

New pterosaur tracks (Pteraichnidae) from the Late Cretaceous Uhangri Formation, southwestern Korea

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Abstract – Numerous footprints of dinosaurs, pterosaurs and birds, together with arthropod tracks, have been discovered in the upper Cretaceous Uhangri Formation which crops out along the southwestern coastline of South Korea. This ichnofauna contains the first pterosaur tracks reported from Asia. The digitigrade tridactyl manus impressions exhibit features of a typical pterosaur hand print. The pes impressions, however, show features that are different from pterosaur footprints reported previously: there is no visible trace of impressions of individual digits, and the toes are triangular or rounded in shape distally without distinct claw impressions. As these features clearly distinguish the Uhangri tracks from *Pteraichnus* and *Purbeckopus*, we assign them to a new genus, *Haenamichnus* which accommodates the new ichnospecies, *Haenamichnus uhangriensis*. The prints are five to six times larger than those of *Pteraichnus*, and are currently the largest pterosaur ichnites known. They show virtually no trace of the 5th phalange of the pes, indicating that they were made by pterodactyls; moreover, features of the tracks suggest that they can be attributed to azhdarchids, the commonest pterosaur of the Late Cretaceous. The longest pterosaur trackway yet known from any track site (length 7.3 m) and consisting of 14 pairs of foot impressions, was also found in the Uhangri Formation and suggests that azhdarchids, at least, were competent terrestrial locomotors. The fossil track site at Uhangri represents the first occurrence of the tracks of pterosaurs, dinosaurs and web-footed birds all on the same level. This demonstrates that pterosaurs and birds visited the same habitat, but the large size disparity suggests that they occupied different ecological niches.

Keywords: tracks, Pterosauria, South Korea, Upper Cretaceous.

1. Introduction

In 1957, Stokes described an unusual trackway from the Morrison Formation in Arizona, named it *Pteraichnus saltwashensis*, and argued that it represented the first evidence for pterosaur tracks. Padian & Olsen (1984) disputed Stokes' interpretation, on the basis of their experimental work on small caimans, and argued that the trackways could have been made by a crocodilian. Subsequent studies (Conrad, Lockley & Prince, 1987; Prince & Lockley, 1989; Unwin, 1989; Lockley, 1991) also cast doubt on a pterosaurian origin for *Pteraichnus*, but the discovery of further *Pteraichnus* and *Pteraichnus*-like tracks (Logue, 1994; Hunt *et al.* 1995; Lockley & Hunt, 1995; Lockley *et al.* 1995; Mazin *et al.* 1995, 2001a,b), with features that could only have been made by pterosaurs, showed that Stokes' original interpretation was correct (Bennett, 1997; Unwin, 1997, 1999). More pteraichnid tracks have been reported recently (Calvo &

Moratalla, 1998; Southwell & Connely, 1997; Wright *et al.* 1997; Krantz, 1998; Calvo, 1999; Lockley, 1999; Lockley *et al.* 2000; Fuentes Vidarte, 2001; Meijide Fuentes, 2001; Meijide Calvo, 2001; Rodríguez De La Rosa, 2001; J. O. Calvo & M. G. Lockley, unpub. data), and our knowledge of the pterosaur track record now consists of more than 20 localities ranging in age from Late Jurassic to Late Cretaceous.

Three ichnospecies have been named so far. *Pteraichnus saltwashensis* was proposed by Stokes (1957) for tracks from the Upper Jurassic Morrison Formation in the Carrizo Mountains, Arizona, and Lockley *et al.* (1995) named a second species, *P. stokesi*, on the basis of tracks from the Upper Jurassic Sundance Formation at Alcova Lake, Wyoming. Lockley *et al.* (1995) proposed a new ichnofamily, Pteraichnidae, for the reception of *Pteraichnus* and a third species, and a new genus was added to this family with the identification of *Purbeckopus pentadactylus* from the Lower Cretaceous Purbeck Limestone Formation of Dorset as being of pterosaurian origin (Wright *et al.* 1997). Other pterosaur tracks, such as

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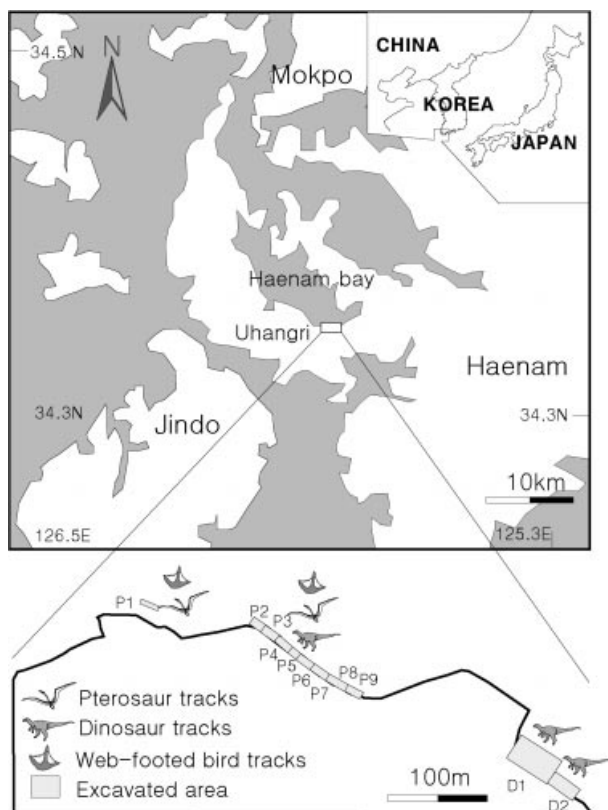


Figure 1. Location map for the Late Cretaceous Uhangri pterosaur track locality in southwestern Korea. Lower part of the figure shows track sites found in the lowest of the three track-bearing layers. Pterosaur tracks were found at sites P1 to P9. Only dinosaur tracks were found at sites D1 and D2.

those from Crayssac (Mazin *et al.* 1995), differ from *Pteraichnus* and *Purbeckopus* but have yet to be formally named.

The first evidence of pterosaur tracks from Asia was found in the Cretaceous Uhangri Formation, which crops out along the southwestern coastline of South Korea, and was initially reported by Lockley *et al.* (1997). The main outcrop of the Uhangri Formation is located about 20 km west of Haenam-gun, Jeollanam Province, South Korea and stretches for about 5 km (Fig. 1). This fossil-bearing bed is 0.3 m thick and dips in an inland direction. Consequently, it took two years (1996–1998), to excavate about 2 km of the coastline. As a result of the excavation, 528 dinosaur footprints, 443 pterosaur footprints, and thousands of footprints of web-footed birds were found in the upper part of the Uhangri Formation (Huh, Lim & Yang, 1996; Huh *et al.* 1997; Lockley *et al.* 1997; Yang *et al.* 1997). These footprints and tracks are of great interest for several reasons: the bird tracks are among the oldest tracks of web-footed birds yet found (Yang *et al.* 1997; Baek & Yang, 1998) while the pterosaur tracks are the stratigraphically youngest found so far, the first to be

