



Figure 10.20. Primitive diapsid reptiles from the Upper Permian of Madagascar. **A**, The terrestrial genus *Thadeosaurus*. **B**, **C**, The aquatic genera *Hovasaurus* and *Claudiosaurus*. From Carroll (1987).

sesamoid element in the tendons of the muscles that extend along the posterior margin of the wrist. In the tarsus, the sequence is as follows: astragalus and calcaneum appear simultaneously, followed by distal tarsal 4, (distal tarsal 3, centrale, distal tarsal 2), then by distal tarsal 1 or 5. Distal tarsal 5 later fuses to distal tarsal 4.

Modern lizards also show irregularity in the sequence of ossification of the distal tarsals. Among the Madagascar genera, the degree of irregularity is greatest in *Claudiosaurus*, in which the order of ossification of the first, second, and fifth distal tarsals varies from specimen to specimen. This degree of irregularity in the sequence of ossification presumably reflects less stringent selection for both the pattern and extent of ossification associated with an aquatic way of life. Ossification of the carpus and tarsus is conspicuously reduced in many, more specialized marine reptiles, for which selection may be acting to produce a more flexible, paddle-like limb that did not have as great a need for the load-bearing capacity of bone.

The most striking difference in limb development between *Claudiosaurus* and both the other Upper Permian genera and most modern reptiles is the relative timing of ossification of the front and rear limbs. In nearly all terrestrial reptiles, the hind limb initiates and completes ossification well ahead of the forelimb. Although the complete ossification sequence is not clear in *Claudiosaurus*, what is known indicates that the carpals reach an advanced state of ossification well ahead of the tarsals. This presumably reflects different use of the limbs in aquatic and terrestrial locomotion. Many more highly derived aquatic reptiles and mammals (e.g., ichthyosaurs, whales, and sirenians) greatly reduce the rear limbs while maintaining the front limbs.

These fossils from the Upper Permian demonstrate that the pattern and sequence of ossification of the carpals and tarsals have remained nearly constant for approximately 250 million years among animals that have retained conservative body