

DINOSAUR FEET IN THE THREE DIMENSIONS: ANATOMY FOR CLIMBING, DIGGING, AND LEAPING

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It is traditional to define the Dinosauria as the clade which evolved a "bird-like" ankle joint that limited motion to a simple flexing of the foot fore and aft. According to this view, most dinosaurs had far less flexibility in foot movement than do most generalized lizards and mammals, animals that can climb trees and shrubs. With few exceptions, textbook and museum restorations show dinosaurs walking and running on flat, level ground, but not engaging in locomotor activity that would require twisting of the sole and grasping by the hind toes.

Birds and their immediate ancestors depart from the basic dinosaurian ankle pattern by evolving a strong, backwardly directed first toe that can grasp branches and other perches by flexing forward against the other three toes.

Superbly preserved specimens of the tiny herbivorous dinosaur *Drinker nisti*, from the earliest Cretaceous at Como Bluff, Wyoming, provide strong evidence that the potential of the dinosaurian foot for movement in three dimensions has been greatly underestimated. Well-defined joint surfaces show that the inner toe was opposable and could grasp objects against toes II and III. Twisting of the foot was encouraged by precise ball-in-socket joints between upper ankle (calcaneum) and mid ankle (cuboid), and between mid ankle and long ankle bones (metatarsals). Fine control of sole movements was accomplished through pivots and slides between the shin (tibia-fibula) and the upper ankle.

Hands of *Drinker* and its close kin *Othnielia* show strong grasping adaptations in the outer two fingers. The grasping geometry of fingers and toes is documented by Early Jurassic footprints of *Anomoepus*, dinosaurs with *Drinker*-like anatomy.

The *Drinker* pattern is primitive for the Dinosauria and can be seen, in less well ossified form, in the earliest carnivores and herbivores of the Triassic. Most families of dinosaurs retained most or part of the grasping adaptations seen in *Drinker*. For small species, tree-climbing was possible. For large species, grasping toes could be employed in digging, nest-building, and manipulating mates and relatives.