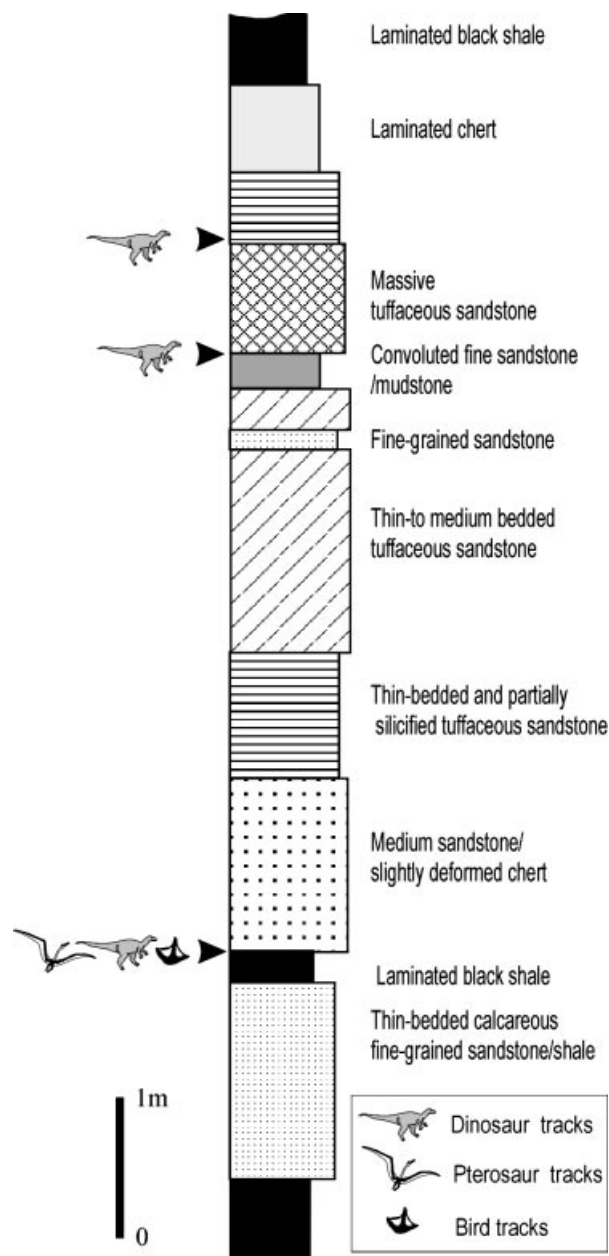


Figure 2. Simplified stratigraphic column for the track-bearing deposits at Uhangri. Dinosaur tracks were found in three levels, and tracks of dinosaurs, pterosaurs and birds were found together in the lowest level.

reported from Asia (Lockley *et al.* 1997), and they include some of the largest prints yet known. Moreover, this is the first reported occurrence of the tracks of birds, pterosaurs, and dinosaurs on the same surface (Fig. 2).

Here, we present the first detailed descriptions of the Uhangri pterosaur tracks and discuss the likely identity of the track-maker. We also consider the significance of the Uhangri tracks for understanding the terrestrial ability, palaeoecology and evolutionary history of pterosaurs.

2. Geological setting

The tracks described here originate from the Uhangri Formation, which forms the middle unit of the Haenam Group in the Haenam Basin. The Haenam Basin is composed of isolated non-marine basins distributed across Haenam-gun County, Jeollanam Province, South Korea (Fig. 1). The Haenam Group contains four formations that are, in ascending order: an andesitic tuff with andesite intrusions and flows, the Uhangri Formation, the Hwangsang Tuff, and the Jindo Rhyolite. The Uhangri Formation comprises an epiclastic fluvio-lacustrine sequence with minor volcanoclastics (Chun & Chough, 1995).

The pterosaur, dinosaur and bird tracks are found in the upper part of the Uhangri Formation in association with ripple marks. The distribution of these traces indicates that part of the formation represents the shallow margin of a lake. The track-bearing layer consists of a well-laminated, calcareous, black shale in an alternating sand/shale succession.

Vertebrate tracks were found in three different levels in the upper part of the Uhangri Formation. Pterosaur tracks, associated with numerous bird and dinosaur tracks, were only found in the lowest track level, which consists of a well-laminated black shale (Figs 1, 2). Pterosaur tracks were found at nine separate sites (P1–P9) in the black shale, while two further sites yielded only dinosaur tracks (D1–D2).

The track-bearing black shale also contains many elongate plant stems, invertebrate traces, and non-marine ostracods. The sandstone above the track layer includes many arthropod trackways and invertebrate trace fossils, including *Planolites* and *Skolithos* (Fig. 3). Despite local volcanic activity, faunal evidence suggests that various organisms thrived in the Uhangri Lake system (Huh *et al.* 1998).

The Hwangsang Tuff and Andesitic Tuff, which respectively overlie and underlie the Uhangri Formation, have been dated at 82.8 ± 1.7 Ma and 94.1 ± 2 Ma (Moon *et al.* 1990). To refine the age of the tracks, whole rock samples were collected and dated from a Lapilli andesite, 36 m below the track-bearing bed. The age date obtained, 83 ± 2.4 Ma ($^{40}\text{K}/^{40}\text{Ar}$), indicates a maximum age for the tracks (Huh *et al.* 1998) and is equivalent to a Santonian–basal Campanian age (Geological Society of America, time scale 1999).

3. Systematic description

Ichnofamily PTERAICHNIDAE, Lockley *et al.* 2000

Haenamichnus ichnogen. nov.

Etymology. ‘*Haenam*’ is the name of the locality where the pterosaur track was found; ‘*ichnos*’ is Latin for trace.

Diagnosis. Pes impressions elongate with narrow heel and postero-lateral impression of digit V rounded.

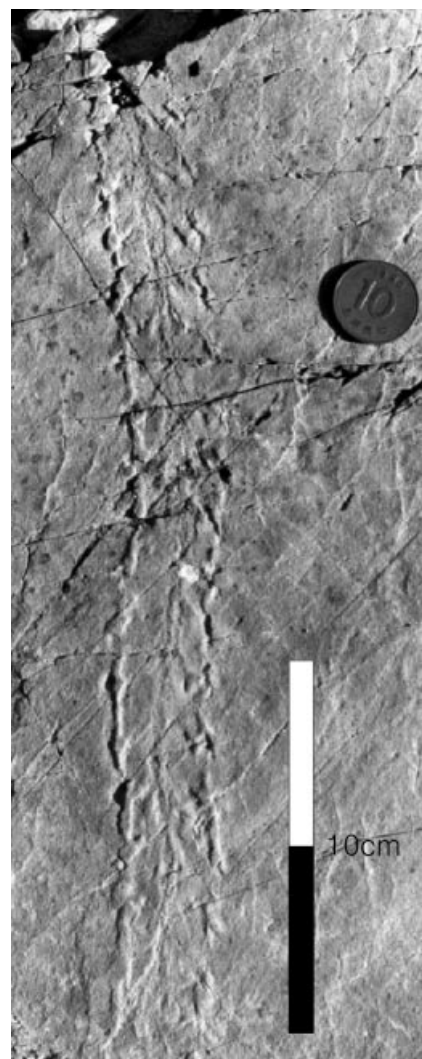


Figure 3. An arthropod trail found in the sandstone above the layer containing pterosaur tracks.

Digital pad impressions sometimes present. Manus tridactyl, occasionally tetradactyl, and usually behind and slightly outside pes.

Haenamichnus uhangriensis ichnosp. nov.

Figure 4

Etymology. Named after the Uhangri Formation, which yielded the holotype.

Holotype. Natural cast of right manus and pes prints, site P2 (CNUPH.P2).

Horizon and locality. Uhangri Formation, Upper Cretaceous; southern coast of Haenam Bay, Haenam-gun, Jeollanam Province, South Korea.

Description. The front part of the pes print is broadly triangular, with no separation of the digit impressions, while the heel region is narrower and rounded. The

