

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

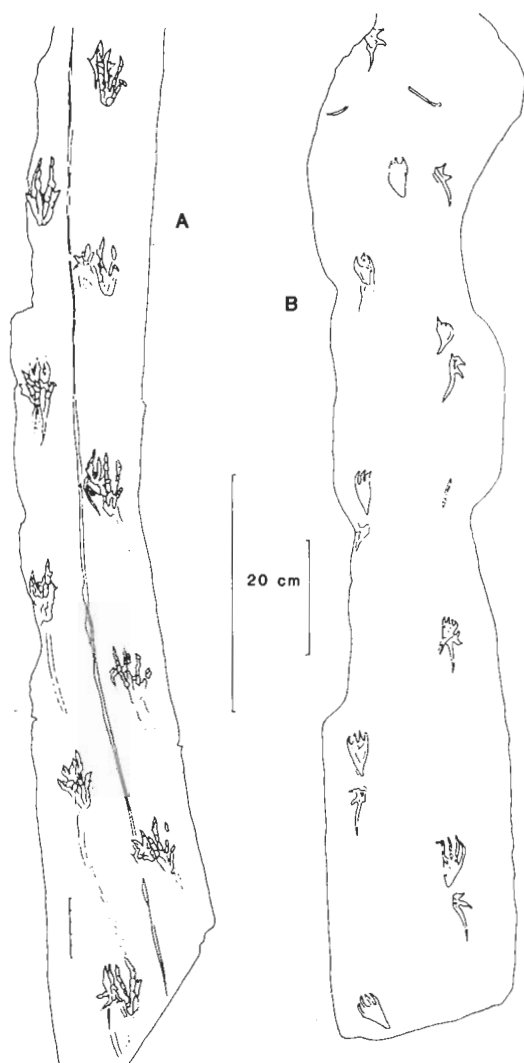


FIGURE 1—A, drawing of a partial trackway of a small *Caiman sclerops* (snout-vent length 23.5 cm). B, *Pteraichnus saltwashensis*, a trackway from the Morrison Formation of Arizona, redrawn from Stokes (1957).

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

noises, threats, and menacing gestures were not effective in producing desirable tracks: usually the caiman's response to such encouragement was to become sullen, to attack, or to walk backwards. The best results were achieved by directing a bright light at a low angle from the near end of the clay bed toward the far end, and staying out of the animal's field of vision. To avoid the light, he would head toward the dark box. The speed of his movement varied, and so a range of trackways was produced.

Figure 2B shows a single set of prints made by the caiman, with the digits of the manus and pes numbered in Figure 2D. This is compared to a similar set from *Pteraichnus* (Figures 2A, C). The variation can be traced both to the kinematics of the step cycle and the condition of the substrate (Figure 2E). The original substrate in which the *Pteraichnus* tracks were made was sandier and not as firm or cohesive as our clay trackbed. It therefore preserved vaguer, although deeper, impressions of digits, and was subjected to slumping. Even so, the trackways are similar enough to allow clear comparison of each digit.

RESULTS

Kinematics of the step cycle can alter appreciably the normal contact of an animal's foot with the substrate. In the "high walk" of the crocodile, the pes moves parasagittally, but the manus is splayed to the side (Schaeffer, 1941; Brinkman, 1980). Some lateral rotation of the carpus occurs in this step cycle, and we have observed that this rotatory thrust is responsible for the deep impression formed

