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Pterosaur Stance and Gait and the Interpretation of Trackways

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The tracks ascribed to pterosaurs from the Late Jurassic limestones at Crayssac, France, must be pterosaurian because the manus prints are so far outside those of the pes, the pes print is four times longer than wide, and the manus prints appear to preserve distinct traces of a posteromedially directed wing-finger. These tracks are different in important ways from previously described *Pteraichnus* trackways, which have been variably considered pterosaurian, crocodilian, or indeterminate. No *Pteraichnus* (*sensu stricto:* those not from Crayssac) tracks have diagnostic features of pterosaurs and in none can a complete phalangeal or digital formula be reconstructed; however, all published Pteraichnidae tracks fulfill the criteria of poor preservation, and some have some diagnostic features of crocodile tracks. Reconstructions of pterosaurs walking in pteraichnid tracks do not fit those tracks well, but crocodiles do.

In contrast, the Crayssac tracks demonstrate the erect stance and parasagittal gait previously reconstructed for pterosaurs. They also demonstrate that the footfall pattern was not as in typical reptiles (LH-RF-RH-LF), but that the manus must have been raised before the next forward step of the ipselateral foot (LH-LF-RH-RF), suggesting that the quadrupedal pattern was secondary. The metatarsus in pterosaurs was set low at the beginning of a stride, as it is in crocodilians and basal dinosaurs. The diagnosis of the Ichnofamily Pteraichnidae comprises features of possible crocodilian trackmakers, but not of possible pterosaurian trackmakers. Trackways considered for attribution to pterosaurs should show (1) manus prints up to three interpedal widths from midline of body, and always lateral to pes prints, (2) pes prints four times longer than wide at the metatarso-phalangeal joint, and (3) penultimate phalanges longest among those of the pes.

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INTRODUCTION

For nearly a century and a half, trackways have been ascribed to pterosaurs (Wellnhofer, 1991). Most of these were later referred to horseshoe crabs, crocodilians, turtles, or simply regarded as indeterminate (Padian and Olsen, 1984; Unwin, 1989; Wellnhofer, 1991; Lockley et al., 1995). Stokes (1957) assigned an unusual and poorly preserved trackway to a new taxon, *Pteraichnus saltwashensis*, and gave reasons why it might have been made by a pterosaur. Padian and Olsen (1984) acknowledged Stokes' insight, but pointed out that on kinematic grounds the trackway was unlikely to have been made by a pterosaur: the forelimbs, much larger than the hindlimbs, could not have articulated in the same parasagittal line as the pedes (this was incorrect for pterosaurs, as the Crayssac tracks show). They also argued that the trackways were made in incompetent substrate and were too poorly preserved to provide phalangeal formulae. Especially problematic was the manus: its long posterior impression, which Stokes took for the imprint of the wing-finger, could be simulated by the action of a small caiman as it dragged its fifth digit into the print. Padian and Olsen concluded that *Pteraichnus* was probably made by a crocodilian (the term "crocodilian" is generally applied to Crocodylomorpha). This view received some general acceptance (e.g., Unwin, 1987; Lockley, 1991) but was later countered by Lockley and Hunt (1995), Lockley et al. (1995), Bennett (1997), and Unwin (1997), all of whom reviewed the history of the problem, but came to somewhat differing conclusions about identification of digits, stance and gait, and terrestrial capability.

The discovery of the Crayssac footprints by Mazin et al. (1995) represents the first unambiguous occurrence of pterosaur tracks. Although they have only been briefly reported so far (Mazin et al., 1995, 1997), they are not disputed because the forelimb prints are so far lateral to the hindlimb prints, and because the pedal prints are approximately four times as long as the width at the metatarso-phalangeal joint (Fig. 1, 2a, b) (crocodilian trackways and pteraichnids are closer to three times as long). They also appear to impress part of the proximal part
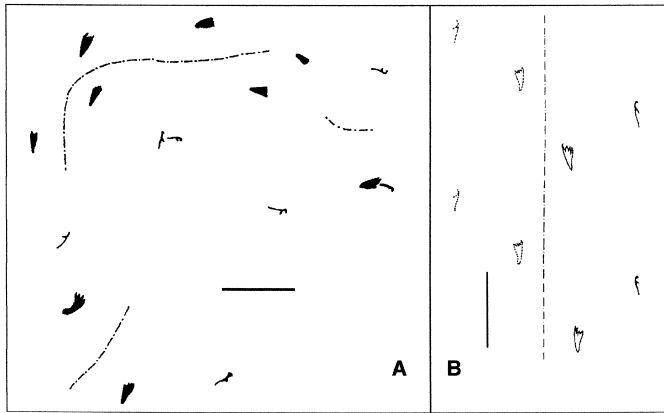
FIG. 1. Drawing (a) and reconstruction (b) of pterodactyloid pterosaur trackways from Crayssac, France (from Mazin et al., 1995). Scale = 10 cm.

of the wing-finger. Because there are other similarities in the manus and pes between the Crayssac tracks and those of pteraichnids, the former have often been referred to *Pteraichnus* or something close to it (e.g., Mazin et al., 1995; Lockley et al., 1995; Unwin, 1997; Wright et al., 1997), and used as further justification that all pteraichnid footprints were made by pterosaurs. However, I suggest here that there are substantial problems with the published evidence adduced to support this assignment.

Throughout this paper I maintain a strict separation between the Crayssac tracks and all tracks referred to as Pteraichnidae. Here, the use of the terms *Pteraichnus* and Pteraichnidae never include the Crayssac tracks, which differ in the ways just noted. I also show that (1) there are no diagnostic features of pterosaur anatomy in typical *Pteraichnus* prints; (2) arguments about these tracks rely on poor preservation for support; (3) it is unlikely that pterosaurs could have made *Pteraichnus* manus prints; and (4) the arguments against a crocodilian origin of *Pteraichnus* tracks are not well established (in fact, experimentally produced caiman tracks fit all the diagnostic features of Pteraichnidae). The poor preservation of pteraichnid tracks, a result of both incompetent substrate and limb kinematics (Baird, 1954, 1957; Padian and Olsen, 1984; Padian, 1986, 1988), has been widely ignored or dismissed, although preservation is critical to the understanding of these tracks.

METHODS

There are two reasons why inferences about the trackmakers of pteraichnid footprints are still disputed. First, known pteraichnid tracks are too poorly preserved to provide phalangeal formulae or diagnostic features of the morphology of any skeletal taxon (Figs. 2g, 3a, 4–6). Part of this is probably caused by the kinematics of the step cycle, and part from substrate incompetence. Second, most workers who discuss this problem do not agree on standard methods of analyzing footprints. As a result, it is difficult to confirm interpretations and assignments.
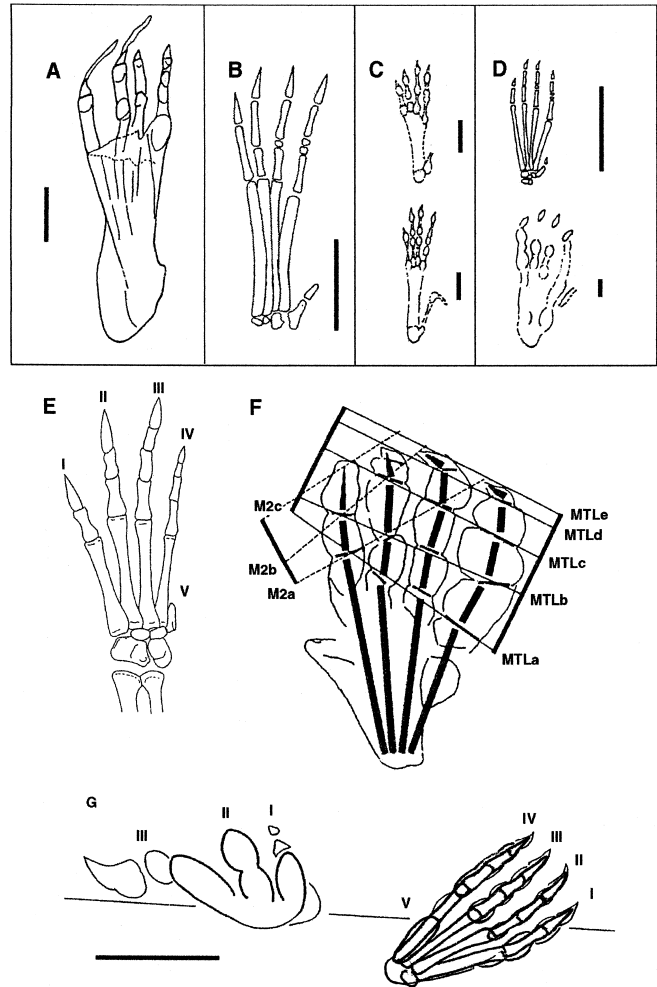