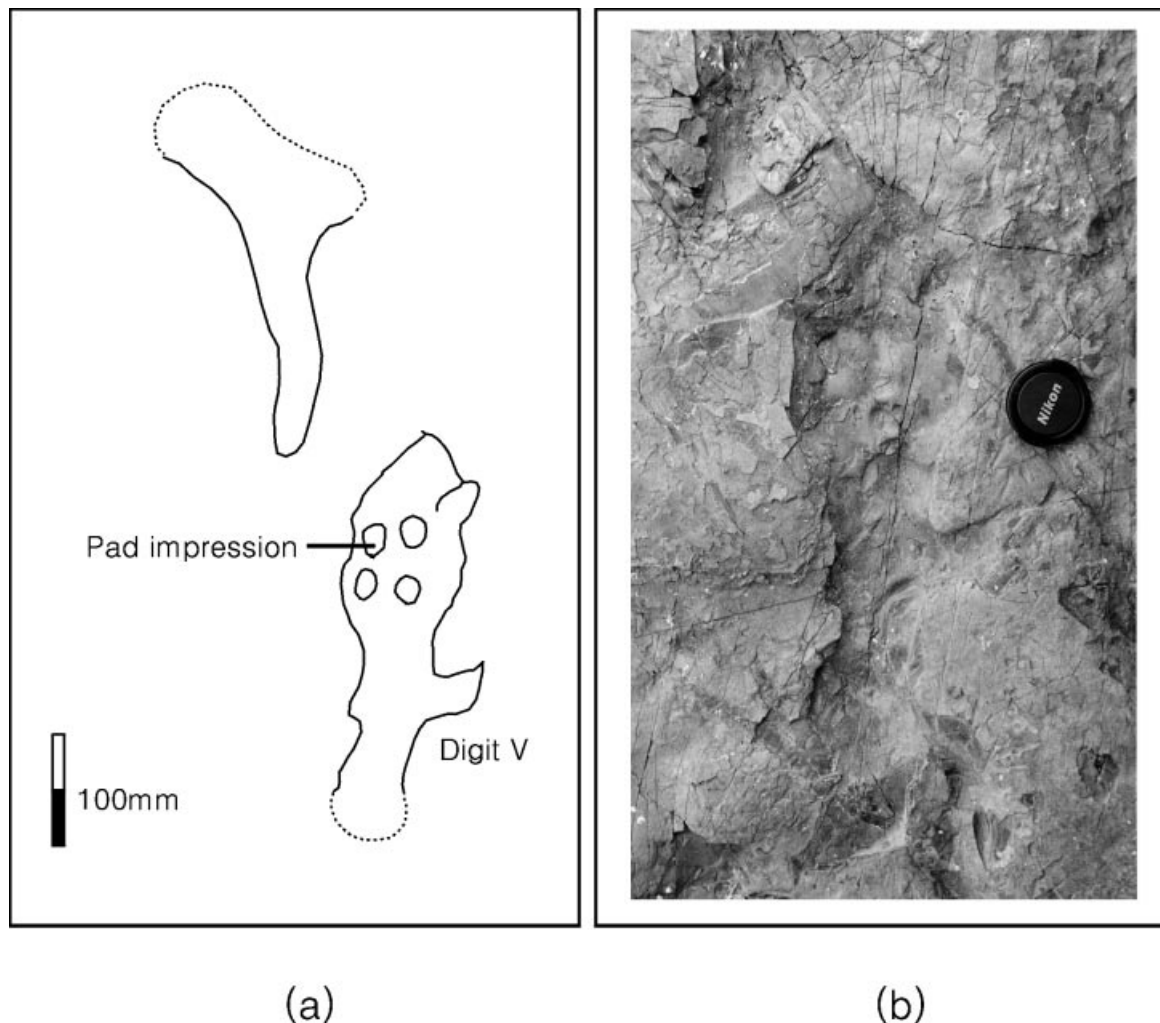


Figure 4. (a) *Haenamichnus uhangriensis*, holotype (CNUPH.P2), impression of right manus and pes pair, site P2 (CNUPH.P2). (b) Pes impression of the holotype.

separation of digits is not evident, but the triangular shape of the anterior margin of the pes impressions suggests that digits II and III may have been the longest. The pes prints have a thick, short impression of digit V and impressions of large interphalangeal pads on pes digits II and III. The pes print is up to 350 mm in length, and 105 mm in width. The manus print, which has a broad knuckle impression, is anterior to the pes impression. The manus impressions are tridactyl, strongly asymmetric, and rotated outward at almost a right angle to the long axis of the track way. The depth of the manus imprint decreases toward the tips of digit prints I and II and they have a round outline without claw impressions. The digit III impression has a clear outline and is much longer and deeper than the other digit prints. The manus print is about 330 mm in length, and 110 mm in width, consequently, the manus and pes impressions are of similar length.

Discussion. The digitigrade tridactyl manus impressions exhibit features of a typical pterosaur hand print (Stokes, 1957; Unwin, 1997; Wright *et al.* 1997; Lockley

et al. 2000). The pes impressions, however, show features that are different from pterosaur footprints reported previously. There is a thick, short impression of digit V and large interphalangeal pad impressions, but no visible traces of impressions of individual digits and claws. Typically, the prints are five to six times larger than those of *Pteraichnus* (Fig. 5).

Previously, the largest known pterosaur prints were those of *Purbeckopus pentadactylus* from the Purbeck Group, which spans the Jurassic–Cretaceous boundary in Dorset, England. However, prints of *Haenamichnus uhangriensis* are about two times larger than those of *P. pentadactylus* (Fig. 5). They also show a number of distinctive features. In *Purbeckopus* the pes imprint is triangular with a short heel impression and the digits are relatively thick, clearly separate and have claw impressions (Wright *et al.* 1997). In contrast, prints of *Haenamichnus uhangriensis* have a narrow, elongate shape with a protruding and rounded heel impression and digit impressions that do not splay outward except for the thick impression of digit V. These features clearly distinguish the Uhangri tracks from *Pteraichnus*

Table 1. Measurements of prints forming the trackways illustrated in Figures 6, 7 and 8

| Trackway | Footprint no. | L/R | Footprint length (mm) | Footprint width (mm) | Footprint depth (mm) | FO (degrees) | Pace length (mm) | Stride length (mm) | Site |
|----------|---------------|-------|-----------------------|----------------------|----------------------|--------------|------------------|--------------------|------|
| A | 1 | P-L | 245 | 70 | 11 | S57E | 515 | 877 | P9 |
| | 2 | M-R | 193 | 126 | 11 | S37E | | | |
| | | P-R | 217 | 69 | 10 | S29E | 646 | 1046 | |
| | 3 | P-L | 231 | 28 | 9 | S64E | 646 | 1092 | |
| | 4 | M-R | 214 | 88 | 10 | S51E | | | |
| | | P-R | 215 | 110 | 10 | S40E | 600 | 892 | |
| | 5 | M-L | 230 | 100 | 9 | S42E | | | |
| | | P-L | 235 | 110 | 11 | S60E | 338 | | |
| | 6 | M-R | 234 | 96 | 11 | S42E | | | |
| | | P-R | 231 | 53 | 10 | S29E | | | |
| | 7 | M-L | 214 | 94 | 11 | S55E | | | |
| | 8 | M-R | 250 | 123 | 11 | S37E | | | |
| | 9 | P-L | 224 | 65 | 11 | S46E | 862 | 1123 | |
| | 10 | M-R | 168 | 115 | 10 | S28E | | | |
| | 11 | M-L | 210 | 120 | 11 | S38E | | | |
| Average | | P-L | 215 | 90 | 11 | S38E | 691 | 1169 | |
| | 12 | M-R | 254 | 127 | 11 | S36E | | | |
| | | P-R | 235 | 108 | 11 | S18E | 631 | 1446 | |
| | 13 | M-L | 235 | 92 | 11 | S37E | | | |
| | | P-L | 202 | 109 | 11 | S42E | | 869 | |
| | 15 | M-L | | 55 | 11 | | | | |
| | | P-L | 254 | 122 | 11 | S56E | | | |
| | | Manus | 220 | 103 | 11 | | | | |
| | | Pes | 228 | 85 | 11 | | 616 | 1064 | |
| | | | | | | | | | |
| B | 1 | M-L | 240 | 150 | 18 | S42W | | | P4 |
| | | P-L | 242 | 102 | 14 | S62W | | | |
| | 2 | P-R | 227 | 99 | 13 | S8E | | | |
| | | Manus | 240 | 150 | 18 | | | | |
| | | Pes | 235 | 101 | 14 | | | | |
| C | 1 | M-R | | | | S11E | | | |
| | 2 | M-L | 170 | 80 | 9 | S17E | | | |
| | | P-L | 170 | 65 | 9 | S22E | | | |
| | 3 | M-R | 170 | 80 | 13 | S12E | | | |
| | | Manus | 170 | 80 | 11 | | | | |
| Average | | Pes | 170 | 65 | 9 | | | | |
| | | | | | | | | | |
| D | 1 | m-R | 159 | 54 | 13 | S23E | 710 | | P1 |
| | 2 | m-L | 202 | 67 | 13 | S2E | | | |
| E | 1 | m-R | 194 | 60 | 16 | N18E | 638 | 877 | |
| | 2 | m-L | 140 | 72 | 16 | N8W | 708 | | |
| F | 3 | m-R | 194 | 91 | 10 | N31W | | | |
| | 1 | M-L | 201 | 64 | 19 | S65W | 654 | 1362 | |
| | 2 | M-R | 165 | 54 | 9 | | 977 | | |
| Average | 3 | M-L | 178 | 38 | 14 | N62W | | | |
| | | Manus | 181 | 52 | 14 | | 816 | 1362 | |

Abbreviations: L/R, left or right print of pes and manus; FO, footprint long axis orientation (in degrees)

and *Purbeckopus* and justify their assignment to a separate ichnogenus and species.

