Pterosaur tracks and the terrestrial ability of pterosaurs

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Unusual tracks of a quadrupedal animal with a three-digit (occasionally four-digit) manus print and four-digit pes print were first interpreted as those of pterosaurs in the 1950s. In the 1980s these tracks were reinterpreted as crocodilian, but new material shows that the original identification was correct. Two features: evidence for elongate penultimate phalanges in digits two to four of the pes, and manus trackways up to three times the width of pes trackways, can only be attributed to pterosaurs. Recent improvements in understanding of pterosaur anatomy and functional morphology explain remaining difficulties regarding the interpretation of ichnites such as the orientation of the manus digits and the absence of some expected ichnological features. *Pteraichnus* and *Pteraichnus*-like tracks show that, when grounded, some, perhaps all, pterosaurs were plantigrade, quadrupedal, and had a semi-erect stance and gait. This is consistent with some functional interpretations of pterosaur anatomy and resolves a long-running debate regarding the terrestrial ability of this group. □*Jurassic, vertebrate, pterosaur, functional morphology, palaeoichnology, PTERAICHNUS.*

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In 1957 William Stokes described some unusual vertebrate tracks from the Late Jurassic Morrison Formation of Apache County, Arizona. Remarkable characteristics of the tracks, including a three-digit manus print and a pes print with a narrow heel and four digits of similar length, suggested a distinctive track-maker that Stokes identified as a pterodactyloid pterosaur and named *Pteraichnus*. Further prints and tracks similar to those of *Pteraichnus* were reported from Wyoming (Logue 1977), Oklahoma (West 1978) and Utah (Stokes 1978; Stokes & Madsen 1979), and by the late 1970s the interpretation of these tracks as those of pterosaurs had become widely accepted (e.g., Wellnhofer 1978, 1980).

In the early 1980s Padian (1983a, b, 1984, 1985) argued that pterosaurs had an upright, bipedal, digitigrade stance and gait, like that of birds and dinosaurs. This style of progression would have resulted in a single set of forward-facing pes prints, arranged in a narrow trackway, quite unlike the broad, quadrupedal tracks of *Pteraichnus* (cf. Unwin 1989, Figs. 10b and 11a). Padian & Olsen (1984) reassessed the *Pteraichnus* tracks and, by comparing them with *Caiman* tracks produced under experimental conditions, concluded that *Pteraichnus* had been made by a crocodile. Taking a rather different approach, Unwin (1989) attempted to reconstruct the likely prints and tracks of pterosaurs from details of their anatomy and functional morphology. Differences between these hypothetical ichnites and the purported trackways of pterosaurs led him to doubt that *Pteraichnus* and other putative pterosaur tracks from Texas (Langston 1974) and New Mexico (Gillette & Thomas 1989) were pterosaurian in origin.

By the early 1990s most workers (Unwin 1986, 1989; Conrad *et al.* 1987; Prince & Lockley 1989; Lockley 1991; Wellnhofer 1991a) were of the opinion that *Pteraichnus* was probably not pterosaurian, and there seemed to be no convincing evidence for pterosaur tracks. On the one hand, this was consistent with the idea, argued by some (Pennycuick 1986; Unwin 1987a, b, 1989; Wellnhofer 1988, 1991b), that pterosaurs had a poor terrestrial ability and probably spent little time on the ground, thereby severely restricting opportunities for track formation. On the other hand, Padian (1983a, b, 1988), Padian & Rayner (1993) and Bennett (1990) were of the opinion that pterosaurs had a good terrestrial ability. In this case, the complete absence of pterosaur tracks from the ichnological record is surprising, particularly in light of recent studies (Hazlehurst & Rayner 1992), which suggest that pterosaurs were present in coastal environments for much of the Jurassic and Cretaceous. Such environments provide competent bipeds, flying or otherwise, with numerous opportunities for track formation (Lockley 1991), as testified by the rapidly growing track record of Mesozoic birds (Lockley *et al.* 1992).

Recently, new *Pteraichnus* and *Pteraichnus*-like tracks have been found in North America (Logue 1994; Hunt *et al.* 1995; Lockley & Hunt 1995; Lockley *et al.* 1995) and Europe (Lockley *et al.* 1995; Mazin *et al.* 1995). Among these, tracks from the Middle to Late Jurassic Sundance Formation of Alcova, Wyoming (Logue 1994) and the Late Jurassic Cazals Formation of Crayssac in France (Mazin *et al.* 1995) are well preserved and exhibit important new details. The similarity of these ichnites to hypothetical tracks reconstructed by Unwin (1989) convinced Logue (1994), Lockley & Hunt (1995), Lockley *et al.* (1995) and Mazin *et al.* (1995) that pteraichnid (= *Pteraichnus* + *Pteraichnus*-like) tracks should be attributed to pterosaurs. Lockley *et al.* further argue (1995) that the ichnological evidence largely settles the debate concerning the terrestrial ability of pterosaurs in favour of the idea that they had a semi-erect, quadrupedal stance and gait. Mazin *et al.* (1995), working independently, arrived at the same conclusion based on the tracks from Crayssac.

Opinions still differ, however, concerning important features of the tracks. For example, Mazin *et al.* (1995) consider impressions of the manus to represent digits one to three, while Lockley *et al.* (1995) interpret them as digits two to four. Further difficulties concern apparent inconsistencies between print details and pterosaur anatomy. For example, manus digits one to three of pterosaurs show a progressive increase in length, whereas manus digits one and two of *Pteraichnus* appear to be relatively short and often of subequal length. This paper has three aims. First, to review the evidence presented in support of a pterosaurian origin for pteraichnid tracks. Second, to show how remaining inconsistencies between skeletal and ichnological details can be resolved through further consideration of the ichnological evidence and recent improvements in our understanding of pterosaur anatomy and functional morphology. Third, to explore the implications of pteraichnid tracks for the terrestrial ability and ecology of pterosaurs.

Pteraichnus: the evidence against a crocodilian track-maker

Padian & Olsen (1984) argued that *Pteraichnus* had been made by a crocodilian on the basis of similarities between *Pteraichnus* and the tracks of a modern *Caiman*. The caiman produced a broad trackway, like that of *Pteraichnus*, with pes prints occasionally overstepping the manus prints (Padian & Olsen 1984, Fig. 1a). The pes prints of *Pteraichnus* also correspond in some respects to those of the caiman: their outlines are similar, and there is a reasonable correspondence in digit lengths (Padian & Olsen 1984, Figs. 2c, d). The manus is more problematic. Stokes (1957) reported three digits in the manus of *Pteraichnus*, whereas crocodilians typically have five digits.
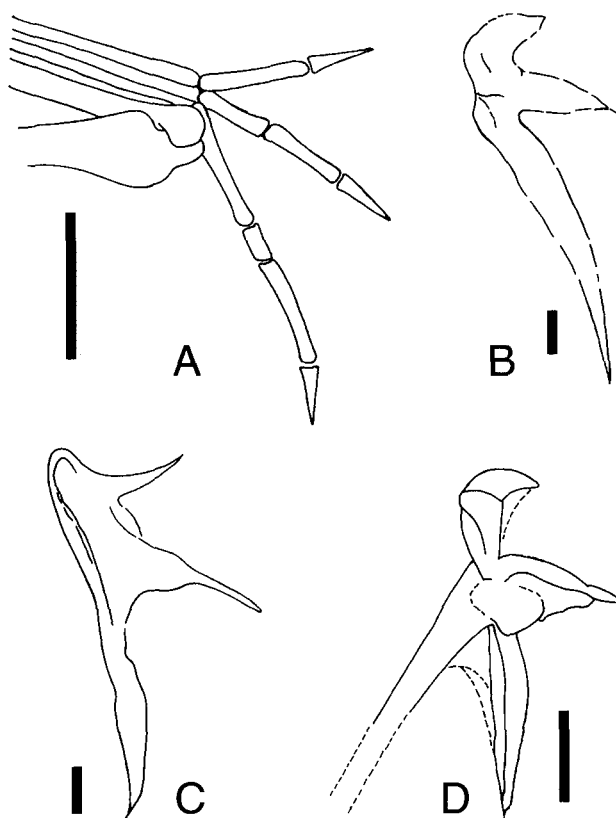

Fig. 1. □A. Right manus of *Pterodactylus kochi* based on 1937 118, Bavarian State Museum for Palaeontology, Munich. □B. Right manus print of *Pteraichnus saltwashensis* (redrawn from Stokes 1957). □C. Left manus print (reversed) of *Pteraichnus* cf. *saltwashensis* (redrawn from Lockley *et al.* 1995). □D. Right manus print of a pterodactyloid pterosaur (redrawn from Mazin *et al.* 1995). Scale bar 10 mm.