FIG. 2. Pterosaur and crocodylian feet and tracks. **(a)** Drawing of a right footprint of a pterodactyloid, from Mazin et al. (1995). Note the length/width ratio is close to four, rather than less than three. The metatarsals are not distally splayed. **(b)** Right foot of *Pterodactylus*, after Unwin (1999). This foot approximately fits the track in (a). **(c)** Hypothetical right pedal tracks of *Pterodactylus* (above) and *Rhamphorhynchus* (below), as predicted by Unwin (1989). **(d)** Right foot skeleton of *Pterodactylus* (above) and pedal track of *Pteraichnus* (below), after Unwin (1989) and Lockley et al. (1995). Note that the distal metatarsals are splayed, but this is not their natural position: compare to (b) and (c, top). Splaying the metatarsals distally makes them resemble a crocodile foot (e, after Wright et al., 1997), but neither this foot nor the *Pteraichnus* track (d, bottom) fits the profile of the pterosaur foot skeleton (b) or predicted track (c, top). In contrast, the crocodile foot skeleton in **(e)** is commensurate with the footprint in (d, bottom). **(f)** Reconstruction of the right foot of *Purbeckopus* (from Peters, 2001, based on Wright et al., 1997), with interphalangeal lines restored. Note that the phalanges as restored do not match those of pterosaurs (the metatarsals splay distally, they are of the wrong relative lengths for pterosaurs, the penultimate phalanges are not the longest, and the length/width ratio is slightly larger than two, rather than close to four). Hence *Purbeckopus* is not a pterosaur track, but its reconstructed skeleton and proportions fit those of crocodilians. **(g)** Left manus-pes set of *Pteraichnus stokesi*, from Bennett (1997), with foot skeleton restored. Bennett interprets an ungual on the posterior manual digit, which means that it must be III, not IV as Lockley et al. (1995) maintained. The foot skeleton, as restored, cannot belong to pterosaurs for the same reasons given for *Purbeckopus*; a crocodylian foot fits it better, though it is not a well-preserved trackway. Note the position of metatarsal V, consistent with crocodiles (e) but not pterodactyloids (b). Following Padian and Olsen (1984), the manual impressions would probably be of digits I (anterior, not marked), II/III, IV, and V. Scale = 5 cm in (g), 1 cm elsewhere.
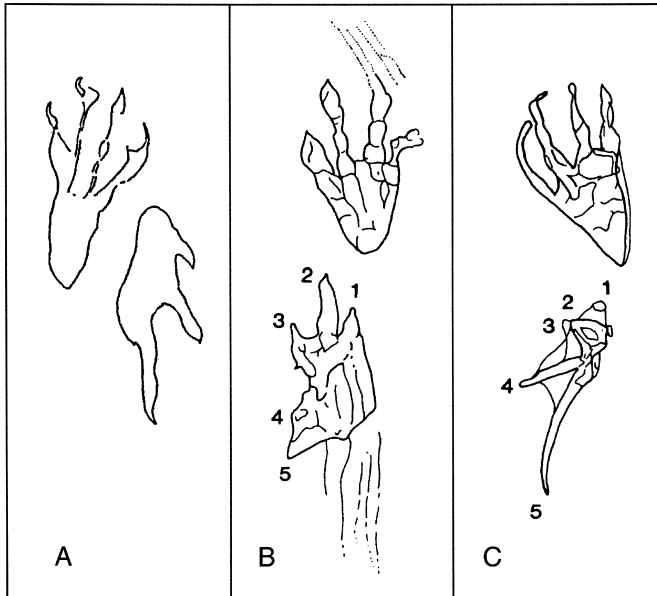
FIG. 3. **(a)** Right manus-pes set of *Pteraichnus* cf. *saltwashensis* from the Summerville Formation of eastern Utah (from Lockley et al., 1995). **(b)** Left manus-pes set experimentally produced from *Caiman sclerops* and **(c)** drawn from the holotype of *Pt. saltwashensis*. (b) and (c) from Padian and Olsen (1984). Note that all three pedes have crocodylian but not pterosaurian features, and all three manus are incomplete records of anatomy, muddied and distorted by kinematics and sediment incompetence.

Baird (1954, 1957) laid out some explicit methods for studying fossil trackways, especially with a view to taxonomy and to the interpretation of trackmakers, gait, and behavior. His methods were codified as laws by Padian and Olsen (1984, 1989b) and Padian (1986). They can be summarized as follows.

1. Baird noted that a footprint is not a simple record of anatomy but of the behavior of an animal executing a particular gait on a particular substrate under certain conditions. This means that if we take literally the shapes that we see preserved as impressions in rocks, we are liable to infer some strange ideas about anatomy and trackmakers. Padian and Olsen (1984; see also Padian, 1986) expressed the factors of anatomy, kinematics, and substrate condition as three corners of a triangle representing influences on footprint form (Fig. 6c). Trackways that are too strongly distorted by kinematics of the step cycle or the incompetence of the substrate destroy anatomical information. They cannot be treated as literal records of anatomy, and they cannot be cursorily inspected with no regard to the influences of kinematics and substrate (see Gatesy et al. [1999] for a classic study that takes these factors into account to reveal unsuspected features of the step cycle in theropods).

2. Poorly preserved trackways cannot be expected to yield zoologically significant information. This means, in plain language, that there is little point in making too much of such remains. Poorly preserved trackways are those in which (1) the number of digits in the manus or pes is not

clear or the digits are clearly not all preserved, (2) a phalangeal formula cannot be unambiguously reconstructed, (3) the kinematics of the step cycle create features that do distort anatomical features in such a way to mislead ichnologists, (4) the substrate was so incompetent as to obscure critical anatomical features, and (5) the preservation of the impressed tracks has been so worn and altered as to remove critical information.

