Table 10.1. *The sequence of ossification of carpal and tarsal elements in the lizard* Cyrtodactylus pubisulcus

ulnare	dc4	radiale	dc3	dc1	dc5	dc2	centrale	pisiform	astragalus	calcaneum	dt4	dt3
									+			
									+	+		
									+	+	+	
+									+	+	+	
+	+								+	+	+	
+	+	+[a]							+	+	+	
+	+	+	+						+	+	+	
+	+	+	+	+	+				+	+	+	+
+	+	+	+	+	+	+	+		+	+	+	+
+	+	+	+	+	+	+	+	+	+	+	+	+

[a]The only exception is FMNH 1249299, where ulnare and distal carpals 4 and 3 are ossified, but not the radiale.
Source: Reprinted by permission of Oxford University Press from Rieppel (1992), *J. Zool. Lond.*, vol. 227.

cellent model for following the temporal sequence in the expression of a developmental pattern. There are few, if any, other parts of the skeleton that are so well suited to determining the importance of developmental constraints in influencing the patterns of evolutionary change.

The first publication specifically on developmental sequences of the carpals and tarsals of fossil vertebrates was by Caldwell (1994), who studied growth series of early amniotes close to the base of the radiation that eventually led to the origin of all the living diapsid groups (lizards, snakes, *Sphenodon,* crocodilians, and birds) as well as diverse fossil groups including dinosaurs and many lineages of Mesozoic marine reptiles (Fig. 10.19). Caldwell determined that the sequence of ossification of both the carpals and tarsals in Upper Permian diapsids was essentially the same as in modern lizards and *Sphenodon,* taking into consideration the loss of some of the distal carpals and tarsals in the modern genera. This showed, without question, that the digital arch ossified in the same sequence 250 million years ago as it does today. This constancy is matched by the identical number of digits and of phalanges within each digit as those in the majority of living lizards.

Caldwell studied three genera from the Upper Permian of Madagascar (Fig. 10.20). One, *Thadeosaurus,* had body and limb proportions very similar to those of modern terrestrial lizards. *Hovasaurus* differed in the lateral compression of the tail that clearly indicated aquatic locomotion. The third genus, *Claudiosaurus,* is thought to be related to the Triassic and Jurassic marine reptiles – nothosaurs, placodonts, and plesiosaurs – on the basis of the small skull with upper but not lower temporal openings, and a long neck.

These genera all had the same complement of carpals and tarsals as adults. As in modern reptiles, the ossification of the mesopodials was much delayed relative to the more proximal and distal limb bones. The area of the carpus and tarsus is completely lacking in ossification in the smallest individuals, in which the rest of the limb is fully formed. The sequence of ossification of the carpals and tarsals is