

difficult to compare in detail with those of later Paleozoic tetrapods. The carpals are small and poorly ossified, whereas the proximal tarsals are very large. The metacarpals and metatarsals are not clearly distinguishable from the succeeding phalanges. Clearly, these limbs represent a period of transition, but one that has all the potential for evolving into the pattern of typical tetrapods. Most significantly, the elbow, wrist, knee, and ankle joints, while primitive, unquestionably presage those of later land vertebrates.

The digits have the general form of those in fully terrestrial amphibians and reptiles, but their numbers differ significantly. In the most primitive Devonian tetrapods in which the limbs are adequately known, there are eight digits in both the front and rear limb, compared with no more than five in any adequately known post-Devonian tetrapods (Coates 1994, in press; Lebedev and Coates 1995). The retention of no more than five digits in the rear limb and either four or five digits in the forelimb of Carboniferous and later tetrapods was almost certainly the result of subsequent reduction.

In contrast with the clear homology of the more proximal limb bones in osteolepiform fish and early tetrapods, no obvious homologues of the digits is evident in any sarcopterygian. These bones appear *de novo* in the Upper Devonian tetrapods. How can this be explained?

The structural similarity of the endochondral bones of the upper limb in osteolepiform fish and all tetrapods suggests a similar mode of genetic control during development. This is supported by the expression of comparable *Hox* genes in forms as phylogenetically distant as the zebra fish *Danio*, chickens, mice, and modern amphibians. Not surprisingly, the gene expression in the distal extremities of fish is clearly different from that of tetrapods. In tetrapods, *Hoxa* and *Hoxd* genes within groups 9–13 are expressed to the very extremity of the limb, and the most distal genes are active throughout development. The early expression of *Hoxa* and *Hoxd* in the zebra fish is similar to that of tetrapods, but their later expression in the more distal portion of the fin differs significantly. *Hoxd-11*, *Hoxd-12*, and *Hoxd-13* are not detected in cells in the anterior half of the fin. Instead, these expression domains are restricted to the posterior margin of the fins early in development and subsequently disappear (Sordino et al. 1995) (Fig. 10.11).

The loss of expression of these genes can be associated both spatially and temporally with the proliferation of cells that form the small, jointed dermal fin rays making up the distal portion of the fin. In early stages of limb formation in bony fish, the fin bud is relatively thick and filled with mesenchyme that differentiates to form the endochondral bones of the girdle and base of the fin (Smith and Hall 1990; Thorogood 1991). At this stage, the distal margin of the fin is formed by a thickened, pseudostratified epidermal ridge, broadly resembling the apical ectodermal ridge (see the following section) of tetrapod limbs (Fig. 10.12). In ray-finned fish, the configuration of this ridge then changes to form the **apical ectodermal fold**, which encloses a very narrow internal space. The mesenchyme at the base of the apical ectodermal fold no longer proliferates to form endochondral bone, but produces two parallel arrays of collagenous fibrils termed **actinotrichia**. The mesenchymal cells then migrate into the distal portion of the limb and generate cells that form the dermal tissue of the lepidotrichia.

Thorogood (1991) argued that formation of the apical ectodermal fold in some