The footprints of every trackway assigned to *Pteraichnus* or Pteraichnidae unexceptionally meet the criteria of poorly preserved tracks. This is evident in Figs. 2–6. Workers do not agree on the number or identification of the digits, especially of the manus; a phalangeal formula has never been reconstructed for even a single manus or pes (the single exception of *Purbeckopus*, discussed below, demonstrates that the track was crocodil-
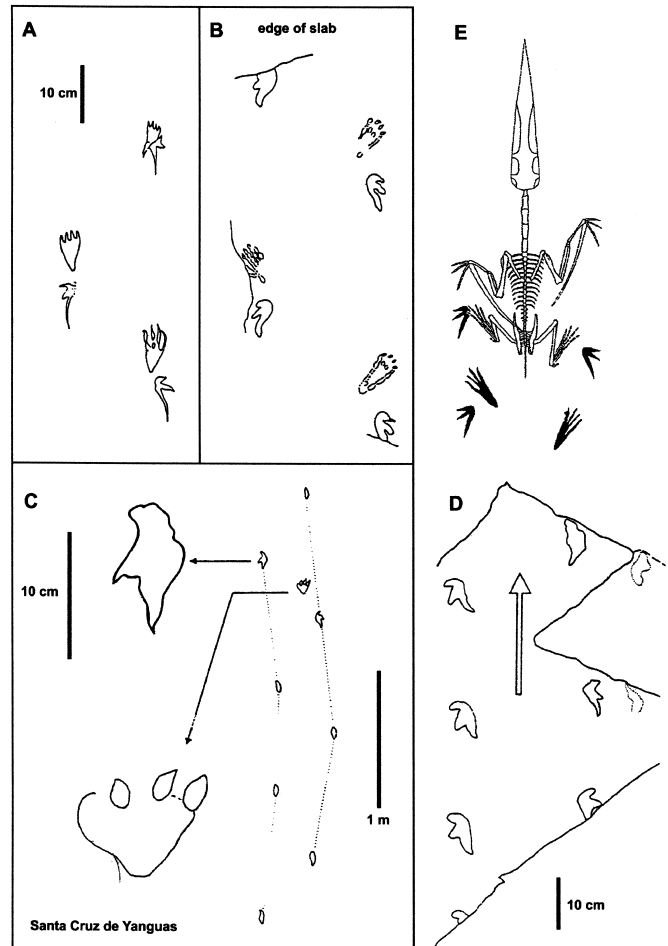
FIG. 4. **(a)–(d)** Trackways referred to Pteraichnidae by Lockley et al. (1995). **(a)** Type specimen of *Pteraichnus saltwashensis*. **(b)** Type specimen of *Pt. stokesi*. **(c)** *Pteraichnus* trackway from the Lower Cretaceous of Spain. **(d)** Manus-only impressions of *Pteraichnus* from the Summerville Formation of Utah. **(e)** Unwin's (1997, 1999) reconstruction of a *Pterodactylus* making *Pteraichnus* tracks. Note that the ratio between stride length and track width is only 1.35 in (e), whereas it is 2.11 in (b) and 3.53 in (a). This means that in order to make *Pteraichnus* tracks (a), the model would have to take steps 2.5 times longer than in (e), which is impossible.
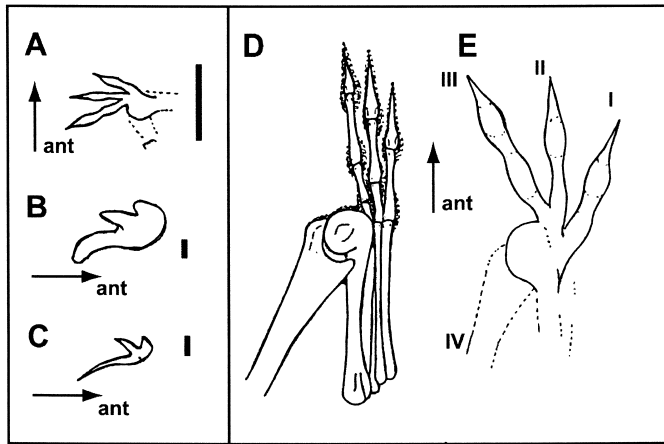
FIG. 5. Manus prints and skeletal reconstructions. (a) Unwin's (1989) reconstruction of the manus print of a pterosaur. (b) and (c) manus prints of *Pteraichnus*. (d) Unwin's (1989) reconstruction of a *Rhamphorhynchus*-like pterosaur manus in natural position, anterior toward the top. (e) Another pterosaur manus reconstruction, also from Unwin, with splayed digits. Note the contradictions: (d) and (e) work only when the wing is retracted and the metacarpus naturally faces forward. (a) is a natural position if anterior is to the top and the arms are extended laterally so that the digits point laterally (and even posteriorly). The digits cannot point laterally and posteriorly if the arm is folded and the metacarpus faces anteriorly (d, e); and in this position the metacarpus cannot abduct 90°. The position with fingers pointing left (a) is 90° from the orientation of the finger traces in (b) and (c) of *Pteraichnus*, which point to the right.

ian); no workers apart from Padian and Olsen (1984) have treated the effects of kinematics or substrate on the footprints, and no other workers have examined the effects of these factors experimentally; and no tracks have been newly exposed to the surface, avoiding further erosion (which is evident in many published pteraichnid trackways). Therefore, regardless of who the pteraichnid trackmakers actually were, the inference that *Pteraichnus* tracks were made by pterosaurs is based on poor quality, not on diagnostic features, a point returned to below.

ANALYSIS

Diagnostic Features of Pterosaur Tracks

Diagnostic pterosaurian trackways should show several features. (1) The manus prints should be lateral to the pes prints (and may be several body widths outside them). (2) The length of the pedal print should be approximately four times greater than its width at the metatarso-phalangeal joint. (3) The penultimate phalanges should be the longest. No known trackway is well enough preserved to satisfy the third criterion. The Crayssac tracks (Fig. 1) satisfy the first two criteria. *Pteraichnus* tracks satisfy none of them.

Manus Prints Should Be Lateral

For reasons discussed by Padian (1983a, b) and Unwin (1989), the manus of pterosaurs cannot be protracted and re-

tracted in line with the pes without dislocating at least one joint of the forelimb. Unwin (1989, p. 270) noted:

> "Padian (1983b) has demonstrated that, with the forelimbs folded up, the manus could not be brought to bear directly upon the substrate, as illustrated by Seeley (1901, Fig. 56, 63). I have been able to confirm this by manipulation of uncrushed wing bones of *Rhamphorhynchu* . . . , *Santanadactylus* . . . , and *Quetzalcoatlus*. . . . The manus could only be used to support or pull the pterosaur forward when the wing was partly or fully extended. Furthermore, the limited degree of fore and aft movement available would only have permitted a very short stride."