Padian & Olsen (1984) reinterpreted the manus print, claiming to have found evidence for five digits, as in crocodilians (Padian & Olsen 1984, Fig. 2d). This interpretation is controversial and has not been supported by more recent studies of the holotype (Lockley *et al.* 1995), or new discoveries, in which only three (e.g., Lockley *et al.* 1995) and sometimes four digits (Mazin *et al.* 1995) have been reported.

Recent studies (Logue 1994; Hunt *et al.* 1995; Lockley & Hunt 1995; Lockley *et al.* 1995; Mazin *et al.* 1995) based on new material of *Pteraichnus* and *Pteraichnus*-like tracks have all rejected the crocodilian interpretation. Logue (1994) and Lockley *et al.* (1995) point out that, typically, crocodilians leave a tail drag mark (Reineck & Howard 1978), whereas no such marks have been found, either in the original *Pteraichnus* trackway, or in any of the newer tracks.

New material has also confirmed Stoke's observation (1957) that *Pteraichnus* and *Pteraichnus*-like tracks typically have a three-digit manus (Logue 1994; Lockley *et al.* 1995). This is most clearly seen in the French prints

(Mazin *et al.* 1995; Fig. 1D herein) and is also visible in well preserved prints from the holotype of *Pteraichnus* (Wellnhofer 1991a, p. 158; Fig. 1B herein) and new tracks from Wyoming (e.g., Lockley *et al.* 1995; Fig. 1C herein). New tracks in which the lengths of phalanges can be observed (e.g., Mazin *et al.* 1995, Fig. 2) show further differences between the pedes of crocodilians and *Pteraichnus*. In the former the phalanges become progressively shorter distally, while in the latter the penultimate phalange of digits two, three, and possibly four, is longer than the preceding phalanges (Fig. 2C).

Other details of the *Pteraichnus* prints are also inconsistent with a crocodilian origin. In dorsal or ventral view, the claws of crocodilians have a triangular outline with relatively broad bases and leave a rather obtusely pointed outline (e.g., Padian & Olsen 1984, Fig. 2c). This is quite different from the slitlike impressions seen in some *Pteraichnus* prints (e.g., Figs. 1C and 2B–D). In addition, crocodilians have relatively thick, robust digits which produce rather broad indentations (Padian & Olsen 1984, Fig. 2c), unlike the relatively narrow digital impressions of *Pteraichnus* (Figs. 1 and 2).

Further differences are evident in the shape and proportions of the prints of *Pteraichnus* and *Caiman*. The pes imprint of *Caiman* is rather short and broad, with a rounded heel (Padian & Olsen 1984, Fig. 2c), while in *Pteraichnus* the pes is relatively long, narrow and has an acutely pointed heel (Fig. 2B–D). There is even greater disparity in manus print morphology. Prints of *Caiman* are relatively short and compact while those of *Pteraichnus* are narrow and elongate (cf. Padian & Olsen 1984, Figs. 2c and d). Moreover, the hindmost digit of *Pteraichnus* is very elongate, in contrast to the lateral digit of *Caiman*, which is rather short. Padian & Olsen (1984) ascribed this ichnological feature to toe drag, but their interpretation can be rejected for two reasons. First, in some examples, the manus is very neatly impressed into the sediment (e.g., Wellnhofer 1991a, p. 158), and there is no evidence of drag. Second, the attenuate hindmost digit is a highly persistent feature, present in all pteraichnid prints from the Late Middle Jurassic to the Upper Cretaceous (Lockley *et al.* 1995). Undoubtedly, it represents a real anatomical feature, an elongate digit, and not an accidental feature of print formation.

Pteraichnus and *Caiman* tracks also differ in respect of print orientation. The long axis of the crocodilian manus almost always lies sub-parallel to the axis of the pes (Padian & Olsen 1984, Fig. 1a). On occasion, it is rotated a little outward, but it never becomes perpendicular to the pes axis, as in *Pteraichnus* (Stokes 1957, Fig. 3). This is also reflected in the orientation of manus digit five which, in *Caiman*, is usually directed outward at about 90° to the axis of the trackway, or sometimes a little further backward (Padian & Olsen 1984, Fig. 2c). By contrast, the hindmost manus digit of *Pteraichnus* (interpreted by
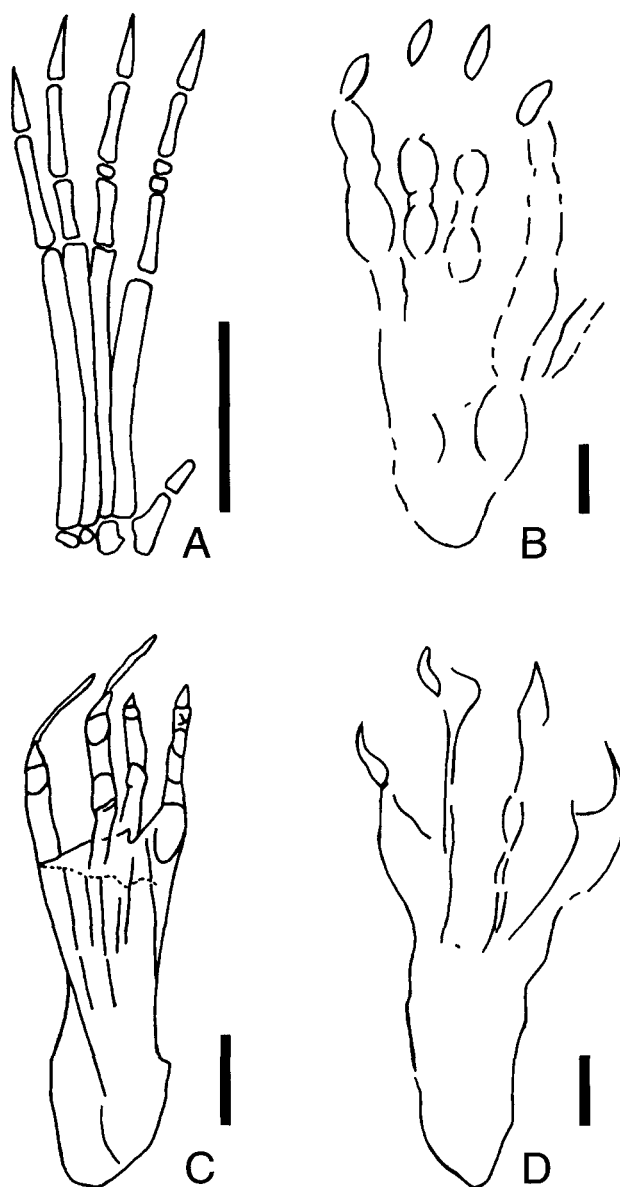

Fig. 2. □A. Right pes of *Pterodactylus* in dorsal aspect (redrawn from Wellnhofer 1978). □B. Right pes print of *Pteraichnus stokesi* (redrawn from Lockley *et al.* 1995). □C. Right pes print of a pterodactyloid pterosaur (redrawn from Mazin *et al.* 1995). □D. Right pes print of *Pteraichnus* cf. *saltwashensis* (redrawn from Lockley *et al.* 1995). Scale bar 10 mm.

