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Footprints of the Komodo Monitor and the Trackways of Fossil Reptiles

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Footprints taken experimentally of a captive Komodo monitor (*Varanus komodoensis*) were recorded in potter's clay and cast in plaster. These show morphologic features, also seen in fossil footprints of large reptiles, that reflect a particular pattern of stance and gait. Footprint form and kinematics must be analyzed separately for fore- and hindlimbs because a certain amount of mosaic evolution occurs in limb morphology and locomotion. Comparisons of footprint form with still photographs of the animal walking reveal that the distinct, unmuddied prints of the manus result from an effectively parasagittal movement of the forearm and hand, rotating around a horizontally-oriented humerus. This differs from the lateral arc of protraction in the forearm movement of crocodiles, whose manus prints are generally less distinct. The monitor's pes moves parasagittally, somewhat as in crocodiles. Tail marks were not conspicuous.

The Komodo monitor tracks are similar in great detail to those of Triassic pseudosuchian thecodonts and (to a lesser extent) Early Jurassic crocodiles. Footprint faunas since the Upper Triassic are completely devoid of similar tracks. The similarities probably reflect retention in all these groups of a primitive reptilian locomotory pattern. Hence, the Komodo monitor tracks underscore the extent to which fossil footprints are classified by grade of organization and locomotion. Lacertilian tracks are uncommon in the fossil record. Similarities of Komodo monitor tracks to fossil footprints of nonlacertilians suggest that analysis of modern lacertilian footprints may provide insight into ontogenetic and functional differences underlying much of the basis of paleoichnologic taxonomy.

FOSSIL footprints have been a valuable source of data to vertebrate paleontologists for nearly two centuries. Footprints often occur in environments of deposition in which bones, the principal source of paleovertebrate data, are rare or absent. They can be used to identify the presence of certain taxonomic groups in otherwise fossil-barren sediments, and to assist in biostratigraphic correlation of other such sediments containing osteological or ichnologic remains (Olsen and Galton, 1977; Olsen, 1980a, b). However, apart from such stratigraphic associations and some rudimentary identification of certain footprint forms with presumed trackmakers, there is as yet no cohesive approach to the study of vertebrate ichnology. Our goal in this and other papers is to compare trackways of fossil and recent reptiles with respect to 1) taxonomy, 2) functional determinants of footprint form and 3) the effects of substrate conditions on trackway form and preservation. Trackmaking processes and patterns of modern animals can shed light on the functional determinants of form in fossil footprints, as well as on the locomotory patterns of the animals that made them.

Interpretation of the trackmakers that left fossil footprints dates back to the early 19th Century, when such tracks were first treated in a scientific context. Early workers (Hitchcock, 1848; Deane, 1861) pressed the feet of stuffed or preserved reptiles into clay molds in an attempt to simulate footprints, but this technique ignored kinematics of the step cycle and its effects on footprint form. Later workers examined tracks of modern reptiles in zoos (von Huene, 1913) or occasionally in the wild (Reineck and Howard, 1978), but few systematic functional analyses of these tracks were made (Rühle von Lilienstern, 1939). Schaeffer (1941) studied the footprints of a small caiman on smoked glass, and Peabody (1948) examined those of salamanders on smoked paper, but neither medium is a good analogue for a natural substrate, and so the animal's normal gait and footprint morphology were both abnormally altered. Footfall patterns of modern animals have been taken in conjunction with studies of lo-