Unwin (1997) changed his mind in reconsidering the Crayssac tracks, and this conclusion partly influenced Lockley et al. (1995) that pterosaurs could indeed have made *Pteraichnus* tracks. (Here I regard this as a conflation of two different kinds of tracks; however, there are many strong superficial similarities.) Unwin (1997, p. 379) explained the revision of his
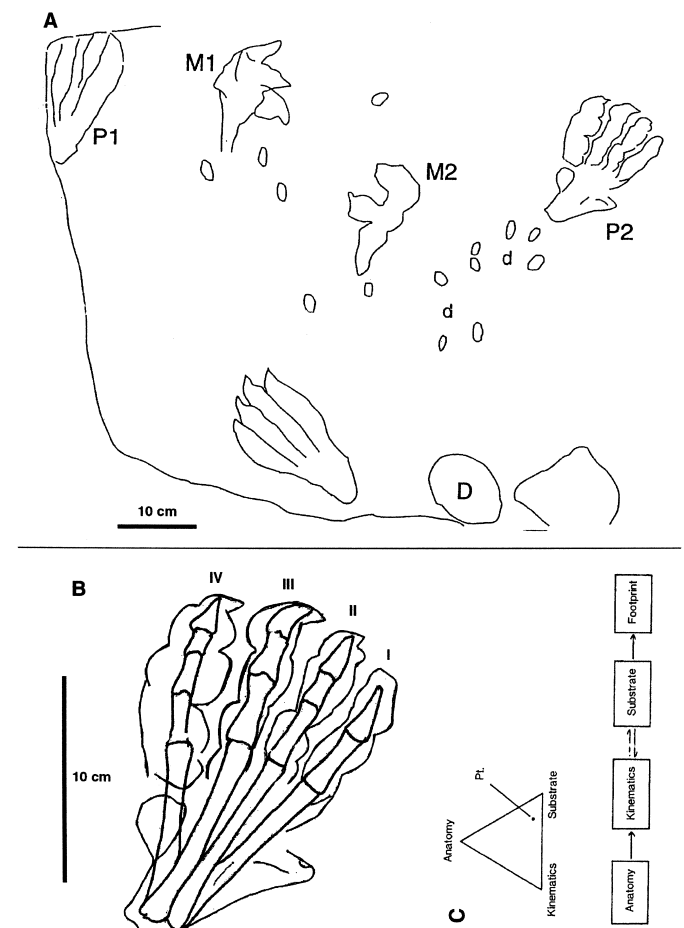
FIG. 6. (a) Slab of *Purbeckopus*, from the Lower Cretaceous of England, from Wright et al. (1995). It is correctly referred to Pteraichnidae, but the trackmaker cannot be pterosaurian, as a restoration of the foot skeleton (b) shows (compare to Figs. 2b and 2e; note caption to Fig. 2). (c) Diagram of the influences on the form of a footprint, from Padian and Olsen (1984), with the condition of the holotype of *Pteraichnus saltwashensis* indicated.

conclusions: "it has not been widely appreciated that in many pterosaurs the shoulder glenoid opens to the rear as well as faces outward. As a result, the humerus could be retracted backward into a position close to the body such that the hinge axis of the elbow joint was oriented perpendicular to the midline."

According to this view, the elbow would flex and extend parasagittally, the wrist would rotate the metacarpus outward and backward, and the small digits would project laterally and posteriorly.

This is an understandable conclusion with respect to certain pterosaurs; I partly agree but suggest at least two caveats. First, in those pterosaurs with a notarium the glenoid faces somewhat posteriorly (rather than mainly laterally), because the scapula, equal to the length of the coracoid, now fits into the midline of the back (Wellnhofer, 1978; Bennett, 2001a). This has been established in some lineages of pterodactyloids, such as pteranodontids and azhdarchids. In more basal pterosaurs the glenoid faced nearly laterally; the humerus could have been adducted against the body, and brought forward to a point somewhat anterior to the glenoid, depending on the taxon (Padian 1983b). But in these basal taxa, when the humerus is brought back against the body wall it cannot rotate; the hand can be raised and lowered by flexing and extending the elbow. So it must be shown and not assumed that the glenoid faced backward in any postulated trackmaker. In protraction, most excursion of the humerus takes place at the distal end.

When the humerus of (at least basal) pterosaurs is protracted, it is also rotated forward and downward from the glenoid (Padian, 1983b). The *Pteraichnus* tracks show no indication of this, and this is not accounted for in the explanations of Lockley et al. (1995), Unwin (1997), and Bennett (1997). Derived pterodactyloids have a more laterally facing glenoid and a deltopectoral crest with less torsion, so there is less rotation during protraction (Hazlehurst and Rayner, 1992). This is not a problem for the Crayssac tracks (Fig. 1), because the shoulder and elbow are already extended, and as noted below, the forelimb is apparently providing support, not mainly powering the stride, so extensive forward rotation at the shoulder is not necessary.

If these inferences are correct, then there is little or no rotation of the forelimb in pteraichnid (non-Crayssac) tracks. This means that the humerus must have been fully adducted against the body (Padian, 1983b; Unwin, 1987), and so the forelimb at the elbow could only have been raised and lowered. In this position it must be accepted that the wrist would have rotated outward to place the three small fingers in the same orientation that they take in the Crayssac tracks, in which the manus is so far outside the pes and the forelimb is so clearly extended (see below). The metacarpals are thought to be directed anteriorly with the arm flexed (Unwin, 1987; Fig. 5d) and laterally with the arm extended (Unwin, 1997; Fig. 5a). If so, the fingers must have made prints of the same orientation when the arm is both flexed and extended.

Length of Pedal Print

An examination of pterosaur feet shows unambiguously that the distance across the appressed metatarsals is no more than a quarter the length of the feet from ankle to unguals (Figs. 2a, b, c; Wellnhofer, 1978, p. 25). This agrees with the Crayssac tracks (Mazin et al., 1995) but not with pteraichnid tracks. Other workers, including Lockley et al. (1995), Unwin (1997), and Bennett (1997, 2001a, b), have argued that pterosaur metatarsals were splayed (e.g., Fig. 2d, top); this would decrease the length-width ratio to a figure closer to three, typical of crocodilians (Figs. 2e, 3b). My observations and others' (e.g., Clark et al., 1998) disagree with the notion that pterosaur metatarsals were splayed (note the hypothetical pedal tracks predicted by Unwin [1989; Fig. 2c] and accepted by Lockley et al. [1995, Fig. 6]). For example, in eight of the ten non-reconstructed pedes pictured by Wellnhofer (1978, p. 25) the metatarsals are closely appressed, as they are in the feet of birds and other dinosaurs. This is the natural position, as can be seen by the snug fit of the metatarsals to each other and the fact that their adjacent surfaces are flattened (e.g., Padian, 1983a). Furthermore, in many pterosaur fossils the metatarsals and phalanges are completely disarticulated, so an apparently spreading metatarsus can be no more than an incipient stage to complete disarticulation. (In the Crayssac tracks, which are indisputably pterosaurian, the toes are separated but the metatarsals are not, Fig. 2a; Mazin et al., 1995, Fig. 2a). Bennett's (2001a, b) careful observations of *Pteranodon* notwithstanding, this was not the case in Late Jurassic and earlier pterosaurs. Certainly some pterosaur fossils show distally and even proximally spread metatarsals, but such disarticulation is characteristic of many fossils such as theropods, whose metatarsals were appressed in life. I disagree with Bennett and maintain that the evidence of metatarsal articulations show that they were closely appressed in all pterosaurs.

For these reasons, the pterosaurian footprint, including metatarsals, should be measurably narrower than in crocodilians. This is true for the Crayssac tracks (Figs. 1, 2a), which do not reflect splayed metatarsals; it is not true for *Pteraichnus*-type tracks (e.g., Figs. 2d, bottom; 2f, g; 4b), with the possible exception of those so poorly preserved that sediment slumping has narrowed the width of the phalangeal and metatarsal impressions, as Padian and Olsen (1984) showed (Figs. 3, 4a). On the other hand, crocodile metatarsals are always splayed, not appressed parallel (Fig. 2e). The pedal print is oblong with a rounded heel in the Crayssac tracks (Fig. 2a; Mazin et al., 1995); it is triangular, expanding distally, in crocodile and *Pteraichnus* tracks (Figs. 2g, 3, 4a, b; Padian and Olsen, 1984).