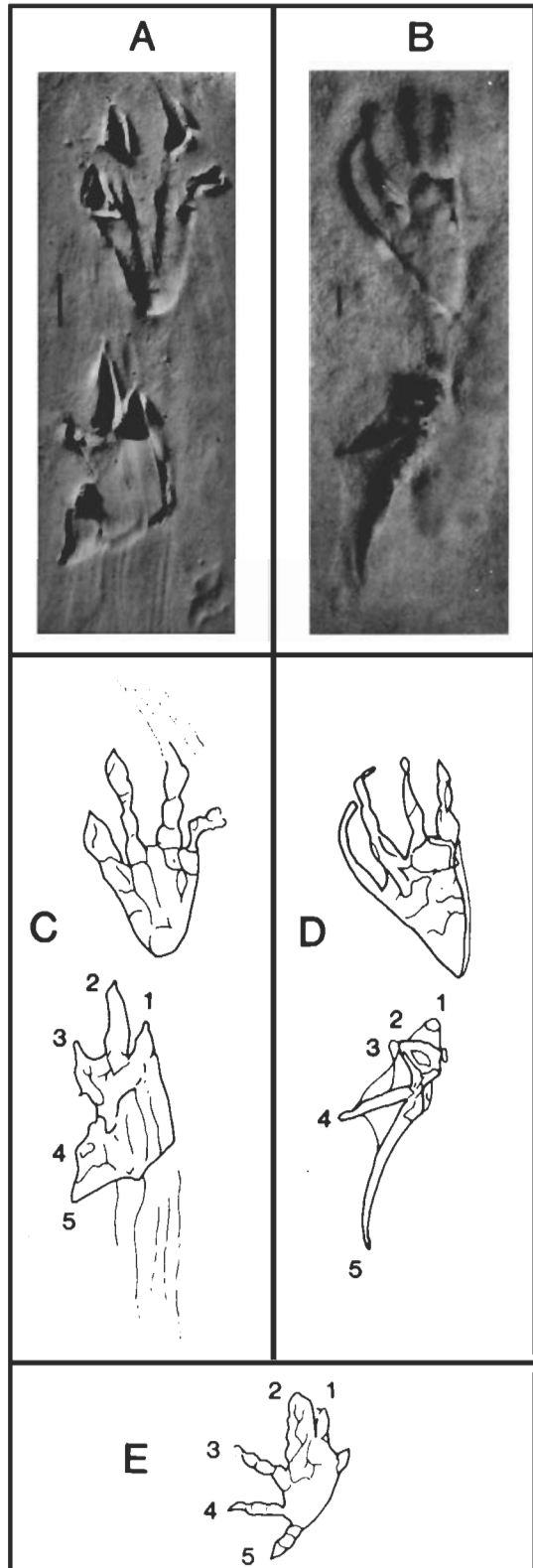


FIGURE 2—Detailed comparison of *Caiman* footprints with *Pteraichnus*. A, pair of left footprints from another part of the caiman trackway of Figure 1A. Length of pes (above) 4.3 cm. Scale = 1 cm. B, pair of right footprints (printed reversed) from *Pteraichnus*, length of pes 7.5 cm. Scale = 1 cm. C, drawing of prints in Figure 2A, with digits of manus numbered. D, similar drawing of Figure 2B. E, an unusually clear left manus print of the caiman, with digits numbered. Compare with manus prints in Figures 2C and 2D: in 2C, sloppy kinematics are responsible for loss of clarity, while in 2D this problem is further compounded by an incompetent substrate. Neither allows accurate representation of anatomy.

in the center of the manus print of the caiman. It is not necessary to ascribe the similar deep depression in the manus print of *Pteraichnus* to the enlarged wing knuckle of a pterosaur, as Stokes (1957) suggested. The depth of this track is not due to size or weight, but to force of the step and incompetence of the substrate. Baird (1957, 1980) has stated that a trackway cannot be regarded as equivalent to the morphology of the animal that made it, but is instead a record of the dynamic process of locomotion. Although it would have been exceedingly difficult to reconstruct this rotatory function in the manus of crocodylians from the footprints alone, it is evident that a deep central depression is the result.

By contrast, the hindfoot undergoes no rotation during the high walk of the caiman (Schaeffer, 1941; Brinkman, 1980). Its print is therefore more distinct and does not show the muddying of the print seen in the manus. Stokes noted that the toes of the pes tended to be curved inward and downward in *Pteraichnus*; this probably reflects a shift in weight as the animal walks, but needs further qualification. Stokes also noted that the claws of the pes were especially recurved, and inferred from this an adaptation to hang from branches and other rough surfaces. As in theropod dinosaurs, the claws of the manus in pterosaurs have a greater curvature than those of the pes, not the other way around as Stokes described for *Pteraichnus*. In fact, the pedal claws of both pterosaurs and crocodiles show very little curvature. The curvature of the toes in the trackways of *Pteraichnus* and the caiman further document the process of trackmaking, as Baird suggested, and are consistent with the step cycle of the caiman described by Brinkman (1980). Their deep curvature, therefore, should not be interpreted as a literal record of morphology.

In all the *Pteraichnus* tracks the hindfoot impression is either superimposed on the forefoot impression or is anterior to it. Stokes believed this indicated "a short body and perhaps the possibility of an occasional bipedal stance." To estimate body length, we have used Baird's (1954, 1957) method of calculating the trackmaker's gleno-acetabular (shoulder-to-hip) length from the pace and stride of the *Pteraichnus* trackway. We then tested this method by comparing the calcu-

lated mean gleno-acetabular length of the experimentally produced caiman trackway to that of the living animal. The calculated gleno-acetabular length of the caiman, based on tracks, is 11.1 ± 0.2 cm and the actual gleno-acetabular length was measured at 11.5 cm. The estimate of the gleno-acetabular length of *Pteraichnus* by Baird's method is 19.4 ± 2.1 cm. The ratio of gleno-acetabular length to foot length, based on tracks, is 2.6 for both the caiman and *Pteraichnus*. It is also 2.6 in the early Mesozoic crocodile *Protosuchus*, as measured from the specimen. In contrast to crocodiles, pterosaurs have relatively shorter bodies for their foot size. In *Rhamphorhynchus* the estimated ratio of gleno-acetabular length to foot length is 2.1, in *Pterodactylus* it is 2.0, and in *Pteranodon* it is 1.5. So, although we agree with Stokes that the *Pteraichnus* trackmaker had a relatively short body, it was no shorter than in other small crocodiles, and it was not as short as in known pterosaurs.