Padian & Olsen 1984 as digit five) is directed backward between 145° and 180° to the direction of travel (Stokes 1957; Lockley *et al.* 1995).

Lockley *et al.* (1995) also draw attention to some important differences in the configuration of the trackways. In the *Caiman* track the manus always lies slightly anterior to the pes or is overstepped by it. By contrast, in *Pteraichnus* the manus is almost always posterior to the pes, indicating a relatively short gleno-acetabular length for the *Pteraichnus* print-maker. More impor-

tantly, while the manus and pes trackways of *Pteraichnus* and similar ichnites are usually of sub-equal width, there are occasions, for example in the Crayssac tracks (Mazin *et al.* 1995, Fig. 4), where the manus trackway is up to three times the width of the pes trackway. This disparity could not be produced by any known crocodilian, living or fossil.

To summarize: *Pteraichnus* shares some general characters in common with crocodilian tracks, but none are unique to crocodilians. Moreover, there are a number of features (elongate penultimate phalanges in the pedal digits and a broad manus trackway) that could not have been produced by crocodilians, and they can be safely rejected as candidates for *Pteraichnus* track-makers.

Pteraichnid tracks: the evidence for a pterosaurian print-maker

There are two features of the tracks, exhibited for the first time by the new material, which can only be attributed to pterosaurs. First, well-preserved pes prints of *Pteraichnus stokesi* (Fig. 2B), *Pteraichnus* cf. *saltwashensis* (Lockley *et al.* 1995) and *Pteraichnus*-like tracks from Crayssac (Fig. 2C) show pad impressions. Assuming that these impressions correspond to the joints between the phalanges (Baird 1954; Thulborn 1990), it can be seen that the penultimate phalange of digits two, three and possibly four, was longer than the preceding phalanges (Mazin *et al.* 1995). This is a very unusual construction and, among Mesozoic tetrapods, is only found in pterosaurs (Unwin 1987a, 1988, 1989). Within this group, elongate penultimate phalanges occur in pedal digits one to four and manus digits one to three, in all taxa in which the extremities are preserved (Wellnhofer 1978, 1991a). This condition seems to have been universal for pterosaurs and is one of the key apomorphies defining the clade Pterosauria.

Second, in some of the Crayssac ichnites the manus portion of the trackway is up to three times the width of the corresponding pes trackway (Mazin *et al.* 1995; Fig. 3A herein). Such an ichnite could only be produced by a tetrapod in which the forelimbs are highly elongate, when compared to the hind limbs, enabling the manus to extend much further from the body than the pes. Pterosaurs are the only Mesozoic tetrapods in which the forelimb is at least 2.5–3.0 times the length of the hind limb, even in the most primitive forms, while ratios of 5.0 or more are achieved in some derived taxa.

The pes prints of *Pteraichnus* and similar ichnites also correspond in many other ways to the hypothetical pes prints of pterosaurs (Unwin 1989). These include: an elongate triangular shape with a well marked heel (Mazin *et al.* 1995), relatively narrow digital impressions, a close correspondence in the relative length and divarication of the digits (Lockley *et al.* 1995) and the same phalangeal formula (2,3,4,5) for digits one to four (Fig. 2C). In addition, the claw marks are deep and slitlike, corresponding to the compressed, bladelike claws borne by the pedal digits of pterosaurs (Stieler 1922; Fig. 2A). Traces of interdigital webbing have been reported in well preserved pes tracks of *Pteraichnus stokesi* (Lockley *et al.* 1995). This is also consistent with pterosaur anatomy, since some taxa, including *Pterodactylus* (Döderlein 1929; Broili 1938), *Rhamphorhynchus* (Broili 1927), and possibly *Sordes* (Sharov 1971), appear to have had webbed feet.

The manus prints of pteraichnid tracks are a little more difficult to interpret. In most cases only three digits are preserved (Stokes 1957, Lockley *et al.* 1995), though in some rare examples, discussed below, traces of a fourth structure have been reported (Mazin *et al.* 1995). Assuming that pterosaurs produced these prints, the identity of the digits can be explained in two ways: as digits one, two and three (Unwin 1989; Mazin *et al.* 1995) or as digits two, three and four (Stokes 1957; Lockley *et al.* 1995).

The latter explanation presents three difficulties, mostly concerning the hindmost digit imprint. First, the fourth digit of pterosaurs is a greatly enlarged structure that forms the outer 60%, or more, of the wing spar (Wellnhofer 1978). The first wing-phalange is at least three times the thickness of either digits one, two, or three, in all pterosaurs (Wellnhofer 1978). By contrast, the hindmost digital impression in *Pteraichnus* and similar ichnites is usually of similar width to the first two digits, and sometimes narrower. It is very difficult to see how the wing-finger could have produced such a narrow impression, especially in those cases where the manus is relatively deeply impressed as, for example, in the holotype of *Pteraichnus saltwashensis* (Stokes 1957). In addition, there are examples in which a very narrow claw impression seems to be present at the termination of the digit (e.g., Lockley *et al.* 1995, Figs. 4 and 5). This cannot have been produced by the wing-finger, which lacks an ungual.

