



Figure 10.18. Sequence of chondrogenic condensations in a generalized tetrapod limb. The primary axis passes through the humerus–ulna or femur–fibula, meeting the digital arch at the ulnare or calcaneum. The digital arch turns preaxially producing the meso- and metapodials by mesenchymal bifurcation. **A**, Front limb. **B**, Rear limb. Abbreviations as in Figure 10.8. From Caldwell (1994).

pal, and so on. The phalanges of each of the digits arise by segmentation from the appropriate metacarpal. The same process occurs in the foot. The fifth digit develops somewhat independently of the rest of the hand or foot, typically appearing after the fourth. The sequence of digit formation is 4-(5 or 3)-2-1.

Aside from the fifth digit, the digital arch in amniotes always develops in a posterior to anterior direction. This is also true of frogs but, surprisingly, is not the case in the salamanders that have been studied: Their digital arch develops from anterior to posterior, with the sequence of digit formation 2-1-3-4-5. Different patterns of limb development led Holmgren (1933) to suggest that salamanders evolved from a different lineage of fish than did all other tetrapods (i.e., the tetrapod limb arose separately in two lineages). Most paleontologists now think that salamanders shared a common ancestry with other living amphibian groups, but there is no answer as to why their limb development differs from that of all other tetrapods, or at what time in their evolution the change occurred.

Shubin and Alberch (1986) documented the basic consistency in the pattern and sequence of chondrification of limb elements. Where differences are observed among living vertebrates, they nearly always follow a consistent pattern. When limb elements are reduced or lost, their reduction typically reverses the sequence of bone formation. The proximal elements of the limb are highly conserved, but distal elements are more variable in expression and most commonly subject to loss. Progressive limb loss from distal to proximal is well documented among lizards, in which scores of lineages have reduced their limbs (Greer 1991), and frogs and salamanders typically lose digits in the reverse order to the sequence of their formation (Alberch and Gale 1985). Experimental work involving termination of