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