In contrast to the usual position of the pes and manus impressions in the pterosaur tracks, the pes impression from Uhangri is posterior to the manus impressions in CNUP.P2. Consequently, these particular impressions may have been made while the track-maker was stationary.

Haenamichnus sp.

Figures 6, 7

Materials. Site P1 (CNUPH.P1) manus-only trackway D, E and F (Fig. 8); site P4 (CNUPH. P4), trackway B

and C; Site P9 (CNUPH. P9) trackway A (Fig. 7). All tracks were found in the black shale layer which is the lowest of the track-bearing layers (Figs 1, 2).

Description. A 7.3 m long trackway of a quadruped from site P9 is designated trackway A. It consists of 14 pairs of impressions (Fig. 6; Table 1). The manus impressions from the 1st and 3rd pairs have been eroded away, and the 14th foot impression is buried in the upper layer. The 7th pair does not contain a pes impression, while the 9th lacks a manus impression.

In the 2nd manus–pes print pair of track A (Fig. 6b) the pes impression, which lies anterior to the manus impression, is relatively elongate with no individual

digit impressions and was made by a plantigrade foot. The manus impression is tridactyl, strongly asymmetric, and rotated outward at almost a right angle to the long axis of the trackway. Digits I and II are directed laterally, while digit III is parallel to the midline of the trackway. The well-preserved 7th manus impression of trackway A has digits I–III that are 65 mm, 51 mm and 98 mm long respectively (Fig. 6c). The claw impression of digit III curves slightly inward toward the axis of the trackway. An elongated impression sub-parallel to digit III, and at a higher angle to the trackway midline, is a trace of what appears to be the impression of the proximal end of the wing-finger (digit IV) as noted by Mazin *et al.* (1995) in some prints from the Upper Jurassic Cazals Formation of Crayssac in France. Some pes impressions forming trackway A at site P9 are irregular and curve in an 's' fashion while the toe region exhibits various shapes. The pes axis shows a strong positive (outward) rotation of about 18° relative to the trackway axis. A short projection can be seen on the external margin of the 12th pes impression and is thought to be a trace of digit V (Fig. 6e). The gleno-acetabular length of the track-maker of trackway A is estimated to be 370 mm.

Many footprints of pterosaurs are irregularly exposed at site P4, but in most cases, individual digit impressions are not distinguishable (Fig. 7). Two trackways, B and C (Fig. 7), are distinctive. Trackway B consists of one manus and two pes prints, and is 0.8 m in width. The pes impressions of this trackway are thicker than those of trackway A and have rounded heel and toe impressions. Trackway C, which consists of three manus prints and one pes print, is 0.5 m in width and thus somewhat narrower than trackway B (Table 1). Among the unusual tracks from site P4 there is a delicate manus–pes print set in which the right pes impression slightly overlaps the manus (Fig. 7b). The manus impression of this set is 265 mm in length and 280 mm in width, and thus has an unusually high width to length ratio ($W/L = 1.06$) compared to the average value ($W/L = 0.4$) for prints in trackways at Uhangri. This distinctive shape is attributable, principally, to a broad central region, but, as in other manus prints, digit I is the shortest and digit III the longest. The plantigrade pes impression lies anterior to the manus impression and is relatively elongate, reaching 280 mm in length, and 128 mm in width.

Discussion. The pes impressions forming trackway A at site P9 are more slender than those of trackway B at site P4, although the prints from tracks A and B are about the same size (Fig. 5). The narrowness of the pes prints of track A do not necessarily reflect an anatomical difference, however, but could be due to differing degrees of abduction of the metatarsals. The 's' shape of the 9th pes impression of trackway A (Fig. 6d) presumably reflects the greater adduction of the digits, as a result of flexion at the joint between the metatarsals

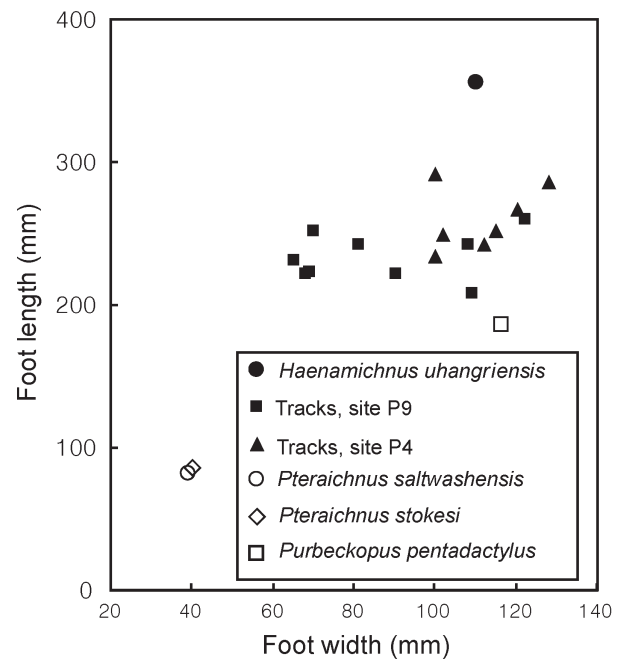


Figure 5. Scatter diagram showing the relationship between foot length and foot width for pterosaur pes prints from the Uhangri Formation. The values for the two species of *Pteraidhnus* and *Purbeckopus* are also included, based on tracks described by Stokes (1957) and Lockley *et al.* (1995) and figured by Wright *et al.* (1997), respectively.

and the digits, than in earlier and later parts of the trackway.

In pterosaur tracks from other localities, the impression corresponding to digit III has occasionally been identified as an impression of the 1st wing-finger phalange (Lockley *et al.* 1995). However, the impression of inter-phalangeal joints in the longest posterior digit impression of the 12th manus print of trackway A (site P9), indicates that, in this case, it is an impression of digit III (Fig. 6e). Moreover, the 7th manus print of this trackway has a fourth, elongate, digit-like impression that is as broad as the impression of digit III and extends toward the mid-line: this probably represents the wing-finger (Fig. 6c).

The morphology of the tracks from site P4 and P9 is similar to that of other pterosaur tracks reported from the USA (Lockley *et al.* 1995), England (Wright *et al.* 1997), France (Mazin *et al.* 1995) and Spain (Pascual Arribas & Sanz Perez, 2000). However, these tracks also show features that distinguish them from pterosaur footprints reported previously: (1) the size of these tracks is much larger than those assigned to *Pteraidhnus*; (2) in *Purbeckopus* the pes imprint is triangular and the digits are distinct and separate, but relatively thick and have claw impressions. By contrast, the pes prints of *Haenamichnus* sp. are narrow, with an elongate shape, and the digit impressions do not splay outward; (3) there are no claw impressions preserved on the pes prints; (4) although the general outline of pes

