limb growth at various stages by removal of the apical ectodermal ridge shows that the distal and anterior limb elements are always the first to be affected by termination of growth. These examples clearly demonstrate how a simple change in the timing of developmental processes can alter the expression of the adult structure according to a particular pattern.

To what extent do these patterns and processes of development constrain or otherwise influence the direction of evolution? To evaluate this, it is necessary to examine one more level of development.

Ossification sequences in primitive diapsid reptiles

Alberch and his colleagues concentrated their studies on the pattern and sequence of formation of the many centers of *chondrification* in the limb. However, they did not continue their studies to the level of *ossification* of the cartilaginous elements. Although it might be assumed that the sequence of chondrification would be followed nearly exactly by that of ossification, the specific degree of congruence between these two processes must be established in order to study patterns of development from the fossil record, in which only ossified bones are likely to be preserved. In fact, there is one major exception to the similarities in the sequence of these two processes.

In both major tetrapod groups, the amphibians and the amniotes, chondrification of the limbs proceeds continuously from proximal to distal; ossification does not. Although it begins proximally and extends through the humerus or femur to the ends of the ulna and radius or tibia and fibula, the ossification sequence does not continue through the carpals or tarsals but jumps directly to the metacarpals or metatarsals and digits, leaving the areas of the wrist and ankle without ossification until significantly later. Thousands of fossils of immature amphibians and reptiles are known in which the proximal and distal bones of the limbs are ossified, but not the carpals and tarsals (see, e.g., Fig. 10.21A,F).

If the carpus and tarsus ossify out of sequence with the rest of the limb, does ossification of the individual carpal and tarsal bones follow the sequence of formation of their cartilaginous precursors? This gap is now being filled through the work of Rieppel (1992, 1993), who has studied members of many reptilian groups to establish the sequence of ossification of carpals and tarsals following their chondrification. Although there is some coossification of originally separate sites of chondrification and some loss of cartilaginous element, the pattern of ossification among the carpals and tarsals does follow the same sequence as the pattern of chondrification (Table 10.1). Based on this information, it is now possible to make direct comparison between sequences of ossification that are known in fossils and those of living vertebrates to determine the degree of constraint on this aspect of development over the past 300 million years.

Emphasis is being placed on the carpals and tarsals specifically because of the delay in their ossification. Ossification of the rest of the skeleton proceeds so rapidly that it is only rarely possible to determine the sequence of ossification of the individual bones in fossil species. In contrast, the development of the carpus and tarsus is significantly delayed, and the rate of ossification is sufficiently slow that one can observe the sequence of appearance of each individual unit in extensive growth series that are occasionally seen in the fossil record. This provides an ex-