tat and ways of life both within and between each major group. They are also among the most difficult evolutionary phenomena to explain. Darwinian selection theory can account for the modification of particular structures so that they are better suited for a given environment, but it is much more difficult to understand how the limbs of early tetrapods could have evolved from the fins of a fish or how the wings of birds could have evolved from the forelimbs of dinosaurs, since these changes involve radical shifts in function between completely different selective regimes. Paradoxically, an equally serious problem is to explain the stability of limb structure within individual groups or lineages, which may retain an extremely stereotyped pattern for hundreds of millions of years.

Changes of limb structures between adaptive zones are frequently both radical and relatively rapid, but they can be attributed to strong, persistent, and unidirectional forces of natural selection. *Within* each major adaptive zone, on the other hand, particular features of limb structure may be so extremely conservative that they seem immune from directional selection or even random fluctuation. It is the latter phenomenon that has led to the concept of *developmental stasis* (Maynard Smith et al. 1985). For instance, among the primates, modern humans have retained five digits on both the forelimbs and hind limbs – the same number as were present in the earliest primates from the early Cenozoic, the earliest mammals from the Late Triassic, and members of the stem group of amniotes from the mid-Carboniferous, nearly 340 mya. Nearly all lizards also have five digits, although their ancestry diverged from that of mammals more than 300 mya. Frogs and most salamanders also had five digits on the hind limb, but four or less on the forelimb, at least since the Early Jurassic, and one or both of these groups may trace its ancestry to lineages that had already lost one of the digits in the forelimb by the mid-Carboniferous. At an even more detailed level, the number of phalanges in each digit, expressed as the phalangeal formula, has been conserved within the mammalian lineage since at least the Early Triassic, when the primitive amniote number of 2,3,4,5,3 (counting from the thumb to the fifth finger) in the front limb and 2,3,4,5,4 in the hind limb was reduced to 2,3,3,3,3 in both hands and feet (Fig. 10.8).

Many amniote lineages have reduced the number of digits and phalanges, but none has evolved more than five true digits, and many have retained the original phalangeal formula, at least in the digits that remain. Except in taxa that have completely lost their limbs, the pattern of the major bones – the humerus, ulna, and radius in the forelimb, and the femur, tibia, and fibula in the hind limb – remains constant, even in groups that have adapted to such different forms of locomotion as swimming or flying. There must be some force acting to retain such stability, beyond selection for particular environments or ways of life.

Understanding how development of the limbs is controlled should contribute substantially to explaining why some aspects of their structure can remain so extremely conservative over hundreds of millions of years in particular taxa, whereas in other lineages comparable features change radically over far shorter periods.

In common with the patterning of the trunk region in both nonvertebrate metazoans and vertebrates, the *Hox* cluster genes are expressed in a linear sequence within the fins of bony fish and the limbs of tetrapods. Neither cephalochordates nor the most primitive jawless vertebrates have paired fins, but the potential for the regulation of their development may have begun with the first stage in the tan-