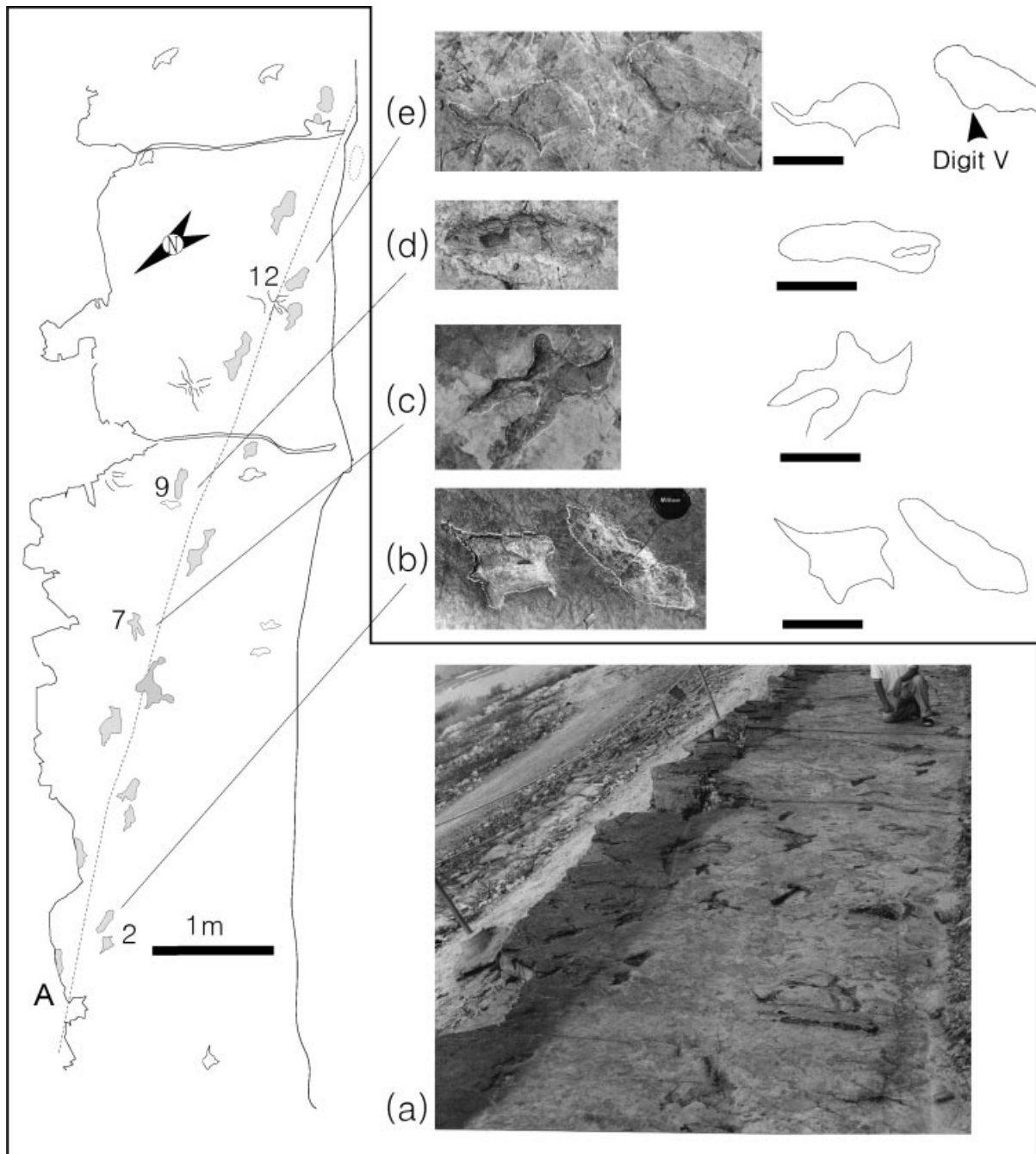


Figure 6. (a) Photograph and map of site P9 (CNUPH.P9) showing the longest trackway (A: length 7.3 m) yet known anywhere in the world; dashed line indicates trackway midline. (b) Impression of 2nd right manus–pes pair. (c) 7th left manus impression. (d) 9th left pes impression. (e) Impression of 12th right manus–pes pair. Scale bar in (b–e) represents 100 mm.

prints from site P4 is similar to those of *P. stokesi*, *Haenamichnus* sp. is distinguished by the presence of rounded posterior projections, similar to those of *Purbeckopus pentadactylus* (Fig. 7b, c).

The estimated gleno-acetabular length (370 mm) for the maker of trackway A is about twice the same dimension for the track-maker of *Pteranichnus stokesi* (about 194 mm). The ratio of the gleno-acetabular length to the pes length for track A is approximately 1.7. This is considerably smaller than the ratio of 2.6

for *Pteranichnus* (Padian & Olsen, 1984), though it falls well within the predicted range for pterosaurs: 1.5–2.1 (Unwin, 1989). It should be noted, however, that the possibility that the trunk may have had a sub-vertical, rather than sub-horizontal, position in some pterosaurs during terrestrial locomotion (Bennett, 1997; Unwin & Henderson, 1999), and the extreme disparity between fore and hind limb lengths, severely complicate estimates of gleno-acetabular length based on pterosaur tracks (Mazin *et al.* 1995; Bennett, 1997).

4. Identity of the *Haenamichnus* ichnogen. nov. track-maker

A number of features of *Haenamichnus* ichnogen. nov. enable a tentative identification of the likely maker of this type of print. The large size of the prints and the absence of any clear evidence for an elongate 5th pes digit suggest that they were produced by a pterodactyloid pterosaur. This is consistent with current understanding of pterosaur evolutionary history in that although basal 'rhamphorhynchoid' pterosaurs may have persisted into the Early Cretaceous (Unwin, Lü & Bakhurina, 2000), they are certainly not known from the Late Cretaceous period.

Two major pterodactyloid clades, Ornithocheiroidea and Azhdarchoidea, are known from the Upper Cretaceous and appear to have been present throughout this interval (Unwin, 2002; Unwin, Lü & Bakhurina, 2000). Toothed ornithocheiroids (*Istiodactylus* (Howse, Milner & Martill, 2001) and Ornithocheiridae) are not certainly known from horizons younger than the Cenomanian (D. Unwin, unpub. data), and only two ornithocheiroid genera, *Pteranodon* and *Nyctosaurus*, both edentulous, are known to have been present in the Santonian–basal Campanian (Wellnhofer, 1991).

Known individuals of *Nyctosaurus* are too small to have produced the Uhangri tracks; moreover, according to Bennett (2000), manus digits I–III may have been lost in this pterosaur, which would firmly exclude it as the Uhangri track-maker. In *Pteranodon*, the metatarsals and pedal digits are long, slender structures (Eaton, 1910) whereas manus digits I–III are much more robustly built. By contrast, the manus and pes prints at Uhangri do not appear to show this degree of disparity, although the broad appearance of the pes in some prints could have been achieved by adduction of the metatarsals and digits. More significantly, in *Pteranodon*, manus digit III is only slightly longer than digit two (Eaton, 1910; Bennett, 2001), whereas in the Uhangri track-maker, digit III seems to have been substantially longer than digit II, even taking into account possible differences in the positioning of the manus digits during print formation. In addition, in *Pteranodon* pes digit III is more than two-thirds the length of metatarsal III (Bennett, 2001), whereas in the Uhangri tracks, the central digits, including digit III, appear to have been only about half the length of the metatarsus (Fig. 4). Moreover, the disparity in digit length in *Pteranodon* (Eaton, 1910; Bennett, 2001) is likely to have resulted in pes impressions that tapered anteriorly, whereas the pes impressions at Uhangri are frequently rounded, indicating that the pedal digits of the print-maker terminated at about the same level, though preservation may have been a complicating factor. Finally, while it seems likely that the largest known individuals of *Pteranodon*, with wingspans of 6–7 m (Bennett, 2001), were capable of generating pes impressions in the region of 200–250 mm

long, it is clear that *Pteranodon* did not reach sizes sufficient to produce the largest prints seen at Uhangri. Upper Cretaceous ornithocheiroids can thus be excluded as likely producers of the *Haenamichnus* type of pterosaur track.

Azhdarchoids include the Tapejaridae, currently known only from the Aptian–Albian (Wellnhofer, 1991; Unwin, Lü & Bakhurina, 2000) and possibly the Cenomanian (Wellnhofer & Buffetaut, 1998), and the Azhdarchidae, which appear to be present in the late Lower Cretaceous (e.g. Martill & Frey, 1999) and are well known from the Upper Cretaceous, particularly the Campanian and Maastrichtian where practically all body fossils appear to be assignable to this taxon (e.g. Unwin & Lü, 1997).