Second, if the impressions are those of digits two to four, why is there no evidence of digit one? The point of articulation of this digit with the metacarpus lies adjacent to digits two and three, and all three digits flexed in the same plane and through approximately the same arc. Deeply impressed manus prints have been reported in *Pteraichnus saltwashensis* (Padian & Olsen 1984). In this case, at least, digit one could not have avoided contact with the substrate. The only reasonable explanation for its apparent absence must be that it was so closely appressed to digit two that they left but a single impression. If this is true, the anteriormost digital impression should be relatively broad, but, frequently, it is narrower than the middle digit impression (e.g., Stokes 1957; Lockley *et al.* 1995).
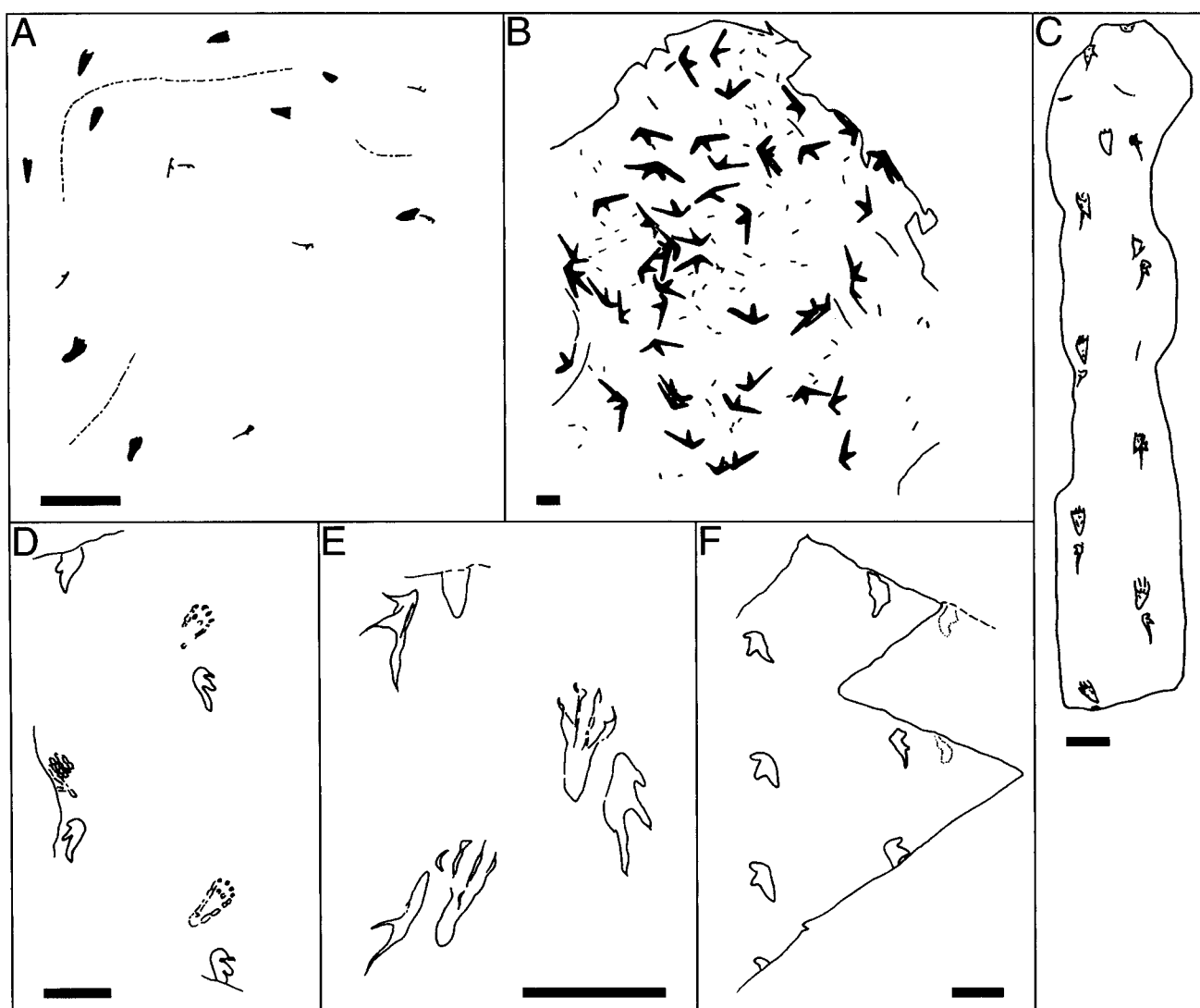
Fig. 3. A selection of pteraichnid tracks. □A. Tracks of a pterodactyloid pterosaur from the Late Jurassic of Crayssac (redrawn from Mazin *et al.* 1995). □B. *Pteraichnus*-like 'manus-only' prints with beak(?) marks from the Late Cretaceous of Utah (redrawn from Parker and Balsley 1989). □C. The holotype of *Pteraichnus saltwashensis* from the Late Jurassic of Arizona (redrawn from Stokes 1957). □D. *Pteraichnus stokesi* from the Late Jurassic of Wyoming (redrawn from Lockley *et al.* 1995). □E. *Pteraichnus* cf. *saltwashensis* from the Late Jurassic of Utah (redrawn from Lockley *et al.* 1995). □F. Manus-only trackway of *Pteraichnus* from the Late Jurassic of Utah (redrawn from Lockley *et al.* 1995). Scale bar 100 mm.

Third, since the proximal section of the wing-finger was impressed, there should also be a prominent rounded impression corresponding to the large joint at its base. There are traces of what may be part of this joint in some examples (e.g., Lockley *et al.* 1995, Fig. 5), but, usually, evidence of this structure is entirely lacking. This is perplexing considering the robustness of the structure and the practical impossibility of the wing-finger leaving an indentation which extends to the base of the other digits, but without the basal condyle contacting the sediment.

If we accept the alternative explanation, that the impressions represent digits one, two and three (Mazin *et al.* 1995), then all these problems are overcome. The nar-

row digital impressions with terminal claw marks correspond to the three slender manus digits of pterosaurs, each of which bears a large, bladelike ungual (Fig. 1A). With the forelimb supported by the first three digits, the wing-finger (and associated wing-membrane) was held clear of the ground, though the condylar region may occasionally have indented the substrate leaving a rounded impression in the medial margin of the manus imprint (Stokes 1957; Mazin *et al.* 1995, Fig. 3a).

Mazin *et al.* (1995, Fig. 3a) identify a long, relatively broad, medially directed impression as an indentation of the proximal portion of the wing-finger. During terrestrial locomotion, the wing-finger is likely to have been

tightly flexed on the wing-metacarpal and thus directed backward and inward toward the body midline. This position corresponds neatly with the long, broad, medial depression and confirms the interpretation of this feature, by Mazin *et al.* (1995), as the wing-finger. This, in turn, further supports the argument that the three-digit impressions typical of all pteraichnid manus prints correspond to digits one to three of pterosaurs.

Other features of the putative pterosaur ichnites are consistent with the morphology of the pterosaur manus. For example, digits one to three always bear large, deep, narrow, bladelike claws with prominent flexor tubercles (e.g., Wellnhofer 1975a, Fig. 14). Long, slitlike claw marks terminating the digit impressions closely match this morphology (Fig. 1C and D). Moreover, the relatively large size of these claw marks, when compared to those of the pes (Lockley *et al.* 1995, Fig. 4), corresponds to the size disparity between the manus and pes unguals of pterosaurs (Wellnhofer 1975b, Fig. 41).

Problematic aspects of the interpretation of pteraichnid manus prints, and their resolution

Some aspects of the manus prints present difficulties. The hindmost digit impression, presumably digit three, is often very long (Fig. 1B–D), up to twice the length of the impression of digit two, whereas in pterosaurs, manus digit three is never more than 1.4 times the length of digit two. Utilizing maximum pes print length as a base line for comparison, the relative length of the hindmost digit impression ranges from 1.3 to 1.6 times pes print length. This compares favourably with the proportions of manus digit three to pes length in pterosaurs, which, typically, is about 1.4. By contrast, the anteriormost and medial digit impressions of the manus seem relatively short when compared with pes print length. If digits one and two were partly flexed during contact with the substrate, or struck the ground at an angle, their prints would appear to be somewhat foreshortened. For the present, this would seem to be the most likely explanation for the apparent disparity in length of the manus digits of pteraichnids, but this discrepancy between skeletal morphology and ichnology deserves further scrutiny.

A second problem concerns the relative lengths of the manus and pes prints. In most trackways the manus prints are shorter than the pes prints. This corresponds to the situation in pterosaurs, wherein the manus (excluding the wing-finger) is shorter than the pes (metatarsus + digits). In some trackways, however, such as the holotype of *Pteraichnus* (Stokes 1957), the manus prints are as long, or even longer, than the pes prints. Examination of the pes prints shows that, in these cases, the metatarsus is shorter

than the digits, the reverse of the situation in pterosaurs, where the metatarsus is always as long or longer than the digits (Wellnhofer 1978, Fig. 25). If these prints were made by a typical pterosaur (and, though not recorded in the fossil record, pterosaurs with short metatarsals cannot be ruled out) then, presumably, in these cases, only the distal portion of the metatarsus made contact with the substrate. Interestingly, trackways containing relatively short pes prints exhibit the longest step and stride lengths, which prompts a possible explanation. These trackways were produced by a relatively rapidly moving pterosaur in which the pes had shifted from a fully plantigrade to a more semi-plantigrade contact. Thus, the unusual manus/pes print proportions probably reflect a not unexpected change in gait at higher speeds. A similar observation has been made for dinosaur tracks (Thulborn 1990, p. 127).

The divarication of the digit impressions, the anteriormost often at right angles to the hindmost, seems unusual, particularly when compared to the pedes in which digits one to four are generally subparallel. Consideration of pterosaur osteology reveals, however, that the metacarpo-phalangeal joint was less restrictive than the metatarso-phalangeal joint and permitted a considerable degree of lateral as well as vertical movement. This is demonstrated by fossil remains of *Dimorphodon* (Owen 1870), *Sordes* (Bakhurina 1986), *Pterodactylus* (Broili 1938; Wellnhofer 1970; Fig. 1A herein) and *Ctenochasma* (Broili 1936), which show that digit three could be abducted up to and beyond 90° to digit one. This is consistent with the details of ichnological evidence and perhaps to be expected since spreading the digits would provide a more stable contact with the substrate.

