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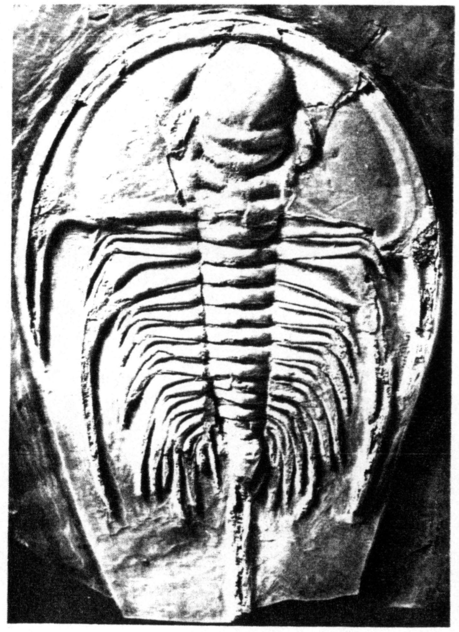

FIGURE 9.3
An early Cambrian trilobite, *Olenellus*, from southern California. The large head and eyes and small tail are typical of many early Cambrian trilobites. The specimen is 12 cm long. (Courtesy of Takeo Susuki, U.C.L.A.)

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Hypotype 2470

that lacked a skeleton, such as the Ediacaran fauna. This is followed by the first shelly fossils that are small, commonly phosphatic, and generally of uncertain affinities. These occur just before the oldest known trilobites.

After the trilobites appear, fossils with skeletons appear regularly in the fossil record until, by the close of the Ordovician Period, almost all major groups of marine invertebrates have appeared. The ammonites and various vertebrate fish groups come on the scene later, as do marine reptiles.

The base of the Cambrian, with the onset of preservable skeletons, marks one of the most important time intervals in geologic history. We will return to this feature a little later in the chapter.

Cambrian Life

Apart from the Ediacaran fauna and the microfossils in the Precambrian, our fossil record for marine communities really begins at the base of the Cambrian rocks and continues without major interruption to the present day. When we first get a good look at marine communities, they are very strange compared to those of modern oceans. Among the first fossils with hard skeletal parts that are likely to be preserved are **trilobites** (Figure 9.3). These are an extinct class of **arthropods**, or jointed-legged animals, related to crabs, lobsters, and shrimp. Arthropods are among the more advanced and complex of any of the various phyla or animals that we call invertebrates—animals without backbones—in contrast to the vertebrates, or animals with backbones. These first trilobites have large eyes and long

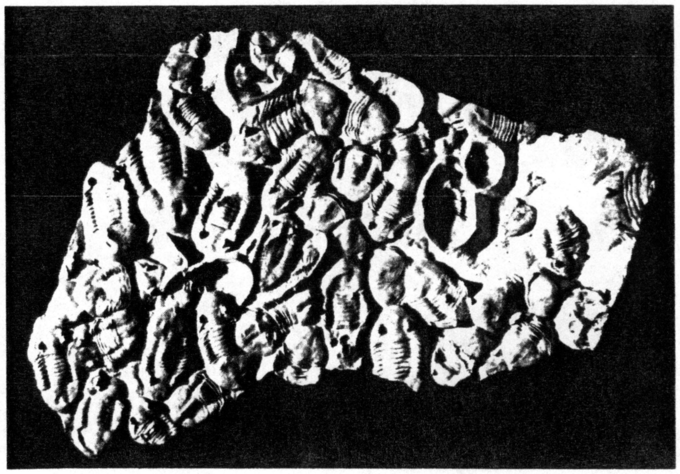

FIGURE 11.1
A slab of Ordovician limestone containing many specimens of a large trilobite, *Homotelus*, characteristic of that period. The block is about 40 cm long. (Courtesy of Los Angeles County Museum of Natural History, photo by Lawrence S. Reynold.)

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hypotype

feeders as the bivalves were present, but they were generally subordinate. Other important members of these communities were sessile carnivores (the corals), a variety of detritus feeders (such as gastropods), and predators (cephalopods and fishes).

Each of the three main groups—brachiopods, bryozoans, and stalked echinoderms—is characterized by two important attributes. First, within each group there is a definite succession of dominance. Those kinds of brachiopods that were predominant in the Ordovician gave way to other types in later periods. The same is true for the other two groups. Secondly, these groups provide the first evidence for conspicuous stratification of marine communities—the brachiopods living just above the sea floor, many bryozoan colonies being raised a few centimeters above the bottom, and stalked echinoderms being generally ten or more centimeters high. This stratification was largely lacking in Cambrian communities. Ordovician communities also differ from Cambrian ones in another respect; in the former, most of the common animals were sessile (fixed to the bottom), whereas in the latter, trilobites were mobile animals. Also, dominant Ordovician animals had a calcium carbonate shell, whereas Cambrian animals most often had a chitinophosphatic shell.