DISCUSSION

There is strong evidence from functional anatomy that a pterosaur could not have been responsible for *Pteraichnus*. The glenoid articulation of the pterosaurian forelimb allowed the wing to be folded against the body, as in birds, with the distal end of the humerus directed posteriorly (Padian, 1980; Figure 3). During the flight stroke the pectoralis muscles brought the huge deltopectoral crest of the humerus, which was oriented laterally and horizontally when the wing was folded, down and forward toward the sternum, from which the pectoralis muscles originated. This action of the flight muscles produced a down-and-forward stroke used in forward flight at slow and medium speeds, as it does in birds and bats. A simple dorsoventral stroke, with the humerus perpendicular to the sagittal axis, was also possible. But the prominent anterior and posterior facets of the glenoid fossa, virtually identical to those of birds, prevented the humerus from being protracted and retracted underneath the body; thus the fore-and-aft motion necessary for the manus print of *Pteraichnus* could not have been produced. The pace length of the elongated forelimb could hardly be the same as that of the hindlimb; and perhaps most importantly, even if a quadrupedal pose were possible, the fore-

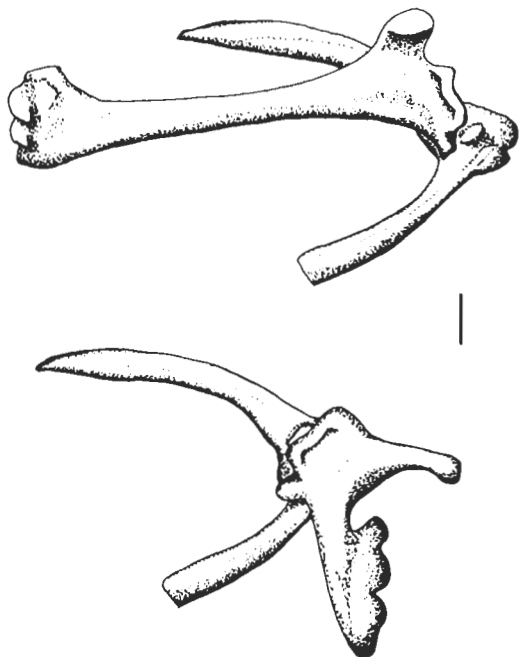


FIGURE 3—Right shoulder girdle and humerus of a generalized rhamphorhynchoid pterosaur in lateral view, with the humerus in retracted (above) and protracted (below) positions. From Padian (1980). Scale = 1 cm.

limb and hindlimb prints could not have been equidistant from the body midline (Bramwell and Whitfield, 1974, figs. 56–57). Pterosaurs, contrary to traditional belief, appear to have been bipedal, digitigrade animals whose stance and gait were very similar to those of birds and small bipedal dinosaurs (Padian, 1980); no trackways corresponding to such a reconstruction have yet been identified.

The track of *Pteraichnus*, in our estimation, was probably produced by a crocodylian (=Order Crocodylia *sensu stricto*, not in the sense of Order Crocodylomorpha proposed by Walker, 1970), although it is difficult to identify the trackmaker beyond this designation. The phalanges are not as distinct in *Pteraichnus* as they are in well-preserved dinosaurian trackways such as *Anchisauripus* (Lull, 1915) or *Anomoepus* (Hitchcock, 1848). For these reasons the trackmaker of *Pteraichnus* can only be described in a general way. There were five digits on the manus, although Stokes noted only three; this is the typical crocodylomorph pattern. The “short

trailing impressions” of the manus, taken by Stokes for the print of the posteriorly directed wing-finger, are actually the tracks made by the fifth digit as it slides *into* position during the recovery stroke of the manus. Reineck and Howard (1978) noted that this long, bow-shaped trail was left continuously in the path of *Alligator mississippiensis* (length 1.25–2 m), walking across damp sand on an island off Georgia. This bow-shaped trail, which they identified as pertaining to the hindfoot, is in fact made by the lateral toe of the forefoot, and is therefore homologous to the similar structure in the caiman track and, by inference, in *Pteraichnus*. The crocodylian hindfoot does not swing in an anterolateral arc like the forelimb, but rather moves more directly forward (Brinkman, 1980). Here again pterosaurs depart from the pattern of *Pteraichnus*: a track made by the wing-finger of pterosaurs would not have curved as this track does, and the smaller digits would have been medial, not lateral, to the wing-finger, provided that a pterosaur was able to rest the manus on the ground.