A more difficult question concerns the orientation of the manus prints. Usually, the anteriormost and medial digits are directed outward at right angles to the direction of travel, while the hindmost digit projects backward almost parallel to the line of travel. Lockley *et al.* (1995) suggested that this orientation of the manus was achieved by outward rotation of the forearm and carpus. Rotation at the elbow is unlikely, since this is essentially a hinge joint. Rotation of up to 45° is possible at the wrist, via movements between the forearm and proximal syncarpal, and the proximal and distal syncarpal (Wellnhofer 1985), but this does not fully explain the orientation of the prints.

Uncrushed remains of the shoulder girdle and forelimbs of *Dsungaripterus* from the Lower Cretaceous of China (Young 1964, 1973) and a variety of pterosaurs from the Lower Cretaceous Santana Formation of Brazil (e.g., Wellnhofer 1991c) throw new light on the orientation and movements of the forelimb during terrestrial locomotion. Various workers have argued that pterosaurs were unable to use the fully adducted forelimbs for terrestrial locomotion and thus produce a narrow manus track-
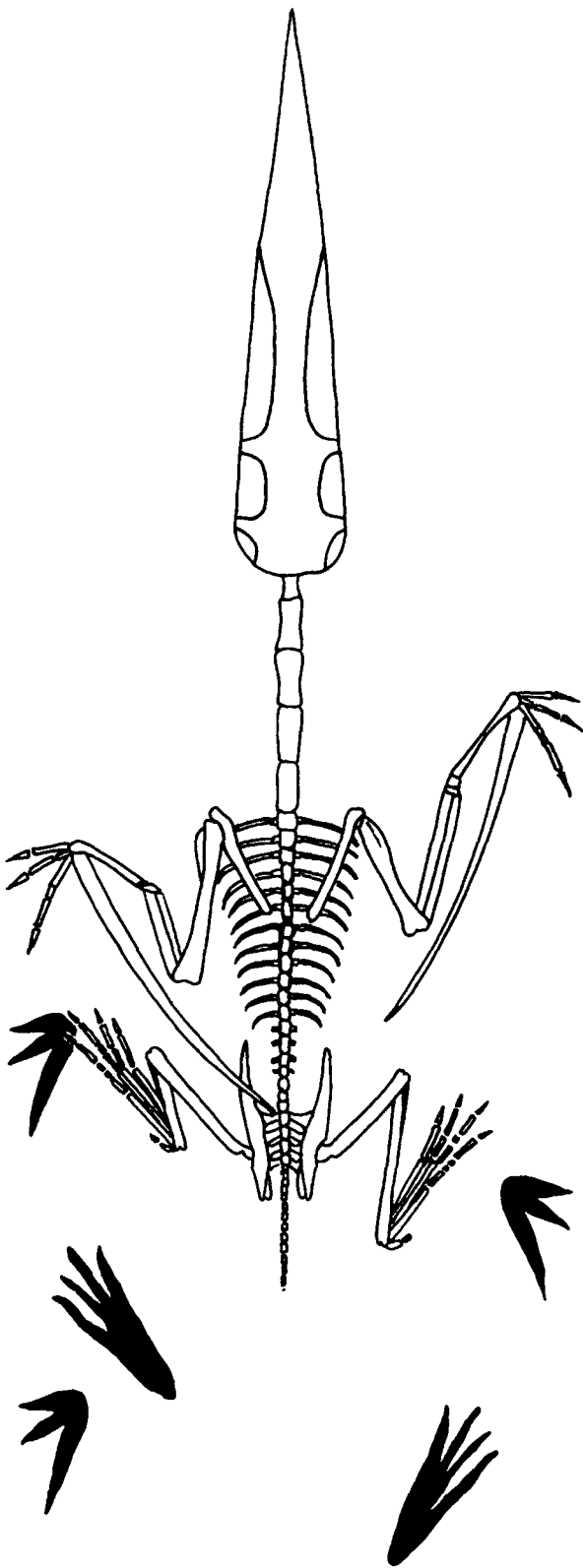
Fig. 4. Pterodactylus walking quadrupedally with limbs partially abducted, as seen from above. The left forelimb is in the middle of the protraction phase, while the right forelimb is fully protracted and in contact with the substrate. The left hind limb is also fully protracted, while the right hind limb is fully retracted and about to be disengaged from the substrate.

way. Indeed, this was Unwin's (1989) principal objection to the interpretation of *Pteraichnus* as a pterosaurian track. However, 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 (Wellnhofer 1975b, Fig. 41; Padian 1983b, Fig. 2a; Fig. 4 herein). Flexion and extension at the elbow enabled the forelimb to swing backward and forward in a parasagittal plane. Movements at the wrist rotated the metacarpus outward and backward, permitting the wing-finger to fold inward, toward the body, as well as upward and clear of the substrate (Wellnhofer 1991b, Fig. 25; Fig. 4 herein). Digits one and two continued the long axis of the metacarpus and thus projected laterally and somewhat toward the rear, while digit three, in its fully abducted position, was directed posteriorally (Fig. 1A). Thus, the posture of the forelimb during terrestrial locomotion is consistent with the orientation of the manus prints in *Pteraichnus* and similar tracks (cf. Fig. 1A with B–D).

This interpretation is further supported by a variety of well-preserved articulated specimens in which the orientation of digits one to three corresponds almost exactly to the position of the digits in the manus prints. Examples include *Dimorphodon macronyx* (Owen 1870, Pl. 17), *Sordes pilosus* (Bakhurina 1986, p. 33), *Rhamphorhynchus longicaudus* (Wellnhofer 1975c, Fig. 22, 1983, Fig. 36), *Pterodactylus kochi* (Abel 1925, Fig. 1; Broili 1938, Fig. 1; Natural History Museum, London, Department of Palaeontology R3949), *Pterodactylus longicollum* (Meyer 1859, Pl. 7, Fig. 1; Wellnhofer 1970; Pl. 11, Fig. 4), *Pterodactylus elegans* (Wellnhofer 1970, Pl. 9, Figs. 1 and 3, Pl. 10, Fig. 1), *Pterodactylus micronyx* (Wellnhofer 1970, Pl. 6, Fig. 1) a large individual of *Pterodactylus* (Natural History Museum, London, Department of Palaeontology R8573), *Germanodactylus cristatus* (State Museum for Natural History, Karlsruhe) and *Ctenochasma gracile* (Broili 1936). In these examples, digit one continues the axis of the metacarpus, digit two is directed somewhat backward and digit three is pointed to the rear, often almost at right angles to the long axis of the metacarpus. The presence of this arrangement in a number of unrelated taxa spanning a large portion of pterosaur evolutionary history strongly indicates that this is a real feature of pterosaurs and not a chance occurrence.

This interpretation of forelimb movement during terrestrial locomotion also solves the problem of narrow-gauge manus tracks. Retraction of the humerus enabled the forelimb to be employed in an almost fully adducted position (Fig. 4). It hinged at the elbow and swung backwards and forwards in a parasagittal plane, close to the body, resulting in a narrow spacing between left and right prints. The greatest rearward development of the shoul-

der glenoid, permitting the fullest adduction of the fore-limb and the closest approach to a parasagittal stance and gait, is found in the dsungaripteroids. It is perhaps not coincidental that, unlike other pterosaurs, most dsun-garipteroids have been recovered from terrestrial deposits (Bakhurina 1992, 1993; Bakhurina & Unwin 1995) and might be expected to show the greatest development of adaptations for terrestrial locomotion.