We will now look at the succession from the Ordovician through the Permian of each of these three major groups of filter feeders in more detail.

Brachiopods

The earliest **brachiopods** have a shell that is chitinophosphatic in composition, and the two valves enclosing the soft parts are not hinged together (inarticulate condition). This kind of brachiopod predominates in Cambrian rocks but is replaced

FIGURE 12.8
A primitive ammonoid, *Tornoceras*, from the Devonian period, has a few very simple wavy septa (goniatite) dividing the shell into chambers. The specimen is 4.4 cm high. (Courtesy of Takeo Susuki, U.C.L.A.)

into chambers. In nautiloids these partitions, or septa, are simple with straight edges. In ammonoids the edges of the septa become fluted and are arranged into a series of waves, so that the edge of the septum, as seen from the shell exterior, traces a series of folds across the shell. The functional significance of this evolutionary change has been much debated. The most generally accepted theory is that the shell edge helps to strengthen the shell, avoiding crushing or implosion of the shell if the animal changes its living depth rapidly. The chambers provide buoyancy, being partly gas filled, and external water pressure on them can be severe. Most ammonoids, and some nautiloids, especially advanced ones, have the chambers coiled so that they are above the living chamber. This helps keep the animal upright in the water, with the lighter gas-filled chambers located above the heavier animal in its living chamber.

Although ammonoids are small and not very common in the Devonian, they rapidly increase in size and abundance through the remainder of the Paleozoic. The most conspicuous change they undergo is increasing complication of the septal edges. The wavy septa develop small, secondary crinkles on them, first on every other fold and then on each fold. The primitive simple type is called a **goniatite septum** (Figure 12.8), the one with secondary crinkles on alternating folds is called a **ceratite** (Figure 12.9), and the most complicated forms are called **ammonite septa** (Figure 12.10). By Permian time, most ammonoids had evolved the complicated ammonite septum. If the prime impetus for this evolutionary change was to strengthen the shell, then some of the more advanced forms must have been living at increasingly greater depths, or else they were accustomed to changing their living depth quite rapidly. The ammonoids underwent a crisis at the close of the Permian. Most of the forms that had been common during that period of time became extinct, and only a few genera survived to provide the ancestral stock for Triassic ammonoids. All of the ones with complicated ammonitic septa became extinct; the survivors were ones with ceratite septa. There are over 300 genera of

FIGURE 12.9
A typical Triassic ammonoid, *Submeekoceras*, with ceratite septa. Alternate waves of the septa have secondary crenulations on them. The specimen is from the Lower Triassic of Idaho. (Courtesy of Takeo Susuki, U.C.L.A.)

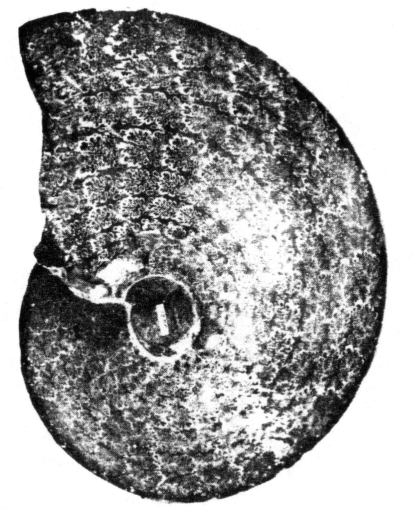

FIGURE 12.10
An ammonoid with complex ammonite septa. This late Cretaceous specimen of *Placenticeras* is from South Dakota and is 22 cm high. (Courtesy of Takeo Susuki, U.C.L.A.)

(Placenticeras whitfieldi Hyatt) in UCLA specimen catalog

ceratite-type cephalopods known from the Triassic. These, in turn, underwent a crisis at the close of the Triassic; all cephalopods with ceratite septa became extinct at that time. A few forms with the advanced ammonite septum had evolved during the Triassic. These persisted into the Jurassic, giving rise to another burst of ammonoid evolution. Several hundred genera are known from the Jurassic.

During the Jurassic and Cretaceous, ammonoids reached their peak of abundance, diversity, and rapidity of evolution. They are used for correlation of marine rocks of these ages on a worldwide basis. The Jurassic Period is divided into about twenty zones based on these fossils, and intervals of about 1.5 million years can be discerned with their use. In the Cretaceous, some of the ammonoids