



**Figure 10.16.** Gene expression and limb development. **A, B,** Expression of *Hoxd* genes in the limb buds of the leg and wing of a bird. White patches indicate where digits are forming (reprinted from *Nature* [Morgan et al., vol. 358]. Copyright © 1992, Macmillan Magazines Limited). **C, D,** Adult structure of the foot and wing. The very similar distribution of the areas of *Hox* gene expression is in striking contrast with the very different adult morphology (from Carroll 1987).

humerus and femur begin to bifurcate. As these areas extend distally, they separate at the base to form the more distal bones of the limb. The pattern of condensation of the cells that will form the radius and ulna and the tibia and fibula illustrate three “rules” of limb development in tetrapods:

1. Bones may originate by bifurcation, but never by trifurcation.
2. Bifurcation is always succeeded by segmentation (no limb bones are forked). Segmentation may, however, occur without bifurcation, as in the bones of the fingers and toes.
3. These bones, and all others in the limbs, are initially arrayed in essentially a single plane; none diverges at a significant angle from this plane.

The bifurcation of the radius–ulna or tibia–fibula establishes a pre- and post-axial series (Fig. 10.18). The preaxial series (beginning with the radius or tibia) nev-