At first sight, manus-only trackways (Lockley et al. 1995, Fig. 3) appear problematic, but are in fact quite con-sistent with pterosaur anatomy. Often the manus prints are deeply impressed into the sediment: some form linear trackways, others exhibit meandering, or even completely disordered patterns, and there are some examples of sin-gle, isolated prints (Lockley et al. 1995, Fig. 8). It is diffi-cult to imagine any known Mesozoic tetrapod habitually proceeding on its forelimbs alone, unless supported by a fluid medium. There is, however, a more simple solution. The tracks were made by vertebrates in which most of the weight was transmitted through the forelimbs, resulting in relatively deep impressions of the manus (Lockley et al. 1995). If little weight were borne by the pedes, they would have produced relatively shallow imprints (Lockley et al. 1995, Fig. 2) or may not have impressed at all, though occasional pes prints, as reported by Lockley et al. (1995, Fig. 5), show that they were operating during terrestrial locomotion.

The body plan of pterosaurs is ideally suited for the production of manus-only trackways. The skull, shoulder girdle and forelimbs of pterosaurs are, almost without exception, much larger than the pelvis and hind limbs. During quadrupedal progression much of the weight was supported by the forelimbs (e.g., Wellnhofer 1991b, Fig. 25b), and the manus is likely to have impressed relatively deeply. By contrast, relatively little weight was transmitted through the hind limbs, and the feet are likely to have left shallower impressions than the hands. It is also worth noting that webbing of the pes has been reported in a number of Late Jurassic pterosaurs (see above). This may have helped spread the weight of the pes, further reducing the degree of impression.

One final problem concerns the discrepancy between gleno-acetabular lengths estimated from trackways and those observed in pterosaurs. Padian & Olsen (1984) cal-culated, from the holotype of Pteraichnus saltwashensis, that the gleno-acetabular length of the animal that made the prints was 2.6 times the pes length, and Mazin et al. (1995) report a ratio of 2.5 for tracks from Crayssac. This is somewhat greater than in pterosaurs, where the pes is only two times, or less, the gleno-acetabular length (Padian & Olsen 1984). The method of estimating gleno-acetabular length from tracks was devised by Baird (1954) and assumes that the fore and hind limbs of the track-maker were of roughly similar length. In pterosaurs, how-ever, there is a much greater disparity in limb length than

in other tetrapods. In Rhamphorhynchus the distance from the shoulder to the manus is more than 1.5 times that of the hip to the pes, and this proportion approaches a factor of two in pterodactyloids. During terrestrial pro-gression this arrangement is likely to have resulted in rel-atively large step and stride lengths for pterosaurs in com-parison to other quadrupeds of similar gleno-acetabular length. Hence, in the case of pterosaur tracks, calculations of gleno-acetabular length and their comparison with pes length are likely to be overestimates. Thus, far from being discrepant, gleno-acetabular length/pes length ratios exhibited by tracks agree with expectations based on pte-rosaur anatomy and functional morphology.

In summary, the new tracks yield evidence that the trackmaker possessed two characters (elongate penulti-mate phalanges and a highly elongate forelimb) that are unique to pterosaurs: they are also consistent in all other important respects with pterosaur anatomy and func-tional morphology. There can be no doubt that pteraich-nid tracks were created by pterosaurs, a conclusion which is strongly supported by the absence of any other Meso-zoic tetrapod capable of producing such unusual tracks. Some aspects of the tracks (such as the rearward directed manus prints) are unexpected, but they can be accommo-dated within our current understanding of pterosaur anatomy and functional morphology. We should not, of course, expect perfect correspondence between anatomy and ichnites; soft tissues and the dynamics of print forma-tion can have profound effects on print and track mor-phology (Thulborn 1990; Lockley 1991). Nevertheless, these unexpected features may be highly informative regarding stance and gait in pterosaurs and deserve fur-ther study.

The track record of pterosaurs

The results of a reassessment of putative pterosaur tracks, based on new understanding of the nature and origin of pteraichnid prints, are presented in Table 1. With the ex-ception of supposed pterosaur tracks from the Navajo Formation (Stokes 1978; Stokes & Madsen 1979), all ich-nites identified as Pteraichnus can be confidently assigned to pterosaurs. Lockley et al. (1995) illustrated manus prints from a number of sites. These, and other unde-scribed examples, seem similar in many respects to the manus prints of Pteraichnus and are very probably ptero-saurian in origin. Enigmatic ichnites consisting of sets of three parallel scratches have been reported from the Glen Rose Formation of Texas and tentatively ascribed to pter-osaurs (Stricklin & Amsbury 1974; Langston 1974). A pte-rosaurian origin cannot be entirely ruled out, but these prints appear to lack typical features of pteraichnid prints, and their identity therefore remains uncertain.

Table 1. The track record of pterosaurs.

Description[a]	Track-maker[b]	Locality	Formation	Age	Material	Authors
Pterosaur tracks						
Pteraichnus salt-washensis	Pterosaur (Stokes 1957; Lockley *et al.* 1995; this paper)	Carrizo Mountains, Apache County, Arizona, USA	Salt Wash Sandstone, Morrison Formation	Late Jurassic	Single track	Stokes 1957; Lockley *et al.* 1995
Pteraichnus cf. *salt-washensis, Pteraichnus* cf. *stokesi, Pteraichnus* ichnosp. indet.	Pterosaur (Lockley *et al.* 1995; this paper)	Bullfrog, Eastern Utah, USA	Summerville Formation	Late Jurassic	Many tracks at multiple stratigraphic levels. Includes 'manus-only' trackway	Lockley *et al.* 1995
Pteraichnus stokesi	Pterosaur (Logue 1977, 1994; Lockley *et al.* 1995; this paper)	Alcova Lake, Wyoming, USA	Sundance Formation	Late Middle– Late Jurassic	Prints	Logue 1977, 1994; Lockley *et al.* 1995
Pterosaur tracks	Pterodactyloid and 'rhamphorhynchoid' pterosaurs (Mazin *et al.* 1995)	Crayssac, Lot, France	Cazals Formation	Late Jurassic	Numerous prints and tracks	Mazin *et al.* 1995
Purbeckopus pentadactylus	Pterosaur (Wright *et al*, in press; this paper)	Langton Matravers, Dorset, England	Middle Purbeck beds	Early Cretaceous	Prints	Delair 1963; Prince & Lockley 1989; Ensom 1984
Possible pterosaur tracks						
Hesperornithiform tracks	Pterosaur(?) (Lockley *et al.* 1995; this paper)	Price, Utah, USA	Mesaverde Group	Late Cretaceous	Prints and tracks with 'beak or peck marks'(?)	Parker & Balsley 1989; Lockley *et al.* 1992; Lockley *et al.* 1995
cf. *Pteraichnus*	Pterosaur(?)	Peñón del Forno, Ribadesella, northern Spain		Late Jurassic	Isolated prints	Valenzuela *et al.* 1988; Lockley *et al.* 1995
Pteraichnus-like trackway	Pterosaur(?)	Santa Cruz de Yanguas, northern Spain	Cameros Basin	Early Cretaceous	Trackway	Moratalla 1993; Lockley *et al.* 1995
cf. *Pteraichnus*	Pterosaur(?)	Los Cayos, Spain		Early Cretaceous	Isolated prints	Moratalla 1993; Lockley *et al.* 1995
Turtle tracks	Pterosaur(?) (Lockley *et al.* 1995; this paper)	Las Hoyas, Cuenca, Spain	La Huergina Limestones Formation	Early Cretaceous	Large, isolated prints up to 270 mm in length	Fregenal-Martinez & Moratalla 1995; Lockley *et al.* 1995
Pteraichnus tracks	Pterosaur(?)	Emery County, Utah, USA	Black Hawk Formation	Late Cretaceous	Tracks	Lockley *et al.* 1995
Pteraichnus	Pterosaur(?)	Como Bluff, Wyoming, USA	Sundance Formation	Late Jurassic	Tracks	Bakker cited in Lockley *et al.* 1995
Footprints of 'hesperornithiform and/or ichthyornithiform birds'	Pterosaur(?) (Lockley *et al.* 1995)	Pouce Coupe River, Alberta, Canada	Dunvegan Formation	Late Cretaceous	Prints and toe drags	Currie 1989
Pterosaur(?)	Pterosaur(??)	Seco Creek, Medina County, Texas, USA	Lower Glen Rose Limestone	Early Cretaceous (Comanchean)	Irregular scratches made by three clawed digits	Stricklin & Amsbury 1974; Langston 1974
Non-pterosaur tracks						
Pteraichnus	Crocodilian (Leonardi 1987), or mammal-like reptile (Lockley & Hunt 1995)	Sand Flats, Grand County, Utah	Navajo Formation	Early Jurassic	Tracks	Anonymous 1973; Stokes 1978; Stokes & Madsen 1979
'Rhamphorhynchus tracks'	Limulid tracks (Caster 1941, 1957)	Altmühl–Alb, Bavaria, Germany	Solnhofen Limestone	Late Jurassic	Tracks	Oppel 1862; Figuier 1863
pterosaur	Crocodilian (Unwin 1986, 1989; Lockley 1991; Bennett 1992)	Clayton Lake State Park, Union County, New Mexico, USA	Mesa Rica Sandstone	Early Cretaceous	Single trackway	Gillette & Thomas 1989

