24 Ratite Footprints and the Stance and Gait of Mesozoic Theropods

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Abstract

Footprints of the rhea *(Rhea americana)* are identical in several diagnostic features to tridactyl footprints of the Mesozoic Era attributed to theropod dinosaurs. Of particular interest, (i) the rhea's feet are placed very close to its body midline as it walks, so that it virtually places one foot in front of the other; (ii) its middle toe (digit III), the central weight–bearing axis, is directed slightly inward under normal conditions; and (iii) the feet are very deliberately placed on the substrate, and the toes and claws leave no drag marks. These are all characteristic of Mesozoic theropod (and ornithopod) trackways, and invite extended comparison of fossil and recent theropods. Modern ratites and Mesozoic theropods are essentially identical in bone morphology and in joint structure and articulations. Their trackways are similar because the structure and function of the hindlimbs of the two groups are also essentially identical. These similarities are to be regarded as homologies because birds are descended from Mesozoic theropods, and the ratites merely retain characters plesiomorphic for the group since the Late Triassic. Mesozoic theropods had fully erect stance and parasagittal posture, as both bone structure and articulation, and footprints reveal. Hypotheses of semi–erect posture based on hypothetical muscle reconstructions are not supported by the available evidence.

Introduction

Dinosaurs were unknown as a group when Edward Hitchcock described gigantic three–toed trackways from the redbeds of the Connecticut River Valley in the early 1830s. Hitchcock (1836) noted that they were first regarded as prints made by giant birds, including "Noah's raven." He named the prints "*Ornithichnites*" to reflect their origin and thereby differentiate them from the tracks of reptiles, or "*Saurichnites*," found in the same beds. Sir Richard Owen named the Dinosauria in 1842, but on such fragmentary material that the Connecticut Valley tracks could not be associated with the osseous remains of dinosaurs until the late 1800s (Colbert 1968, Desmond 1975), when relatively complete skeletons of carnivorous and herbivorous dinosaurs became known from places as diverse as Belgium and the western United States. By the time Lull published the first edition of *Triassic Life of the Connecticut Valley* (1915), footprints could be referred not only to dinosaurs but to other archosaurian groups, often at the family or even genus levels. The parataxonomy of fossil footprints is still preserved, but in specific cases the inference that certain bones and trackways may have been left by the same animals has been of great use in reconstructing stance, gait, and functional morphology of extinct tetrapods, particularly reptiles (Haubold 1971).

Experimental studies (e.g., Schaeffer 1941, Peabody 1959, Padian and Olsen 1984a,b) of the trackways of living tetrapods have been able to shed light on the process of trackmaking and how it relates to the structure of the foot, the kinematics of the limb, and the competence of the substrata (Baird 1954, 1957; Padian and Olsen 1984a). In many cases, the form of a footprint can reveal not only the identity of the trackmaker and the condition of the surface, but also the animal's stance and gait, which may vary with behavioral and environmental circumstances. The experimental approach is especially powerful when comparing fossil and living members of a single phylogenetically restricted group. For example, the earliest known crocodilian trackways *(Batrachopus,* reviewed in Olsen and Padian 1986) differ in no appreciable way from those of living crocodiles (Padian and Olsen 1984a), which suggests that crocodilian locomotory trends have remained conservative over nearly 200 million years.

The present study is an attempt to test alternative hypotheses of the stance and gait of Mesozoic theropod dinosaurs, using the evidence of fossil and recent footprints. No living vertebrates have precisely the same pelvic structure as Mesozoic ornithischian and saurischian dinosaurs. Some lines of evidence, such as the shapes of pelvic and hindlimb joints and the inferred angles of articulation of