

## THE FOSSIL TRACKWAY *PTERAICHNUS*: NOT PTEROSAURIAN, BUT CROCODILIAN

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**ABSTRACT**—The fossil trackway *Pteraichnus saltwashensis* Stokes 1957, from the Morrison Formation of Arizona, originally attributed to a pterodactyloid pterosaur, is reassessed. We conclude that the assignment was incorrect because: 1, *Pteraichnus* has five toes on the manus (all pterosaurs have four); and 2, pterosaurs did not walk quadrupedally. However, trackways similar in detail to the poorly preserved *Pteraichnus* can be simulated experimentally by a small caiman, and we suggest that *Pteraichnus* could have been made by a crocodilian. Experimental work on trackways, coupled with considerations of limb kinematics and substrate conditions, will permit the most robust inferences about paleoichnologic trackmakers, and will thus maximize the utility of fossil footprint data.

### INTRODUCTION

IN 1957 Stokes described a trackway (*Pteraichnus saltwashensis*) from the Morrison Formation (Upper Jurassic) of Apache County, Arizona, which he assigned to a "pterodactyl" (=Pterodactyloidea *sensu stricto*) because of the narrow V-shaped heel, the four subequal toes of the pes, and the unusual manus print, which seemed to preserve an impression of the hypertrophied wing-finger (digit IV) as well as two of the three small digits I-III. Stokes added: "The apparent reduction of digits in both manus and pes is distinctive and is the chief reason for placing the animal in the Pterodactyloidea." For twenty years these tracks have served as the principal fossil evidence in support of the idea that when pterosaurs landed on the ground, they must have walked quadrupedally (e.g., Wellnhofer, 1978).

Stokes' taxonomic inference on the basis of these tracks was ingenious, but we think it must be called into question on at least two grounds. First, detailed studies of anatomy and functional morphology show that the *Pteraichnus* tracks could not have been made by a pterosaur. There are not four digits on the manus print of *Pteraichnus*, as Stokes believed, but five, although all five are not always clearly preserved. This automatically removes pterosaurs, which have only four digits, from eligibility as possible trackmakers of *Pteraichnus*. Crocodiles, like pterodactyloids, have a four-toed pes with a V-shaped "heel." However, crocodiles are plantigrade,

whereas pterosaurs were digitigrade and would not have left a heel impression as seen in *Pteraichnus* and the caiman tracks. Furthermore, the articulation of the pterosaurian forelimb (Padian, 1980) indicates that even if pterosaurs could have walked quadrupedally, which is unlikely, their trackways would have differed considerably from *Pteraichnus*.

Second, when the *Pteraichnus* track is considered in the light of kinematics of the step cycle and interaction of the foot with the substrate, it corresponds in all appreciable respects to a similarly made trackway of a crocodilian—a fact which we demonstrate experimentally with a living caiman. Our purpose in this paper is to show how these results might fit into a conceptual framework of animal-sediment interactions, and to propose criteria for paleoichnologic analysis.

### *PTERAICHNUS*: DATA AND MEASUREMENTS

Stokes' (1957) reconstruction of the *Pteraichnus* trackway, shown in Figure 1B, consisted of a manus print of variable length, averaging around 3¼ inches (8.3 cm), and a pes approximately three inches long (7.5 cm). Stokes described the manus print as a deep impression formed by the wing knuckle, with shallower impressions of two of the three smaller digits splayed *laterally* (not medially, although they are the medial digits). A longer posterior process of this track was taken for the impression of the wing-finger.

There is some confusion in Stokes' measurements of the trackway, which should be