a. This column lists the first name or identification to be applied to the ichnite.
b. Current identification of the track-maker. In many cases, earlier workers (listed in the final column) assigned the tracks and prints to other tetrapods.

Tracks from the Early Jurassic Navajo Formation of Grand County, Utah, were ascribed to *Pteraichnus* by Stokes (1978) and Stokes & Madsen (1979). They lack typical features of pteraichnid prints, however, and have recently been reidentified as mammaloid tracks (Lockley & Hunt 1995). A series of six prints in the Early Cretaceous Mesa Rica Sandstone of Clayton Lake State Park, New Mexico, were described as a pterosaur trackway (Gillette & Thomas 1989) consisting solely of manus prints. At least one of the prints appears to contain four digits of similar thickness, thus these prints cannot have been made by a pterosaur manus. In a re-examination of the tracksite, Bennett (1992) found evidence of further prints and tail drags and put forward a convincing argument in favour of a crocodilian trackmaker, as others have argued (Unwin 1986; 1989; Lockley 1991).

In summary, pteraichnid tracks are now reliably reported from Europe and Northern America. They range from the Late Middle Jurassic to the Late Cretaceous but are most abundant in the Late Jurassic. Lockley *et al.* (1995) have shown that this abundance correlates with a peak in pterosaur diversity in the Late Jurassic. Both the body fossil and ichnological records of pterosaurs are probably highly biased, however, and this correspondence should be interpreted with caution until the nature of the bias is better understood.

Terrestrial locomotion in pterosaurs

The terrestrial ability of pterosaurs has recently become the subject of some controversy. Padian (1983a, b, 1984, 1985, 1987, 1988, 1991), Padian & Rayner (1993) and others (Paul 1987; Bennett 1990) have argued that pterosaurs were digitigrade bipeds with an upright stance and gait. This is in strong contrast to the traditional idea, still supported by Pennycuick (1986), Unwin (1987a, b, 1989), Wellnhofer (1988, 1991b) and Wellnhofer & Vahldiek (1986), that pterosaurs were quadrupedal plantigrades, with a semi-erect or possibly even sprawling stance and gait. These conflicting views stem from differing interpretations of skeletal anatomy, arthrology and limb kinematics, especially as applied to the pelvis and hind limb, and are related to a wider debate concerning the relationships of pterosaurs to other diapsids. Recognition that pterosaurs were responsible for pteraichnid tracks marks a critical step forward in this debate, since these ichnites provide direct and unequivocal evidence of the stance and gait of pterosaurs during terrestrial locomotion. Consideration of the tracks and comparison with anatomical and functional studies of pterosaurs reveal the following:

1 Pterosaurs were quadrupedal, using both fore and hind limbs during terrestrial locomotion. Discounting manus-only trackways (discussed above), no bipedal

tracks have been reported, though such tracks may have been produced during the final stages of a take-off run, when much of the body mass was already supported by lift from the wings (see also Lockley *et al.* 1995, p. 18).

Considerations of mass distribution within pterosaurs also favour a quadrupedal stance and gait (Bramwell & Whitfield 1974; Pennycuick 1986). Pterosaurs have relatively large skulls, a stout shoulder girdle and greatly enlarged forelimbs, but a relatively small pelvis and hind limbs (Wellnhofer 1991a). As is evident in lateral view, much of the body mass was located in the anterior half of the body, and the centre of gravity lay well forward of the pelvis (Bramwell & Whitfield 1974; Pennycuick 1986). A bipedal stance and gait is thus largely precluded (unless the body is partly supported by lift from the wings), since, even with the femora fully adducted, the centre of balance lay well in front of the feet. Thus pterosaurs were forced to adopt a quadrupedal stance, as is confirmed by the tracks.

2 The pes was plantigrade. Digits one to four and their metatarsals struck the substrate during the contact phase of the step cycle. At relatively slow speeds the ankle came into contact with the substrate, but at higher speeds, as exemplified by the holotype of *Pteraichnus saltwashensis*, the ankle and proximal end of the metatarsus was raised, resulting in a smaller contact area.

The design of the pterosaur pes is suitable for plantigrady, but not for digitigrady. By contrast to the situation in bipedal dinosaurs and birds where the digits are divergent, enhancing stability of the single pes in contact with the substrate during locomotion, the digits are closely aligned. In addition, the penultimate phalange of digits one to four is elongate. Though best suited for sustaining loads in tension, this arrangement is adequate for plantigrady in that loads experienced during locomotion are distributed throughout the pes. It is a very poor design for digitigrady, however, in that during this type of locomotion loads are concentrated toward the distal end of the digits. For this reason, the pedal phalanges of digitigrades decrease in length distally.

3 The breadth of the trackways and positive rotation of the pes prints indicate a semi-abducted hind limb posture (Lockley *et al.* 1995). The key determinant of this posture was the femur. The head of the femur is usually set off at about 135° to the shaft in pterosaurs. With the caput in maximal congruence with the acetabulum, the shaft of the femur was directed outward at about 45° to the body, in a semi-abducted position (fig. 4). During the step cycle, the femur probably underwent a relatively small excursion, moving

from subhorizontal to a steeply inclined position, directed forward and outward. Displacement of the pes was mainly achieved by a large excursion of the tibiotarsus at the knee combined with smaller movements at the ankle.

There is some variation in trackway width and the degree of pes rotation. For example, the tracks of *Pteraichnus stokesi* from the Sundance Formation of Wyoming are relatively broad and the pes is angled outward at about 45° to the midline, whereas the tracks of *Pteraichnus saltwashensis* are relatively narrow and the pes is directed forward (cf. Figs. 3D and C). This is principally related to femur morphology, in that the angle of the caput to the shaft, while typically 135°, varies from 120° to 160°. The more acute the angle, the greater the adduction permitted and hence a narrower trackway, while the more obtuse the angle the greater the abduction and the broader the trackway. Since the knee and ankle were essentially hinge joints (Padian 1983b), the more obtuse the femur caput to the shaft the greater the degree of lateral rotation of the pes. This is reflected in the ichnological record, wherein narrow trackways have forward-pointing pedes while broader tracks consist of more laterally directed pes prints. Incidentally, these observations support Lockley *et al.*'s decision (1995) to assign these tracks to different taxa.

It could also be argued that variations in trackways reflect the ability of pterosaurs to vary the stance and gait of the hind limbs, rather than differences in osteology. However, until it can be shown that the same pterosaur was responsible for differing trackways, this must remain the less likely of the two explanations outlined here.