The Uhangri tracks show a good match with the skeletal morphology of azhdarchids, in so far as it is known. In azhdarchids such as *Zhejiangopterus* (Cai & Wei, 1994; Unwin & Lü, 1997) manus digits I–III and pedal digits I–IV show a similar degree of robustness and are likely to have left prints of similar dimensions, as is evident in the Uhangri tracks. Additionally, the central digits of the pes (II and III) are only a little more than half the length of the metatarsus, as also appears to be the case in the Uhangri tracks.

A complete pes is currently unknown for any azhdarchid, but is preserved in an azhdarchoid from the Crato limestone Formation of Brazil (Frey & Tischlinger, 2000). A distinctive feature of this pes is that the distal ends of digits I–IV terminate at about the same level. The pes of *Zhejiangopterus* is incompletely preserved, but, in so far as comparisons can be made, it is very similar to the pes of the Brazilian azhdarchoid. Presuming, therefore, that the pedal digits of azhdarchids terminated at about the same level, their pes is likely to have left an impression with a relatively round anterior margin, as is seen in many of the Uhangri tracks.

Finally, the typical foot print size seen at Uhangri (200–220 mm) is consistent with an azhdarchid wingspan of 5–6 m, and individuals of at least this size have been reported from a number of Upper Cretaceous localities (Wellnhofer, 1991). Moreover, giant individuals capable of generating footprints in the region of 350 mm in length have been reported from the Upper Cretaceous of Texas (Lawson, 1975; Langston, 1981), Canada (Currie & Russell, 1982), Jordan (Frey & Martill, 1996; Martill *et al.* 1998) and Spain (Ruiz-Omeñaca, Pereda-Suberbiola & Company, 2000).

We argue for the present, therefore, that the pterosaur tracks at Uhangri may have been made by azhdarchids, because the size, proportions and features of the tracks left by azhdarchids, as reconstructed from their skeletal anatomy, show a much better match with the Uhangri tracks than those for *Pteranodon* or, indeed, for other ornithocheiroids. This conclusion is consistent with an earlier, preliminary study of the Uhangri

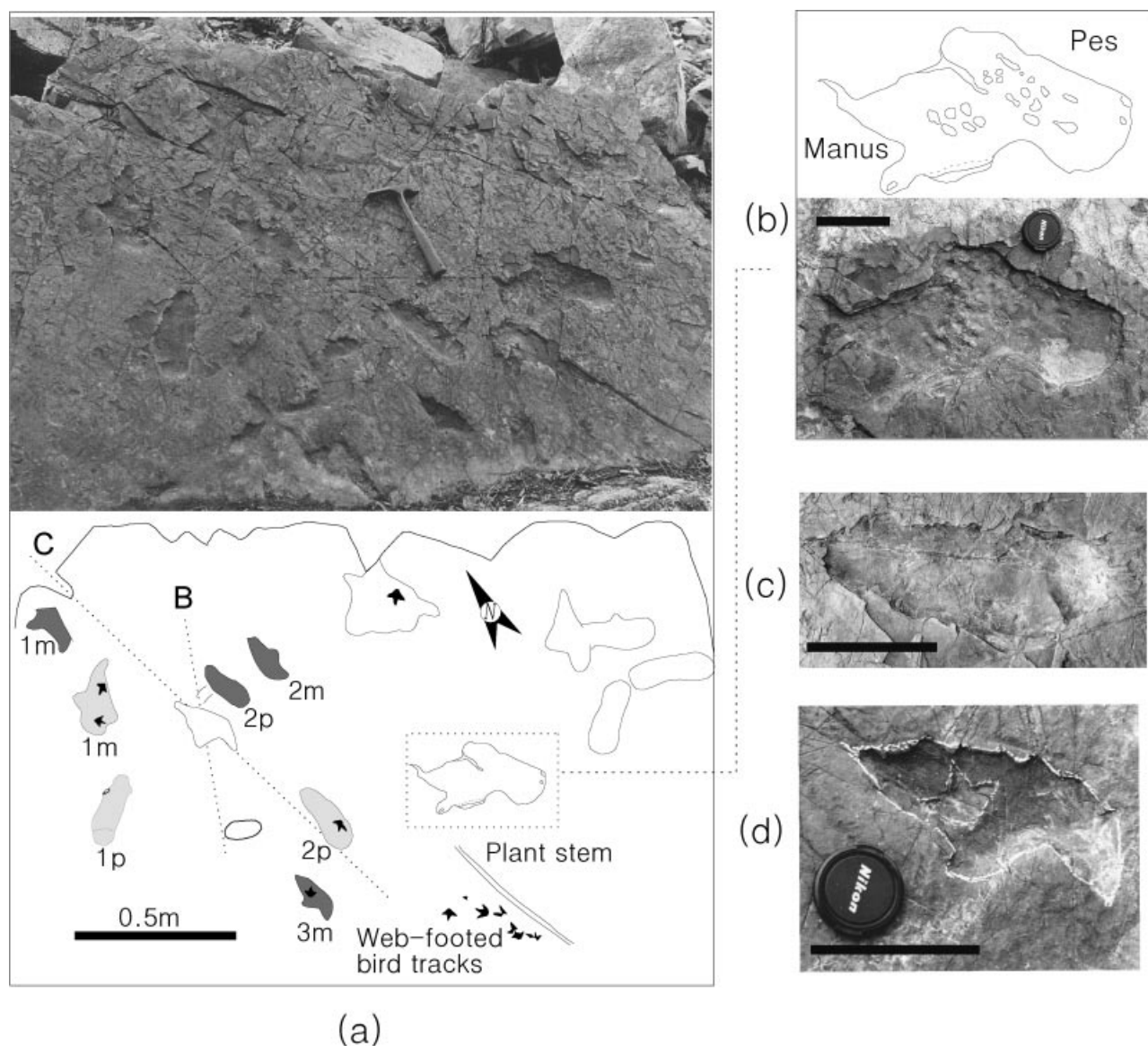


Figure 7. (a) Photograph and map of site P4 (CNUPH.P4) showing a relatively wide, irregularly exposed trackway. Two principal trackways (B and C) are highlighted in different shades; dashed lines indicate the trackway midline. (b) Well-preserved right pes impression which slightly overlaps the manus. (c) 1st right pes impression, track B, showing the round posterior projections. (d) 3rd right manus impression associated with a well-preserved print of a web-footed bird. Scale bar in (b–d) represents 100 mm.

tracks, which also tentatively identified the track-maker as an azhdarchid pterosaur (Lockley *et al.* 1997).

5. Discussion

The Uhangri pterosaur tracks provide a variety of new insights into pterosaur biology, including pterosaur anatomy, the terrestrial ability of large pterodactyls and pterosaur ecology. They also form an important addition to the fossil record of pterosaur tracks and, in combination with other records, further emphasize the remarkable congruency between the track and body fossil record.

5.a. Pterosaur anatomy

An interesting feature of the Uhangri tracks is the rounded anterior termination of the pedal impressions, and the lack of any distinct outlines of the digits. Some bird tracks inside the pterosaur tracks are less clear than those outside the latter. This means that the mud inside the pterosaur tracks was soft and wet. It might be supposed that these features could be attributed to preservational factors, such as obliteration of the digit impressions by submersion seepage or water flow, or as a result of the relative deepness of the impressions compared to pterosaur prints from other sites. These explanations are not entirely satisfactory,