Penultimate Phalanges the Longest

Unwin (1989, 1997) noted that the penultimate phalanges of pterosaur feet were generally the longest (Fig. 2b; Wellnhofer, 1978, p. 25), and that this should characterize their tracks. However, no footprints have definitively shown this, although in some the feature has been alleged but not substantiated

(Wright et al., 1997). No known pterosaurian or alleged ptero-saurian footprint is well enough preserved to permit the unam-biguous reconstruction of a phalangeal formula (Figs. 2g, 6b; see below) or to demonstrate that the penultimate phalanges are the longest. Crocodile feet (Fig. 2e) and pterosaur feet (Fig. 2b) are similar in having four major digits in which the metatarsi are usually about as long as their respective phalangeal series (Wellnhofer, 1978; Padian and Olsen, 1984; Peters, 2001). Moreover, in all but some of the most basal pterosaurs, digits II and III are slightly longer than I and IV, as in crocodiles. (Unwin [1988] was correct that the fourth toe is the longest in *Dimorphodon*; my reconstruction [Padian 1983a] was incor-rect.) But these shared similarities cannot be used to support the inference that a trackmaker was either pterosaurian or croco-dylian. Conversely, the structure identified as metatarsal V in *Pteraichnus* by Bennett (1997; Fig. 2g) is confluent with meta-tarsal IV as in crocodilians (Fig. 2e), lateral and ventral to the other metatarsals.

Overstepping: A Clarification

Lockley et al. (1995) stated that there was no overstepping in crocodylian tracks, which is not true (Padian and Olsen, 1984). Crocodiles overstep (Fig. 3b), as do many animals in which the hindlimb is longer than the forelimb, or in which the hindlimb is mainly powering the stride, especially at moderate and higher speeds. Overstepping is seen in all four trackways that Lockley et al. (1995, Figs. 1–4) refer to *Pteraichnus*, in-cluding the holotype (Figs. 3a, c, 4a–c). No overstepping was illustrated in the Crayssac tracks (Mazin et al., 1995), but J.-M. Mazin (pers. comm.) has kindly informed me that this has since been discovered. Overstepping would not be expected in ptero-saurs if they used a typical reptilian step pattern (LH-RF-RH-LF), because the hindlimb would have had to step around the long forelimb and the posteriorly directed wing-finger. But in these tracks the pedal tracks are medial to the manual tracks and the hindlimbs moved parasagittally, which means that the feet did not have to move around the wings. In most pterosaurs the forelimb from the glenoid to the base of the fingers was at least as long as the hindlimb from the hip to the ankle. There-fore, overstepping would have been possible if the forelimbs were lifted before the hindfoot stepped past the manus track (LH-LF-RH-RF; Bennett, 1997). This would not be a problem if pterosaurs were capable of handling the weight of the skele-ton on the back legs (Padian, 1983b, 1991). The manus prints in the Crayssac tracks frequently are impressed more deeply than the hindlimb tracks, reflecting the weight-bearing as the animal leans forward to feed; the center of mass in pterosaurs was considerably anterior to the hip, and they normally bal-anced by placing the toes well in front of the hip joint (Padian, 1983b; Padian and Olsen, 1989).

Questions of Pterosaurian Stance and Gait that Bear on Ichnology

The question of pterosaur stance and gait has received con-siderable attention in the past two decades (e.g., Padian, 1983b, 1985, 1991, 1995; Unwin, 1987, 1988, 1989, 1997, 1999; Welln-hofer, 1988, 1991; Bennett, 1990, 1997, 2001; Clark et al., 1998). It is important in the first instance to separate the questions of stance—quadrupedal or bipedal—and gait—sprawling or para-sagittal. Many animals use different options of stance and gait at different times. There is some direct and some indirect evi-dence for stance and gait, but only some possibilities are ex-cluded by what we know. A complete review of this problem is beyond the scope of this paper; only some elements related to the interpretation of footprints are discussed here.

Forelimb

The forelimbs of pterosaurs are longer than the hindlimbs, and in most (derived) species they are far longer, for two rea-sons. First, large species have proportionally larger wings, so the forelimbs are relatively longer; second, pterodactyloids even further elongated the metacarpals. Most Crayssac ptero-saur tracks appear to be from pterodactyloids because they show no trace of a fifth toe. (Non-pterodactyloid tracks have re-ceived a preliminary report [Mazin et al., 1995, 1997] but will be described separately.)

The shoulder joint in basal pterosaurs through most basal members of pterodactyloid lineages faces laterally and slightly posteriorly, and the head of the humerus is a complex concave-convex saddle joint (Padian, 1983a, b). It is not at all typical of tetrapods, but it bears some similarities to the shoulder of a mole, an echidna, and some dicynodonts. All these animals ro-tate the humerus, and this was the principal function of the shoulder in *Dimorphodon*, along with an up and down motion (Padian, 1983a, b). This rotation seems to have been necessary for getting up speed, for generating thrust in low-speed flight, and for landing, as in birds. A more up and down motion would have been used in faster flight (Rayner, 1988).

However, the humerus in basal pterosaurs such as *Dimor-phodon* could not have protracted and retracted much unless it was almost fully abducted. The bony stops on the anterior and posterior sides of the glenoid fossa would seem to have pre-vented a fore and aft motion (protraction and retraction while abducted) of more than about 60°, less further constraint by soft tissues (Padian, 1983a, b). This means that the protraction and retraction of the distal end of the humerus (i.e., the contri-bution of the humeral excursion to forward progress) would have been only about as great as the length of the humerus, or about half the length of the torso. If terrestrial progress de-pended on fore-aft excursion of the humerus, the steps would have been exceedingly short (e.g., Fig. 4e; Unwin, 1999, which is not the case with *Pteraichnus* tracks). If the narrow-gauge tracks of the *Pteraichnus* manus were made by a pterosaur with humerus adducted (Lockley et al., 1995; Unwin, 1997), then the forearm could not have increased the pace length, but only moved up and down at the elbow. Conversely, if the elbow is extended as in the Crayssac tracks, the pace length of the fore-limb can be much greater; but in that case the manus print must be far lateral to the pes print.

Because the pace length in *Pteraichnus* is longer than the arc of humeral protraction and retraction, and the forearm does not lengthen the stride by its excursion, the pace length is too long

to have been made by a pterosaur such as Unwin (1999; Fig. 4e) reconstructs. That reconstructed pace and stride length is less than half of the distance seen in pteraichnid tracks (e.g., Lockley et al., 1995, Figs. 1–5), and demonstrates that pterosaurs, according to that model, could not have made pteraichnid tracks. In Fig. 4, take distance Y from the right heel anteriorly to the level of the second left toe anterior to it. Take distance X as the lateral width between the outer borders of successive left and right feet. Distance Y/X is 3.53 in the holotype of *Pteraichnus saltwashensis* (Fig. 4a) and 2.11 in the holotype of *Pt. stokesi* (Fig. 4b); yet it is only 1.35 in Unwin's reconstruction of a pterodactyloid walking in *Pteraichnus* tracks (Fig. 4e). This reconstruction cannot account for pteraichnid tracks unless it can increase its stride length by a factor of 2.5. However, its body is too short and its legs are both too short and too laterally oriented to do so. Unwin's reconstruction, if correct, shows that pterosaurs cannot have made pteraichnid tracks.

Even if *Pteraichnus* were made by a pterosaur, the forelimb could not have powered locomotion, but only gone along for the ride. Unwin (1989: 270) echoed Padian (1983b) and Padian and Olsen (1984):

> The elbow was a hinge and there was little rotation possible at the wrist, as Bramwell and Whitfield and others have shown. And in forward locomotion, the forearm can only follow what the humerus does. So the outer joints up to the fingers are of no help extending the stride. And once the humerus is protracted, during which phase it must be rotated forward or pronated, it cannot retract without supinating. This would have been of no help in supporting the body in locomotion. If these inferences are correct, then the conclusion that the forelimbs could have not supported the body significantly in terrestrial locomotion means that such a gait must have been secondary, and facultative.