4 The manus was employed in a digitigrade position, supported by digits one to three. The digits were splayed, presumably to provide a more stable podium, and the claws were used to grip the substrate. Occasionally, the wing-finger came into contact with the substrate, but this was probably accidental. The wing-finger supported the main wing membrane which, though undoubtedly robust, probably functioned more efficiently if kept clean and protected from wear and damage.

5 Usually the forelimb adopted a semi-adducted posture, resulting in manus and pes trackways of similar width. During the step cycle most of the movement took place at the elbow, which permitted a wide arc of extension and flexion. Some movement was also possible at the wrist and could be used to modify the posture and orientation of the manus. The Crayssac tracks show that, on occasion, pterosaurs deployed the forelimb in a semi-extended position (Mazin *et al.* 1995; Fig. 3A). Presumably, the humerus was abducted and

the forearm extended, but as there are no indentations on the sediment surface lateral to the imprints of the clawed digits of the manus, it must be assumed that the wing-finger remained flexed on the wing-metacarpal.

Discussion

The wide stratigraphic range (Late Middle Jurassic to Late Cretaceous) and general uniformity of pteraichnid tracks suggests that a quadrupedal, semi-erect, plantigrade stance and gait was typical for pterosaurs. This is consistent with the uniformity in skeletal anatomy of pterosaurs, particularly with respect to the hind limb, which is remarkably conservative, varying little across a time interval of more than 140 million years. Narrow pterosaur trackways, consisting only of pes prints (Unwin 1989, Fig. 27.10b) and indicative of a fully erect, bipedal, digitigrade stance and gait (e.g., Padian 1983a), have never been found, and this functional model is also inconsistent with evidence for extensive involvement of the hind limbs in the flight apparatus (Unwin & Bakhurina 1994; Bakhurina & Unwin 1995).

It may be of some significance that virtually all the tracks reported so far appear to be those of pterodactyloid pterosaurs. Mazin *et al.* (1995) mention 'rhamphorhynchoid' tracks from Crayssac, but these have not yet been described. Lockley *et al.* (1995, Fig. 6c) illustrate a pes imprint which appears to contain the impression of an elongate fifth toe, a structure common to all 'rhamphorhynchoids' but strongly reduced in pterodactyloids (Wellnhofer 1978). The print illustrated is a composite restoration, however, and detailed descriptions of the prints on which it is based have yet to be published.

'Rhamphorhynchoids' are the only pterosaurs known from the Late Triassic to the Middle Jurassic and dominated pterosaur faunas until almost the end of the Jurassic. However, apart from the exceptions noted above, they seem to have left no track record, despite achieving considerable diversity and a world-wide distribution by the Early Jurassic (Wellnhofer 1991a). By contrast, the known track record of pterosaurs (Late Middle Jurassic to Late Cretaceous) closely matches the known stratigraphic distribution of pterodactyloids (Upper Jurassic to Late Cretaceous).

A possible explanation for these patterns may be related to differences in the construction of the flight apparatus of 'rhamphorhynchoids' and pterodactyloids, and their significance for the terrestrial ability of pterosaurs. It has recently been shown (Unwin & Bakhurina 1994; Bakhurina & Unwin 1995) that in the Late Jurassic 'rhamphorhynchoid' *Sordes pilosus* the main wing-membrane extended to the ankle and there was a uropatagium stretched between the hind limbs and supported by the fifth toe. This arrangement was probably typical for

'rhamphorhynchoids' in that they all have a long fifth toe and similar hind limbs (Unwin & Bakhurina 1994). The patagia of pterodactyloids were comparatively reduced: the main wing membrane appears to have been restricted to the femur (Wellnhofer 1987) and the fifth toe was strongly reduced or lost altogether, indicating a similar reduction and perhaps eventual loss of the uropatagium. Comparing these two models it seems clear that, when grounded, 'rhamphorhynchoids' must have been somewhat impeded by the uropatagium, which prevented large excursions of the hind limb and was constantly at risk of snagging on obstacles or projections. Pterodactyloids, with hind limbs relatively free of the flight apparatus probably had a less restricted terrestrial ability and thus would be expected to leave more tracks.

Pteraichnid tracks and pterosaur body fossils also show a clear correlation in size from the Late Middle Jurassic to the Late Cretaceous. Middle to Late Jurassic ichnites indicate pterosaurs of small to medium size, as also occurs in the skeletal record where most taxa are between 0.5 and 1.5 m in wingspan, reaching a maximum size of about 3 m. Prints from the Lower Cretaceous represent larger animals. This is consistent with body fossils which show that most Lower Cretaceous pterosaurs were 2–4 m in wingspan, though individuals with wingspans in excess of 5 m (e.g., *Coloborhynchus*, '*Ornithodesmus*') had appeared by the Hauterivian. Very large prints, probably of pterosaurs, have been reported from the Late Cretaceous of Price, Utah (Lockley *et al.* 1995). Again, this is consistent with the body fossil record in that the largest pterosaurs, with wingspans in excess of 10 m (e.g., *Quetzalcoatlus*) are known only from the Late Cretaceous (Wellnhofer 1991a). This interval has also yielded some small, possibly pterosaurian prints (Lockley *et al.* 1995; Table 1). If confirmed, this record will not be inconsistent with osteological data in that, although large pterosaurs seem to have been predominant in the Late Cretaceous, adults of small to medium-sized forms, such as *Nyctosaurus* (Williston 1902) and *Montanazhdarcho* (Padian *et al.* 1995) have been reported.

The wide stratigraphic distribution of pteraichnid tracks (Table 1) and their great abundance at some sites (Lockley *et al.* 1995; Mazin *et al.* 1995) provide two further insights into pterosaur biology. First, although quadrupedal, some, though perhaps not all, pterosaurs may have had a reasonably proficient terrestrial ability. Dsungaripteroids (Late Jurassic – Early Cretaceous) seem best adapted for terrestrial locomotion, which is consistent with their occurrence in continental environments (Bakhurina 1992, 1993).

Second, the association of large numbers of tracks, as for example at Crayssac (Mazin *et al.* 1995), is unlikely to be fortuitous. The most probable explanation for these associations is that they represent areas in which the trackmakers were feeding. Almost all the tracksites (Table 1) have been interpreted as mud flats or sand bars adjacent to large water bodies. These locations provide numerous feeding opportunities and at the present day are intensely exploited by a wide variety of birds. It seems likely that such environments were also highly productive during the Mesozoic and would have provided pterosaurs with an important food resource. The abundance of pterosaur tracks indicates that pterosaurs certainly visited these environments and the report of possible 'beak' marks (Parker & Balsley 1989) at a putative pterosaur tracksite in Price, Utah (Lockley *et al.* 1995), suggests that feeding took place on at least some occasions. This is supported by a peculiar feature of some pterosaur tracksites. Lockley *et al.* (1995) and Mazin *et al.* (1995) describe small areas bearing large numbers of disorganized tracks. This may represent 'trampling', an activity carried out by gulls and ducks and intended to bring infaunal organisms to the surface where they can be caught and consumed (Cadèe 1990).

Conclusions

New ichnites from Europe and America have provided the key to two outstanding problems: the identity of the *Pteraichnus* trackmaker, and the nature of terrestrial locomotion in pterosaurs. Pteraichnid tracks were made by pterosaurs employing a plantigrade, quadrupedal stance and gait with the hind limb partly adducted and the forelimb in a variety of postures from partially abducted to fully adducted. The majority of tracks were produced by pterodactyloids, probably engaged in feeding. Only a small proportion of known tracks have been reported or described in detail and few have been illustrated. The study and description of the wealth of new material should help resolve unexpected features of pterosaur ichnites and provide new insights into the functional morphology and behaviour of pterosaurs.

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