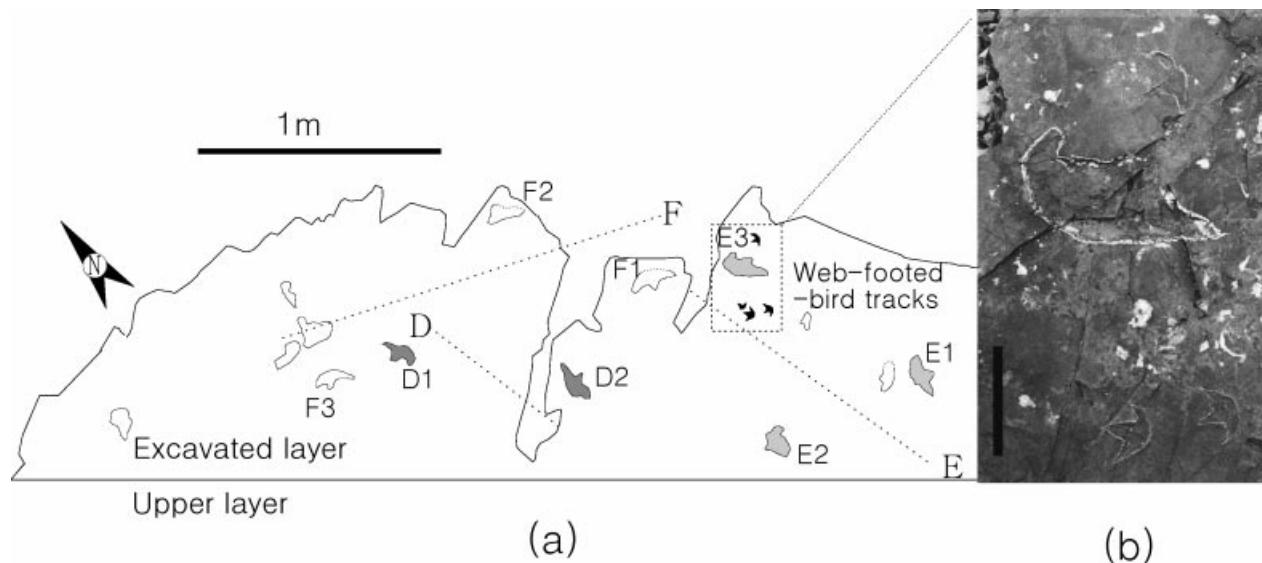


Figure 8. (a) Detailed map of the manus-only trackway, site P1. Three distinctive manus-only trackways have been found; trackway D, trackway E and trackway F. Much of this site is covered by tracks of web-footed birds. (b) Right pterosaur manus print associated with well-preserved tracks of web-footed birds (scale bar = 100 mm).

however, because the prints are moderately well formed with clear margins, and typically reach only a depth of 10 mm. Moreover, many tracks of web-footed birds, some superimposed on the pterosaur prints (Yang *et al.* 1997), are found on the same horizon, indicating that there was little disturbance of the pterosaur tracks after the track-maker had passed by (Figs 7d, 8b). Most importantly, even though there are a large number of pes prints, covering an area of more than 200 m², they consistently lack digit impressions. This suggests that the print morphology could be related to an anatomical feature rather than preservational factors, which are likely to have resulted in far greater variation in print morphology.

We propose, instead, that the pes print morphology indicates that the track-makers may have had webbed feet. Webbing would explain the lack of digit outlines, exactly as is seen in the prints of web-footed birds from the same locality and track-bearing horizon (Yang *et al.* 1997). Pterosaur pes prints with what has also been interpreted as webbing, have recently been reported from the Upper Jurassic site of Crayssac (Mazin & Hantzpergue, 1999; Billon-Bruyat & Mazin, 2001), but have not yet been described in detail, while 'faint traces of interdigital webbing' were also mentioned by Lockley *et al.* (1995) in their description of the prints of *Pteraichnus stokesi*. Our interpretation of the Haenam prints is also supported by evidence of foot webbing in the pterosaur body fossil record. Exceptionally well-preserved remains of *Pterodactylus* from the Upper Jurassic Solnhofen Limestone, that show evidence of soft tissues, appear to have webbing between pedal digits I–IV (Wellnhofer, 1970; Frey & Tischlinger, 2000). Moreover, illustrations of the webbed pes of this pterosaur show a similar outline to

the Uhangri pes prints (Figs 6b, 7b). Apart from *Pterodactylus*, webbing of the pes also appears to be present in the 'rhamphorhynchoids' *Sordes* (D. Unwin, unpub. data) and *Rhamphorhynchus* (Wellnhofer, 1975), and, most significantly, in an azhdarchoid from the Crato limestone Formation of Brazil (Frey & Tischlinger, 2000). As the Uhangri print-maker appears to have been an azhdarchid, the presence of webbed feet in a related form lends support to our interpretation of these tracks as those of a web-footed azhdarchid.

Like the pes prints, the manus prints at Uhangri also often appear as single, irregularly shaped, wide impressions, without clear evidence of the digits, other than where represented by claw marks that project from the margins of the impressions (e.g. Figs 6b, e, 7b). Following the same line of reasoning as for the pes prints above, we suggest that webs of skin may have been present between manus digits I and II, and II and III of the Uhangri print-maker. Such soft tissue structures have not been reported so far in pterosaurs, but appear to be present in an azhdarchoid from Brazil (Frey & Tischlinger, 2000). Interestingly, although digit outlines are clearly preserved in the prints of *Pteraichnus saltwashensis* there is also some evidence for the presence of webs of skin between manus digits I and II, and II and III, as is most clearly seen in the single manus print illustrated by Wellnhofer (1991, p. 158).

5.b. Pterosaur terrestrial locomotion

An important feature of the Uhangri tracks is the insight they provide into the stance and gait of large Late Cretaceous pterosaurs, possibly azhdarchids

if the identification of the print-maker is correct, as morphology and geological age suggest. It is clear from the Uhangri ichnites that the track-maker was a quadrupedal plantigrade, with a near fully erect stance and gait. Moreover, although details of the manus and pes prints distinguish the Uhangri tracks from other pterosaur ichnites, the orientation of the manus and pes with regard to the midline of the track, the relative lengths of the pace and stride, and the relative width of the tracks, are remarkably similar to the corresponding components of other pterosaur trackways. This suggests that the Uhangri track-maker locomoted in a similar fashion to other pterosaur track-makers which have also been reconstructed as quadrupedal plantigrades, with the limbs held in a near fully erect position (Bennett, 1997; Unwin, 1997).

In the Uhangri Formation, manus-only pterosaur trackways were found at site P1 on the same horizon as other quadrupedal trackways (Fig. 8). Manus-only, or manus-dominated, bipedal trackways, which have also been reported from the Lower Cretaceous Oncala Group of Spain (Mejide Fuentes, 2001) and the Summerville Formation of Utah, have been explained as artefacts of preservation (Lockley *et al.* 1995) and linked to a mass distribution in which most of the body weight is supported by the forelimbs (Unwin, 1997).

In the Uhangri tracksite, the tracks of web-footed birds are found together with pterosaur tracks on sediment surfaces that show few mud cracks, indicating that pterosaurs and birds walked across the same slightly wet surface (Figs 7d, 8b). It seems puzzling that birds should have produced prints, whereas the pterosaur pes did not. It needs further study to solve this problem.

5.c. Pterosaur palaeoecology

The Uhangri track site is the first locality where tracks of pterosaurs, birds and dinosaurs occur together on the same surface, although the co-occurrence of pterosaur and bird tracks has also been reported from the North Horn Formation of Utah (Lockley, 1999) and the Oncala Group of Spain (Fuentes Vidarte, 2001). Many bird tracks have been found in and around the pterosaur tracks at Uhangri (Figs 7d, 8b), from which it can be deduced that birds and pterosaurs either were present simultaneously on the mud flats, or that birds visited the flats very soon after the pterosaurs, sometimes stepping in their tracks. The co-occurrence of skeletal remains of pterosaurs and birds has been reported from a number of localities including the Upper Jurassic Solnhofen Limestone of Bavaria (Wellnhofer, 1983), the Lower Cretaceous Yixian Formation of Liaoning, China (Wang *et al.* 1998), the Crato Formation of Brazil (Martill, 1993; Martill & Frey, 1998; Martill & Davis, 2001), the Cambridge Greensand of England (Seeley, 1869), the

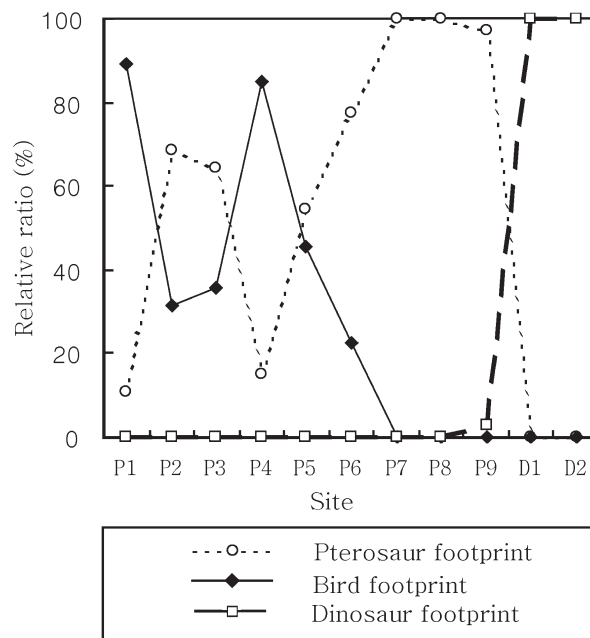


Figure 9. Relative incidence of vertebrate footprints (pterosaurs, birds, and dinosaurs) from various sites at Uhangri.