This is important when considering the Crayssac tracks. They tell us that some pterosaurs could walk on four legs. They do not tell us that all or most did, nor that any pterosaurs had to do so. We know these animals are pterosaurian because their forelimbs are so far outside the midline of the body, beyond the forelimbs. To contribute to forward progress, the humerus must protract and retract. As noted, to do so the humerus must be directed mainly laterally. This automatically places the forearm segments even farther from the body, as they are during the flight stroke. This is why the manus tracks are so far outside the pes tracks in many Crayssac footprints. When the manus tracks are closer to the midline, the limbs must have been folded close to the body wall, and the humerus performed little protraction and retraction.

Hindlimb

The often-repeated statement that pterosaurs could not stand bipedally, in an erect stance (e.g., Unwin, 1999, pp. 265–266), that is with the femur pointing forward as it does in birds and other dinosaurs, has been strongly contested; for example, Padian, 1983a, b, 1985, 1991 and Bennett, 1990, 1997 accept the erect stance in all pterosaurs, but conclude that only large pterodactyloids were bipedal. The Crayssac tracks show that the hindlimbs are quite close to the body midline, and they do not

toe out as in *Pteraichnus* (*contra* Unwin, 1999, Fig. 5d). (Often, when they appear to toe outward, the animal is turning.) The Crayssac tracks indicate that the pterosaurs had an erect stance and a parasagittal gait in the hindlimbs (Padian, 1983b).

The erect gait and parasagittal stance follow from the construction of the hindlimb joints. The femoral head is either a flattened, rounded, offset structure as in most dinosaurs, or a ball-and-socket joint as in birds, many other dinosaurs, and most mammals, and this is where nearly all the abduction and adduction and mediolateral rotation occur in the hindlimb. The knee is a hinge with no possibility of significant rotation. Although disagreement with this has been expressed (e.g., Unwin, 1988), there are no muscles to rotate the knee significantly because the fibula is so much smaller than the tibia and set immovably against it, like the knee of a bird or human. So the distal portions of these bones plus the proximal tarsals (which are also fused to the tibia) cannot support rotation, as they can in a crocodile or lizard.

The ankle is a hinge, like those of birds and other dinosaurs. Motion at the bases of the digits appears to have been restricted (Clark et al., 1988), and the interphalangeal joints are also hinges (Unwin, 1999). Therefore virtually all the non-orthal movement can only come from the hip. The acetabulum is shallow and subhemispherical. The head of the femur is offset from the shaft by an angled neck, much as in humans and birds and other dinosaurs. In all these animals, some mediolateral rotation is possible. If the distal condyles of a three-dimensional femur are held parallel to the ground, the femoral head reaches up and into the hip socket as it does in a bird. All available evidence indicates that pterosaurs stood erect and moved their hindlimbs parasagittally. No pterosaur trackways reported from Crayssac indicate any kind of sprawling.

Without soft tissues we cannot quantify mobility at the hip in pterosaurs. But we can say that the most efficient mode of locomotion would have been parasagittal, as it is in the living forms just mentioned (Padian, 1983b). The reason is that all the other joints are hinges; any deviation from this angle by the hip joint would have resulted in a "dancing Cossack" or "waddling" syndrome, as Unwin (1987) pointed out. This would have been inefficient because it would have directed the action of the limbs anteriomedially, whereas the progression of the animal is anteriorly directed. It is difficult to think that pterosaurs would have persisted in this awkward situation over 160 million years of evolution. In fact, the feet of the Crayssac tracks point nearly anteriorly, as we would expect from birds and other bipedal dinosaurs, which walk parasagittally (Unwin, 1987; Olsen and Padian, 1989a). Crocodiles also proceed parasagittally when they do the high walk, as Brinkman (1980) and Padian and Olsen (1984) showed. So one thing that these hindfoot tracks show us is that pterosaurs did not sprawl. Instead, they maintained a parasagittal gait close to the body midline.

The Metatarso-Phalangeal (MP) Joint

Clark et al. (1998) provided an important interpretation of the metatarso-phalangeal joints in basal pterosaurs that suggests far less mobility than previously supposed (Padian, 1983a, b). The

bones that meet at this joint have comparatively squared-off ends. The tight spaces connecting all the joints of the foot do not suggest the presence of an extensive cartilaginous cap that could extend and round out these articulations to any significant degree.

These observations have important bearing on interpretations of locomotor function in basal pterosaurs (Padian, 1983b, 1991; Unwin, 1988, 1999; Bennett, 1997). Clark et al. (1998) concluded that the total arc of extension possible along the joints of the pterosaur toes was only about 50°, and they inferred from this that pterosaurs must have walked with a "flat-footed" gait.

However, the hindlimb kinematics were more complex than this term would suggest, as the available functional and phylogenetic evidence shows. A broader comparative study indicates that the MP joints of other basal dinosauromorphs are comparable to those of pterosaurs, not to those of living birds as Clark et al. (1998) contrasted them. Even basal dinosaurs do not approach the condition in living birds. But the metatarsals of ornithodirans, including pterosaurs, differ from those of crocodiles in at least two functionally important ways: they are relatively longer and they are not distally splayed, so their individual bones do not move independently; thus there is no mediolateral rotational push as seen in the plantigrade step cycle (Brinkman, 1980; Gatesy, 1990).

The second problem is that the term 'plantigrade' denotes only that the heel touches the ground at some stage in the step cycle; it says nothing about weight-bearing, kinematics, speed, or substrate conditions. As crocodiles walk (the "high walk" at low to moderate speeds) they place one foot deliberately in front of the other at the edge of the body; their claws contact the ground first and contact proceeds posteriorly to the heel (Brinkman, 1980; Gatesy, 1990). Hence their footfall pattern is initially digitigrade, even though the whole foot appears to strike the surface almost simultaneously. They are plantigrade because their soles then impress (in reverse order from human heel-toe plantigrady, a condition also seen in bears and badgers). But the body's weight (the principal ground reaction force) is not borne by the heel in crocodiles; rather, the heel touches the ground as a consequence of pedal flexure. Crocodiles are not always sole-walkers; trackways of small basal crocodiles from the Early Jurassic are digitigrade (Olsen and Padian, 1986), and during rapid locomotion the heels of living crocodiles often do not touch the ground (Brinkman, 1980).

In slow progression or on incompetent substrates even bipedal, digitigrade dinosaurs record metatarsal impressions (Lull, 1953). Purported trackways of pterosaurs, like those of crocodiles, do not suggest a heel-first step (*contra* illustrations in Clark et al., 1998, Fig. 1b, which also show little phalangeal motion), so the term "flat-footed" is a misnomer if it recalls the human motion of that pes. Heel impression also depends on the competence of the substrate, because heels of digitigrade animals will impress soft ground (Gatesy et al., 1999). The ubiquity of slumping and substrate incompetence in pteraichnids provides no reason to suspect that they reflect true plantigrady, although the Crayssac tracks demonstrate at least that the metatarsus was held at a low angle and that the heel characteristically met the ground at slow speeds. This pattern is commensurate with small basal theropods (Gatesy et al., 1999).

The "flat-footed" interpretation requires an explanation of why other basal ornithodirans should not be interpreted as similarly restricted in gait. Clark et al. (1998) also disputed the argument (Padian, 1983a, b) that the comparative mesaxial symmetry of the digits of the pterosaur pes supports digitigrady (a valid point, considering crocodiles, though recall that they impress their toes before the heel), and they showed that in some basal pterosaurs (though not in others) the fourth toe was slightly longer than the third (Unwin, 1988). However, this digital asymmetry is even more exaggerated in the basal ornithodiran *Lagerpeton*, in which digitigrady has never been questioned (e.g., Sereno and Arcucci, 1993; Sereno, 1991). It seems logical to infer that if a set of hindlimb features is invoked to infer digitigrady for some groups, it should apply to any group with the same features, especially if they are closely related.

