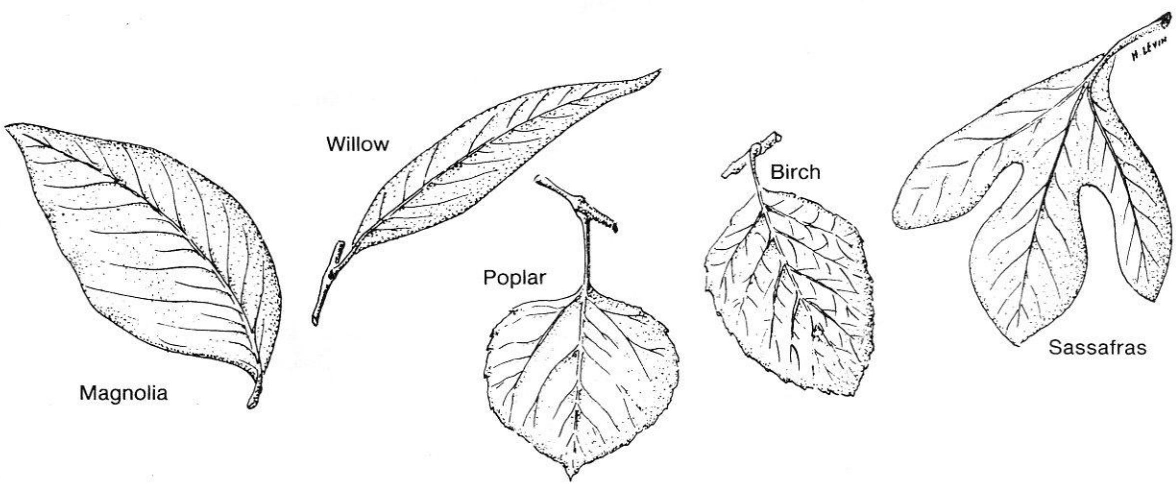


Figure 11.45 Leaves of angiosperms found fossilized in Cretaceous rocks.

From Levin, H. L., *The Earth Through Time,* Philadelphia: Saunders College Publishing, 1992.



3. What advantages, in terms of assurance of success in reproduction, do gymnosperms have over seedless, spore-bearing plants?

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4. A traditional interpretation of the relationship between insects and flowering plants is that the flowering plants evolved first, stimulating the expansion of flower-dependent insects. Some scientists suggest the reverse may have been the case. How might this question be resolved?

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TERMS

ambulacral Pertaining to the rows of openings through which the tube feet of echinoderms are extended, or along which food grooves are located.

amphineuran A group of mollusks having shells that are composed of eight plates on the dorsal side of the body. The chitons are amphineurans.

angiosperm A plant with true flowers, in which the seeds are enclosed in the fruit (the fertilized and developed ovary). Examples include grasses, orchids, elms, and roses.

antagonism The relationship that exists between two different organisms that live in close association, in which one organism suffers through the actions of the other.

Aristotle's lantern A system of calcareous elements that surround the mouth and function as jaws in echinoids.

beak The projection at the initial point of shell growth in pelecypods.

belemnites Members of the molluscan Class Cephalopoda having straight internal shells.

blastoid Sessile (attached) Paleozoic echinoderm, members of which have a stem and an attached cup or calyx composed of relatively few plates.

calyx That portion of the skeleton that surrounds the viscera in crinoids, blastoids, and cystoids.

***camerae* (cephalopods)** The chambers in the conch of a cephalopod.

carapace A bony or chitinous case or shield covering the whole or part of the back of certain animals.

cephalon The major anterior body segment (the "head") of a trilobite.

cephalopods Mollusks characterized by a chambered conch.

chitin A resistant organic compound that is the common constituent of various invertebrate skeletons such as insect exoskeletons and the inner tests of foraminifers.

columnella The medial pillar surrounding the axis of a spiral gastropod shell, formed by the coalescence of the inner walls of the whorls.

conch Any of various marine shells of invertebrates, including bivalve mollusks and brachiopods.

crinoid A stalked echinoderm with a calyx composed of regularly arranged plates from which arms radiate for gathering food.

crustacean A member of the Class Crustacea of the Phylum Arthropoda that includes such animals as lobsters and crayfish.

cycads A gymnosperm having compound leaves and naked seeds borne separately on leaves or in simple cones. Cycads were abundant during the Triassic and Jurassic and declined during the Cretaceous.

cystoid An attached echinoderm with an irregular arrangement and number of plates in the calyx and with calyx perforated by pores or slits.

echinoids Globular or discoidal members of the Phylum Echinodermata, having a firm shell (test) composed of symmetrically arranged plates, including such animals as sand dollars, sea urchins, and heart urchins.

gastropoda A class of mollusks having a well-developed head region, ventral foot for creeping, and unchambered conch. Includes snails and limpets.

graptolites Extinct colonial, marine invertebrates frequently found as fossils in dark shales of Paleozoic age.

gymnosperm A plant whose seeds are commonly in cones and never enclosed in a fruit. Examples include cycad, ginkgo, and the conifers (pine, fir, and spruce).

mantle The pair of fleshy folds that secrete the shell in mollusks, brachiopods, and certain other invertebrates.

monoplacophoran Primitive marine mollusks with simple, cap-shaped shells.

operculum A calcareous or chitinous plate that develops on the posterior dorsal surface of the foot of a gastropod and that serves to close the aperture.

ophiuroidea A class of the Phylum Echinodermata characterized by the presence of five slender, jointed, flexible arms, as in the so-called brittle stars.

ostracode A small, bivalved crustacean.

pallial line Linear depression on inside of pelecypod. Shell marking inner margin of thickened mantle edges.

pallial sinus An indentation in the pallial line in pelecypods. The pallial sinus marks the position of the siphon.

palynology The study of pollen of seed plants and spores, both living or fossil, including their dispersal and applications in stratigraphy and paleoecology.

pollen Tiny reproductive bodies produced in the anthers of flowering plants.

psilophyte A primitive vascular plant, generally without roots or leaves, having spore-bearing organs at the stem tips. Geologic range: Late Silurian to Early Devonian. Also called psilopsids.

pteridospermophytes Extinct seed-bearing plants with fernlike leaves.

pygidium The major posterior portion of a trilobite.

rhizome A horizontal, subterranean stem that permits a plant to grow laterally.

scaphopod Mollusks characterized by a simple, tusklike, unchambered shell that is open at both ends.

septa Vertical partitions in the theca of a coral.

siphuncle A long membranous tube extending all through the camerae and septa from the protoconch to the base of the body chamber of a cephalopod shell.

sporangia Structures that produce spores.

spore Any single-celled body, produced as a means of propagating a new individual, often adapted to survive unfavorable environmental conditions.

stipe A branch of a graptolite colony, along which are arranged the thecae.

symbiosis The relationship that exists between two different organisms that live in close association, with at least one being helped without either being harmed.

theca The external skeleton of an echinoderm. Formed of calcium carbonate (corals) or chitin (graptolites).

tube feet The locomotor organs in starfish and echinoids.

umbo Elevated and convex area of the valves of pelecypods and brachiopods that is adjacent to the beak.

valves One of the two usually convex plates that form the shell in brachiopods and pelecypods.

vascular plant A plant with a well-developed conductive system and structural differentiation. The majority of visible terrestrial plants are vascular.

whorl One of the turns of a spiral or coiled shell.