Upper Cretaceous Beleuta Formation of Uzbekistan (Bakhurina & Unwin, 1995) and Niobrara Chalk of western North America. The traces from the Uhangri and North Horn formations (Lockley, 1999) and the Oncala Group (Fuentes Vidarte, 2001) provide the first clear evidence that pterosaurs and birds inhabited, or at least visited the same environments. It also seems probable that, because of their large disparity in size, the two taxa occupied rather different ecological niches and thus, in this instance, were not in direct competition.

A broader assessment of the vertebrate tracks at Uhangri shows that even though all tracks are found on the same surface, the pterosaur and bird tracks appear together in the west, while dinosaur tracks appear alone in the east (Fig. 9). This disjunction might reflect different habitat preferences, but it could also be related to the suitability of the substrate for locomotion. Web-footed birds and pterosaurs were probably able to move across sediments that were too soft to support heavier animals such as dinosaurs.

5.d. The pterosaur track record

The Uhangri tracks represent a valuable addition to the pterosaur ichnological fossil record. An important feature of the tracks is their relative size. Until their discovery, the largest known tracks were those of *Purbeckopus*, which with dimensions of 187–225 mm, are of a similar size to the common print type at Uhangri (Table 1). The largest prints at Uhangri far exceed in size any prints found so far, but are con-

sistent with the largest known pterosaurs, which also date from the Upper Cretaceous (Lawson, 1975; Langston, 1981; Currie & Russell, 1982; Frey & Martill, 1996; Martill *et al.* 1998; Company *et al.* 2001).

An interesting aspect of the Uhangri tracks is their distinctness from pterosaur tracks found heretofore. Initial discoveries of pterosaur tracks at a number of sites in the Jurassic of North America suggested a great deal of homogeneity in the basic shape and structure of the hand and foot prints (Unwin, 1997) and in other aspects of the trackways. As the pterosaur track record has expanded, however, through the discovery of new sites and the re-identification of older tracks (see Unwin, 1997, table 1 and references listed above) evidence of morphological diversity has begun to emerge (Lockley, 1999). Thus, while most of the North American tracks can be assigned to the two species of *Pteranichnus*, the Crayssac tracks, which include at least two distinct track types (Mazin & Hantzpergue, 1999), appear to be somewhat different, and the slightly younger *Purbeckopus* is different again, distinguished both by its much larger size and features of the prints (Wright *et al.* 1997).

The Uhangri tracks add to this diversity since they clearly cannot be assigned to any of the named track types, as discussed above, nor do they appear particularly similar to the various unnamed or unassigned tracks reported from Europe and South America.

The challenge in the future will be to match these track types to particular clades of pterosaur. Peters (2000) has suggested that all pterosaur tracks were made by members of the Ctenochasmatidae, a group of filter-feeding pterosaurs restricted to the Upper Jurassic and Lower Cretaceous (Wellnhofer, 1991). This seems extremely doubtful, however, partly because the morphological disparity of pterosaur tracks does not match the known skeletal morphology of ctenochasmatids and partly because members of this group did not achieve very large or giant size and do not appear to have survived beyond the late Early Cretaceous period (Unwin, Lü & Bakhurina, 2000). Consequently, they are unlikely to have been responsible for any Upper Cretaceous pterosaur tracks including those from the Uhangri Formation.

The Uhangri tracks are important in two further respects. They represent the first Asian record for pterosaur tracks (Lockley *et al.* 1997), prior to which they had been reported from Europe and North and South America. This geographic range extension is encouraging, but not necessarily surprising, since pterosaurs are known to have had a world-wide distribution throughout the Jurassic and Cretaceous (Wellnhofer, 1991).

The Uhangri site also represents one of the very few Upper Cretaceous records for pterosaur tracks. The only other records reported so far are from the North Horn Formation of Emery County, Utah (Lockley,

1999), the Blackhawk Formation, also in Emery County (Lockley *et al.* 1995), and possibly also from the Dunvegan Formation, Alberta, Canada (Lockley *et al.* 1995).

5.e. Pterosaur body fossils and tracks: a remarkable degree of congruency

Combined with other records of pterosaur ichnites, the Uhangri tracks further emphasize the remarkable congruency between the pterosaur track record and the history of the group as currently understood from the body fossil record (e.g. Unwin, 2002). All tracks found so far appear to be have been made by pterodactyloid pterosaurs, and have a stratigraphic range that almost exactly matches that of pterodactyloids: Upper Jurassic–Upper Cretaceous. The modest degree of anatomical diversity shown by the manus and pes of pterosaurs (Wellnhofer, 1978) is now also apparent in the track record (Lockley, 1999). Moreover, in some cases, such as the Uhangri tracks, the ichnites show good correspondence with the skeletal anatomy of contemporaneous taxa, probably, in this example, azhdarchids. Incidentally, of the two known Upper Cretaceous pterosaurs, ornithocheiroids are thought to have been albatross-like forms that spent much of their time at sea (Wellnhofer, 1991; Unwin, Lü & Bakhurina, 2000), whereas azhdarchids have been reported from a variety of continental localities (Langston, 1981; Currie & Russell, 1982; Nesov, 1984; Padian, 1984; Cai & Wei, 1994; Padian, de Ricqles & Horner, 1995; Company, Ruiz-Omeñaca & Pereda-Suberbiola, 1999) though they are also known from marine strata (e.g. Frey & Martill, 1996). The expectation that, in the latest Cretaceous, azhdarchids are more likely to have left tracks than ornithocheiroids seems to be borne out by the Uhangri records.

The congruence in size between tracks and taxa is particularly striking. Upper Jurassic pterosaurs are of small to medium size (Wellnhofer, 1978, 1991), as are Upper Jurassic tracks (Lockley *et al.* 1995; Bennett, 1997; Unwin, 1997), Lower Cretaceous pterosaurs reached large sizes (Wellnhofer, 1991; Unwin, 2001), as do some of the tracks (Wright *et al.* 1997), and tracks of giant pterosaurs occur in the uppermost Cretaceous (Lockley *et al.* 1997; this paper) at the same time as giant azhdarchids (Lawson, 1975; Langston, 1981; Currie & Russell, 1982; Frey & Martill, 1996; Martill *et al.* 1998). Some Upper Cretaceous pterosaurs were of only medium size (Cai & Wei, 1994; Padian, De Ricqles, & Horner, 1995), but tracks of medium-sized pterosaurs have also been found in this interval (Lockley, 1999).

6. Conclusions

A large series of pterosaur ichnites at Uhangri represent a distinct type of track named here as *Haena-*

michnus. Anatomical comparisons suggest that the print-maker may have been an azhdarchid pterosaur. Details of the prints suggest that the pes and possibly the manus bore webs of skin between the digits. This is consistent with rare examples of soft tissue evidence from the body fossil record. The tracks also show that at least one clade of large-giant Late Cretaceous pterosaurs had a quadrupedal, plantigrade stance and gait, as seems to be the case for other pterodactyloid pterosaurs. The Uhangri site also shows that birds and pterosaurs inhabited the same environments, but probably occupied distinct ecological niches. Finally, the Uhangri tracks provide further evidence for a remarkable degree of congruency between pterosaur tracks and the pterosaur body fossil record.

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