How then did pterosaurs walk? The ankle allowed a flexion and extension of some 180° (Padian, 1983a, b). This is comparable to the excursion of most dinosaurian ankles but perhaps greater than in some other ornithodirans (*Lagerpeton*, *Lagosuchus/Marasuchus*: Sereno and Arcucci, 1993, 1994). Unless these animals have all been mistakenly interpreted as digitigrade, we must conclude that flexing and extending some joints more than others can achieve the same locomotor effects. The MP joint of many birds is held off the ground and is not the primary joint of flexion and extension of the foot while walking. This sub-unguligrade to digitigrade stance is how all basal ornithodirans are currently interpreted (Sereno, 1991; Sereno and Arcucci, 1993, 1994; Gatesy et al., 1999). The phalangeal joints appear to have sustained most of the body's weight during locomotion in ornithodirans primitively.

To understand pterosaur gaits the entire hindlimb must be considered, and its features are consistent with those of other bipedal ornithodirans with digitigrade stance and parasagittal gait (Padian, 1983b, 1991; Sereno, 1991). In short, the full comparative evidence suggests that pterosaurs had a low-angled metatarsus that quite often impressed, especially during slow progression, that they walked with a toe-heel step cycle, and that the ankle and interphalangeal joints may have sustained most of the distal hindlimb motion.

Arguments about Crocodylian Assignments of Trackways

Several authors have assigned various, mostly poorly preserved footprints to *Pteraichnus* or to the Pteraichnidae Lockley et al. 1995. They have argued that these tracks are pterosaurian and cannot be crocodylian. I agree that insofar as their features can be determined, most should be referred to Pteraich-

nidae, but on the basis of the criteria discussed above they lack pterosaurian synapomorphies and are too poorly preserved to provide any diagnostic information.

Lockley et al. (1995) referred a gallery of thirteen trackways and isolated tracks from the western U.S. and Europe to *Pteraichnus*. But in no case did they outline features diagnostic of *Pteraichnus* and Pteraichnidae and demonstrate that the referred tracks shared these features; rather, these were assigned on the basis of general similarity. Unfortunately, each of their illustrated specimens (Figs. 3a, 4 a–d) fails every test both of diagnostic pterosaurian features and of good preservation. The manus print is not up to several interpedal widths lateral to the pes; the pedal imprint is three times (or less), not four times as long as the width across the MP joint; the metatarsals are far wider at their distal than at their proximal ends; and there is no evidence that the penultimate phalanges are the longest. So there is no evidence that any of these tracks are pterosaurian, but substantial evidence that they are not. Furthermore, in each case it is difficult to determine how many digits were present on the manus; it is impossible to reconstruct a phalangeal formula for either manus or pes; the kinematics of the step cycle and the poor condition of the substrate have conspired to destroy or distort crucial anatomical features; and the illustrations do not show the crisp preservation of freshly excavated tracks, suggesting that some erosion and scouring have occurred. Hence they are by definition poorly preserved. (This is also the case with the type specimen of *Pteraichnus*, as Padian and Olsen [1984] noted. Most authors do not discuss preservational conditions.) One interesting feature of the Spanish trackway (Fig. 4c) illustrated by Lockley et al. (1995, Fig. 5) is that it is extremely short-footed, suggesting that only the phalanges are imprinted, or that the foot was far too short and broad to belong to any pterosaur. This would mean that the trackmaker was walking digitigrade, unless the metatarsal print was lost or unexposed (both pterosaurs and crocodiles could do this).

Lockley et al. (1995, p. 12) diagnosed the Ichnofamily Pteraichnidae as follows:

> Wide trackway of a quadrupedal animal with elongate, symmetrical, functional-tetradactyl, plantigrade pes impressions and asymmetric tridactyl manus. Impression of manus digit IV [this is identified as digit III by some other workers] elongate, curved and posteriorly directed, parallel to the trackway axis. Manus impressions often more deeply impressed than pes impressions.

The problem with this diagnosis is that all of these features were found in the tracks of the small caiman experimentally produced by Padian and Olsen (1984). Hence, whatever else they may be, Pteraichnidae are demonstrably consistent with the footprints of crocodilians. Therefore these features cannot be diagnostic of the tracks of pterosaurs as well. As Padian and Olsen showed (Fig. 3c), frequently only three distinct manual digit impressions are produced by crocodiles (though both crocodiles and pterosaurs have more than three manual digits); hence, the "tridactyl manus" is an artifact of preservation, not

an anatomical feature. Furthermore, as Padian and Olsen (1984) showed, and Unwin (1989) and Bennett (1997) concurred (see also Wellnhofer, 1978, 1991), the proximal end of the first phalanx of digit IV is not curved in pterosaurs. By its own diagnosis, *Pteraichnus* and other such tracks are consistent with crocodylian trackmakers.

Lockley et al. (1995) argued that the type specimen of *Pteraichnus* did not reveal five manual digit impressions, but they did not make detailed drawings of each print and superimpose them, reversed as necessary, as Padian and Olsen (1984) did (and showed that two digits are frequently impressed together: Fig. 2b). Lockley et al. stated that the pterosaur manus and pes fit well into the preserved tracks (Fig. 4a), but they did not actually show this, and they did not compare the manus and pes of crocodiles, so their statement is unsupported. Furthermore, it can be challenged because the metatarsals of the *Pteraichnus* trackmaker are obviously splayed (not the case in pterosaurs), the digit impressions are too slitlike to accommodate actual phalanges (Fig. 3c, 4a), and the manus can only be fit into the manus print if the forearm and metacarpus are directed laterally, but there is not enough room for this in the *Pteraichnus* trackway. Their statement that the *Pteraichnus* trackmaker was semi-erect with a wide straddle does not agree with anatomical evidence (Padian, 1983b; Bennett, 1997; see above), which they did not examine. Their reliance on Unwin's (1997) revised reconstruction is based on a lack of documentation of the trackmaker or of forelimb kinematics, as noted above. The strongest statement that Lockley et al. (1995) offer in support of their assignment is that "the *Pteraichnus* trackway is more or less consistent with many of the classic reconstructions of pterosaurs in quadrupedal poses," though they acknowledge that "the position of digit I remains uncertain." The statement "more or less consistent" is not sufficient to establish the identity of a trackmaker, especially when the question has been debated in as much detail as this one has.

Lockley et al. (1995) provided a series of reasons to support their inference that *Pteraichnus* could not have been made by a crocodylian. They claimed the absence of a tail drag in *Pteraichnus* in this regard, but crocodile trackways, especially fossil ones, are frequently preserved without tail marks (e.g., Haubold, 1984; Olsen and Padian, 1986), and crocodylian feet may or may not drag as well (Padian and Olsen, 1984, Fig. 1a). They claimed that the pes did not overstep the manus in crocodilians, whereas in *Pteraichnus* the manus print is anterior to or overprinted by the pes print. This is not correct; Padian and Olsen (1984, Fig. 2 A–B) showed the identical overstepped position in both the caiman track and the type specimen of *Pteraichnus* (Figs. 3b, c). I agree with Lockley et al. (1995, p. 16) that the speed and gait of the animal affect the relative position of manus and pes (Padian and Olsen, 1984; Padian, 1998), which makes their previous statement difficult to understand. They state that it was easy for pterosaurs to overstep because their trunk was so much shorter than in crocodiles. They fail to note how much longer the forelimb is than the hindlimb

in pterosaurs, and how difficult it would have been to move the pes into a track anterior to the manus with its enormous, posteriorly protruding wing-finger (another difficulty with Unwin's reconstruction [Fig. 4e]).

