tetrapods were able to continue elaboration of the endochondral skeleton to the very end of the limbs. This is correlated with the complete absence of lepidotrichia in association with the limbs in Devonian tetrapods (Coates 1994). Carboniferous tetrapods do have dermal scales covering their limbs, but these resemble the trunk scales rather than the distal fin scales of bony fish, and were presumably elaborated after the loss of the lepidotrichia from the paired limbs.

The hands and feet of land vertebrates were formed not by a symmetrical extension of endochondral ossification from the end of the osteolepiform fin, but rather by sustained proliferation of the posterior portion. In sarcopterygian fish, including the immediate sister-group of tetrapods, the endoskeleton of both pectoral and pelvic fins are essentially linear structures, with a major proximal-to-distal axis. The *Hox* genes in modern ray-finned fish show a comparable pattern of linear expression. Modern tetrapods show a similarly linear pattern of gene expression for

Figure 10.11. Change in the axis of development and the expression of *Hox* genes between bony fish and tetrapods. **A,** Endochondral bones of the limb of a modern lungfish, showing both preaxial (anterior) and postaxial (posterior) radials, extending from the main axis of development (from Coates 1994). **B,** Endochondral bones of the osteolepiform fish *Eusthenopteron,* in which all radials are preaxial. **C,** Hind limb of the early tetrapod *Ichthyostega,* in which the axis of development angles forward and the distal tarsals and digits develop in a posterior to anterior sequence (B,C modified from Sordino et al. 1995). **D,** Area of expression of *Hoxd* genes in the living zebra fish. **E,** Area of expression of *Hoxd* genes in modern tetrapods (D,E reprinted from *Nature* [Nelson and Tabin, vol. 375]. Copyright © 1995, Macmillan Magazines Limited). Abbreviations as in Figure 10.8.