At least four genera of crocodylians are known from the Morrison Formation, including *Goniopholis*, *Hoplosuchus*, *Eutretauranosuchus*, and an undescribed protosuchian from the Fruita region of Colorado (J. M. Clark, in preparation). At the present time it is not necessary or desirable to attempt to assign the *Pteraichnus* trackway to any particular genus of crocodylian. More work is needed to assess the relationship of variations in size and foot form to trackways before the possibility of linking fossil trackways to trackmakers can be realized. Stokes (1978) also assigned prints from the underlying Navajo Formation (Lower Jurassic) to *Pteraichnus*, although they are much more poorly preserved than those from the Morrison. These cannot be regarded as the earliest evidence of pterosaurs (Stokes, 1978; Anonymous, 1973), which in any case are known from the Norian-(Upper Triassic) of Italy (Zambelli, 1973); but if they are indeed like *Pteraichnus*, then the crocodile *Protosuchus*, which has been recorded by Camp from the Navajo Sandstone (Galton, 1971), could be considered as a possible trackmaker. Stokes and Madsen (1979) have assigned other tracks from the Sundance Formation, which overlies the Morrison, to *Pteraichnus*; if this sim-

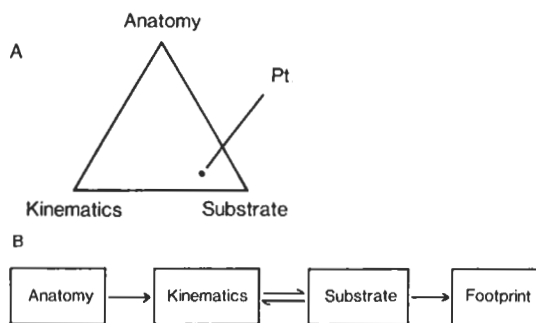


FIGURE 4—A, ternary diagram of factors influencing footprint morphology. *Pt*, *Pteraichnus*. B, flow chart of the same factors. For explanation see text.

ilarity can be established, it follows that these tracks are also crocodyloid.

In this reassessment of *Pteraichnus* we have tried to follow Baird's (1980) maxim that "a footprint is not the natural mold of a morphological structure but is, instead, the record of that structure in dynamic contact with a plastic substrate." We believe this idea can be usefully conceptualized in two ways. Figure 4A is a ternary diagram intended to represent the morphology of a footprint. At the corners of the triangle are the three principal determinants of this morphology: anatomy of the foot, kinematics of the limb, and conditions of the substrate. A point within the triangle can represent subjectively the morphology of the footprint as it has been influenced by each determinant. The kinematics of an animal's locomotory cycle may distort the reflection of anatomy, whereas a poor substrate may render the tracks indistinct. The point labeled *Pt* in Figure 4A represents, somewhat subjectively, the condition seen in *Pteraichnus*. In Figure 4B we have tried to express this idea in the form of a flow chart; this diagram also shows how substrate conditions can influence kinematics to remove the footprint even further from the anatomy of the trackmaker.

Further attention to kinematic patterns of step cycles among living tetrapods and to variables in substrate conditions should allow important advances in paleoichnologic study. There have been few studies of the relationships between patterns of locomotion and footprints of living reptiles, and most accounts have been anecdotal (see Huene,

1913 and Reineck and Howard, 1978 on crocodiles). We have recently taken trackways of the Komodo monitor (*Varanus komodoensis*) and compared the prints to those of fossil reptiles (Padian and Olsen, in preparation). But much more work is needed on the anatomical and kinematic bases of ichnologic classification. Particular attention should be devoted to allometric changes in footprints from both ontogenetic and phylogenetic aspects. Through these approaches, the real data available in fossil trackways could be more fully explored.

CONCLUSIONS

The conclusions we draw from this study are these. First, the *Pteraichnus* tracks are poor trace fossils, not sufficiently preserved to allow detailed inferences about their morphology or their trackmaker. Second, Stokes' (1957) inference that a pterosaur was responsible for these tracks must be rejected on the grounds of anatomy and functional morphology: *Pteraichnus* has five toes on the manus, while pterosaurs have only four, and pterosaurs would not have been able to draw all four limbs into the same plane of movement or to make tracks like *Pteraichnus*. Third, a reasonable approximation of *Pteraichnus* can be simulated by a living caiman, and the morphology of the *Pteraichnus* trackmaker can, by careful comparison, be shown to correspond in all decipherable particulars to a crocodylian. This conclusion would not be possible without experimental analysis of living animals, which we see as an encouraging prospect for further advances in the science of ichnology.

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