Finally, Lockley et al. (1995) stated that *Pteraichnus* and crocodylian tracks differ because crocodilians have a pentadactyl manus, whereas *Pteraichnus* tracks only show evidence of three fingers, including an elongated digit IV. This statement is of limited utility because, as noted previously, both pterosaurs and crocodiles have more than three fingers, so clearly some are not being imprinted. Padian and Olsen (1984) showed that (1) digits I and II of the caiman are frequently impressed together, and sometimes digit I itself crosses digit II, and that (2) the elongated "digit IV" (which Unwin and Bennett regard as digit III) in the caiman track is the impression of crocodylian digit V, which slides into the trackway (Figs. 3b, c). This would seem to remove both objections of Lockley et al. (1995). Bennett (1997) noted that this posteriorly directed digit (his digit III, Lockley's digit IV) has an ungual impression at the end (Fig. 2g), but because a realistic phalangeal formula cannot be determined from this manus print, it is difficult to know what is a faithful anatomical record and what is kinematic or preservational artifact. If Bennett is correct, of course, it would be diagnostic of a pterosaur's third finger, not the fourth, which would challenge the identifications by Unwin (1997), Lockley et al. (1995), and others. Clearly further work is needed in this area, and much of it may depend on the discovery of better-preserved trackways.

Wright et al. (1997) suggested that *Purbeckopus* (Fig. 6), a large (ca. 20 cm pedal length), poorly preserved collection of seven scattered pes prints and a few manus prints (none clearly associated) on three slabs, was made by "the same type of animal" as *Pteraichnus*, and inferred that the trackmaker was pterosaurian because (1) "the pes tracks show indications of elongate penultimate phalanges" and (2) "the impression of the manus lies well outside that of the pes." These are indeed pterosaurian features, but they do not appear in *Purbeckopus*. Only one pes print, as reconstructed by Wright et al., has any possibility of reconstructing any phalanges at all. These authors, in fact, did not reconstruct the phalanges, but Peters (2001; Fig. 2f) did. It is clear from his reconstruction that *Purbeckopus* lacks all features of pterosaur tracks: the pedal length is only a little over twice the MP width, and there is no evidence that the penultimate phalanx is the longest. I differ from him in suspecting that the metatarsals were rather more equal in length, with II and III slightly longer than I and II (Fig. 6b); but even so, the foot is clearly crocodilian in form and proportions, and there are no pterosaurian features. Insofar as the specimens permit reconstruction, *Purbeckopus* could have been made by a crocodylian, but not a pterosaur. The heel is narrow and the metatarsals are divergent, not parallel—features found in crocodylian tracks, but not in pterosaur tracks.

Bennett (1997) provided cogent and lucid arguments why *Pteraichnus* was made by pterosaurs, although he took issue with Lockley, Unwin, and their colleagues on most interpretive points. For example, to Bennett, the preserved manual digit impressions are I, II, and III, and the hindlimb prints demonstrate erect posture and parasagittal gait. Most of his arguments cannot be reviewed here in sufficient detail but should be read carefully. My interpretations differ from his in several respects that have already been noted. However, I agree that the *Pteraichnus* trackmakers did not have all four feet in contact with the substrate simultaneously at any point in the step cycle (Bennett, 1997, p. 107) for the reasons he notes. Regrettably, Bennett's illustrations of pterodactyloids making *Pteraichnus* tracks picture the animals in side view and do not include the trackways, so it is difficult to evaluate his arguments that these pterosaurs fit the tracks. Bennett did not reconstruct the digits, but I do so in Fig. 2g. A comparison to Figs. 2b and 2e shows that the foot skeleton that fits this pedal track cannot be pterosaurian, because it is far too short and the penultimate phalanges are not the longest; but it can easily be crocodylian. The only ambiguity is the lack of clear separation in the impressions of the smaller phalanges of digits III and IV, but it is at least clear that the penultimate phalanges cannot be the longest, so the pterosaurian trackmaker inference fails.

I conclude from the foregoing that pteraichnid trackways are not demonstrably pterosaurian; that the diagnosis of Pteraichnidae itself is consistent with a crocodilian but not a pterosaurian trackmaker; and that pteraichnid footprints, insofar as they preserve definitive features, were probably made by crocodilians.

CONCLUSIONS

The trackways of crocodilians and pterosaurs are similar, at least when they are not perfectly distinct in preservation. This is why the problem has been so difficult to untangle, and why it is essential to agree on diagnostic features that separate them. The Crayssac tracks must be pterodactyloid, for reasons noted above and by Mazin et al. (1995). However, other tracks, beginning with those originally called *Pteraichnus* by Stokes in the 1950s, as well as many examples referred to this form by Lockley, Wright, Unwin, and their colleagues, are quite different from the Crayssac tracks. Moreover, the posteroventrally directed print of the large bone reported in the Crayssac tracks, which presumably represents the wing-finger, has never been reliably reported in *Pteraichnus* tracks.

In none of the fossil trackways referred to pterosaurs has it been possible to reconstruct a reliable phalangeal formula, let alone one characteristic of pterosaurs. The only possible examples (Bennett, 1997; Wright et al., 1997), if correctly illustrated, are consistent with crocodylian feet but not with pterosaurian feet. In none of the examples shown by Lockley, Unwin, or their colleagues is it possible to determine the configuration of the phalanges.

Proponents of the pterosaurian identity of these tracks do not agree on how many digits are represented in these presumed pterosaur tracks, which digits they are, or how many

phalanges or which phalanges are present. These are poorly preserved tracks that preserve no diagnostic pterosaurian features. Other features of the trackways are too strongly affected by the locomotion of the animal and by the incompetence of the substrate, two factors that conspire to destroy anatomical interpretation. This is why resolution of the *Pteraichnus* problem is so difficult and complex.

The hypotheses advanced above would be falsified if adequately preserved tracks with diagnostic features of pterosaur feet were discovered. The Crayssac tracks are different in these respects, and their manus prints also differ in detail. They should not be referred to *Pteraichnus*, but rather belong to a different ichnotaxon, diagnosed by the following features:

> Lateral distance between manus tracks up to three times that between those of the pedes; manus print with three small digits (I–III) directed anteriorly, laterally, and posteriorly, respectively, and a much larger fourth digit directed posteromedially from the junction of the other three; pedal print plantigrade, a long oblong in shape, with rounded heel; metatarsal prints parallel, not divergent; length of pes from ankle to ungual tips approximately four times the width of the foot at the metatarso-phalangeal joint; four toes of generally subequal length, of which II and III are longer and I is slightly the shortest. It is to be expected that the impressions of the penultimate pedal phalanges are longer than those of other phalanges, but this feature cannot be confirmed in known trackways.

Critics may object that the manus prints of pteraichnids and of the Crayssac tracks are so similar that they should not be separated, and undoubtedly there are similarities. However, because none of these tracks is well enough preserved to provide phalangeal formulas and unambiguous assessment of digits, this is tantamount to arguing that poor preservation is a diagnostic feature. Poorly preserved tracks of tridactyl theropods can look like poorly preserved tracks of tridactyl ornithopods, but this is not a diagnostic feature either of the tracks or of their trackmakers.

Before referring any further trackways to *Pteraichnus* or making attempts to interpret their trackmakers, their paleoecology, and their global distribution, ichnologists should focus more on determining whether there are really diagnostic features, the extent to which kinematics and behavior influence trackway form, and the extent to which the conditions of the sediment affect their appearance and features.

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