

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

KEVIN PADIAN AND PAUL E. OLSEN

Department of Paleontology, University of California, Berkeley 94720; and  
Department of Biology, Yale University, New Haven, Connecticut 06511

---

**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

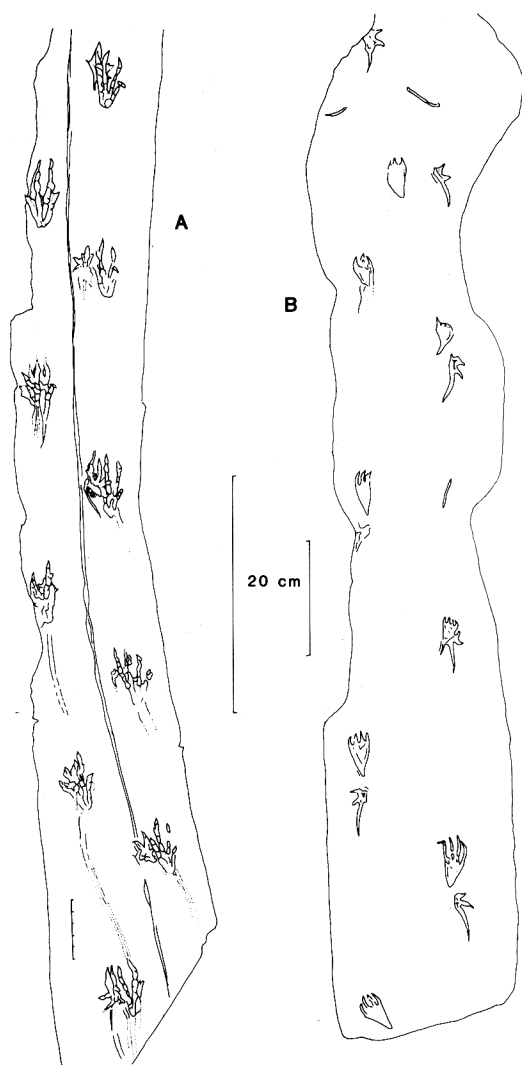


FIGURE 1—A, drawing of a partial trackway of a small *Caiman sclerops* (snout-vent length 23.5 cm). B, *Pteraichnus saltwashensis*, a trackway from the Morrison Formation of Arizona, redrawn from Stokes (1957).

rectified. Stokes gave a pace length of 14" (35.5 cm) and a stride length of 28" (71 cm) for the 3" (7.5 cm) pes of *Pteraichnus*, although his photographs and our measurements of the actual slab clearly show that the pace ranges between 7–10" (18–25 cm) and the stride between 14–18" (35.5–46 cm) for the hindfoot, which was correctly listed as 3".

There are nine pairs (fore and hind) of prints, representing more than two complete

step cycles, with the first three pairs more clearly preserved than the other six. The quality of these prints ranges from fair to indecipherable. In the better ones it is possible to determine the number of digits on the manus, which is always more poorly preserved than the pes. But in no track is it possible to determine a phalangeal formula, and no other details of structure are evident, as they would be in good to excellent trackways. We agree with Stokes' inference that the tracks were made in moist to very moist sand, with the moisture increasing toward the last tracks. The impressions of the digits are slitlike, which indicates that they were filled in by sediment slumping from the sides of the digits. This is one of two main reasons why details of the trackway are obscure. Evidently the animal was entering deeper water. The prints are relatively deep for the size of the foot, so the substrate must have held a great deal of moisture in order to allow the animal to sink to that extent.

#### MATERIALS AND METHODS

Figure 1A shows the outline of the trackway of a small caiman (*Caiman sclerops*) with a snout-vent length of 23.5 cm and a total length of 48.6 cm. The length of the manus is 2.1 cm, and that of the pes is 4.3 cm, so the caiman track is roughly 60% the size of *Pteraichnus*. The caiman was run under a range of conditions, in order to simulate trackways at several different speeds. The set reproduced here was made during a rapid walk, according to the following procedure.

To make a suitable bed for tracks, we cut slabs of potter's clay approximately 2 cm thick and laid them end to end. We worked water into the surface of the clay to make a suitable mud, and smoothed the surface with a straightedge. Then we conditioned the surface with a very thin coat of glycerine to simulate natural algal and bacterial growth, which acts as a natural parting medium. This prevented the substrate from sticking to the caiman's feet as he moved, the most frequent problem in producing experimental trackways.

The clay bed was placed between two high barriers, and a dark open box was placed at the far end of the bed. The animal was placed at the opposite end and was encouraged to walk along the clay bed. We found that loud

