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DAVID W. E. HONE & ERIC BUFFETAUT (Guest Editors)

**Flugsaurier: pterosaur papers in honour of
Peter Wellnhofer**

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Flugsaurier: pterosaur papers in honour of Peter Wellnhofer

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Umschlagbild: Reconstitution of a *Rhamphorhynchus* from the Upper Jurassic of Eichstätt, Bavaria. Concept: P. Wellnhofer;
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A global overview of pterosaur ichnology: tracksite distribution in space and time

By

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Abstract

At least 50 pterosaur track sites have been reported from Late Jurassic through Late Cretaceous localities in North America, Europe, East Asia and South America, plus one possible site from north Africa. Tracks from these sites have been assigned to 11 ichnospecies in four ichnogenera. Of these, *Pterainchus* is by far the most prevalent, well-preserved, and represented by multiple (presently eight) ichnospecies. The majority of *Pterainchus* tracksites are Late Jurassic or earliest Cretaceous (Berriasian) in age. In contrast, the other three ichnogenera – *Purbeckopus*, *Haenamichnus* and possibly *Agadirichnus* – are all represented by single ichnospecies from single localities and are based on relatively poorly-preserved, earliest through latest Cretaceous material. At least 16 Late Jurassic, well-preserved *Pterainchus* samples from marginal marine deposits in western North America are dominated by small tracks (pes length ~2–10 cm), often in trackways. The two ichnospecies from this region (*P. saltwashensis* and *P. stokesi*) are both based on trackway segments and differ in style of preservation. Other Late Jurassic trackways from marginal marine deposits in France and Poland are also small (pes length typically ~3–5 cm); much larger tracks (pes length 18 cm) are known from a single locality in Asturias, Spain. It is unclear whether most *Pterainchus* represent pterodactyloid or “rhamphorhynchoid” pterosaurs because the diagnostic impressions of pedal digit V are rarely clearly and unambiguously impressed. Six basal Cretaceous (Berriasian) *Pterainchus* ichnospecies from at least a dozen sites in Soria, Spain are also mostly small (footprint length ~1–5 cm) and based on as yet insufficiently described, isolated footprints, not trackways. As a result, several of these ichnospecies are probably *nomina dubia*. The contemporaneous *Purbeckopus* from England is much larger (foot length ~19–22 cm). Although small, *Pterainchus*-like tracks have been reported sporadically from the post-Berriasian Cretaceous, most are much larger (foot length 10–20 cm) and, in the case of *Haenamichnus* from Korea, reach 30–33 cm. It is unclear

whether *Agadirichnus* from the Late Cretaceous of Morocco (foot length 10–12 cm) is pterosaurian. Most Cretaceous sites represent lacustrine, not marginal marine, habitats. Both Jurassic and Cretaceous assemblages often contain very high track densities and a range of track sizes associated with invertebrate traces. This suggests that diverse pterosaurian flocks may have congregated in large numbers to feed. Some assemblages reveal swim tracks that suggest pterosaurs floated in shallow water, touching the submerged substrate with only their hind feet. These swim track assemblages also contain possible beak traces that may indicate feeding.

Key words: footprint, *Pterainchus*, paleoecology, behavior

Zusammenfassung

Mindestens 45 Flugsaurier Fahrtenorte vom Obere Jura zur Obere Kreide sind bekannt in Nordamerika, Europa, Fernasien und Südamerika, und ein möglicher Ort in Nordafrika. Fahrten an diesen Orten wurden 11 Ichnospezies in vier Ichnogenera zugeschrieben. Von diesen ist der *Pterainchus* bei weitem der häufigste und am besten präservierte. Er ist vertreten von mehreren (augenblicklich acht) Ichnospezies. Die Mehrzahl der *Pterainchus* Fahrtenorte stammen vom Obere Jura oder der beginnenden Unteren Kreide (Berriasian). Im Vergleich sind die anderen drei Ichnogenera – *Purbeckopus*, *Haenamichnus* und möglicherweise *Agadirichnus* – von einzelnen Ichnospezies an einzelnen Fundorten vertreten und basieren auf relativ schlecht erhaltenem Material datierend von der frühen bis zur späten Kreide. Mindestens 16 guterhaltene *Pterainchus* Abdrücke vom Obere Jura in seitlichen Meeresablagerungen im westlichen Nordamerika werden von kleinen Abdrücken dominiert (Fusslänge 2–10 cm). Sie erscheinen häufig in Trampelpfaden. Die beiden Ichnospezies in dieser Region (*P. saltwashensis* und *P. stokesi*) basieren beide auf Trampelpfadsegmenten und unterscheiden sich im Erhaltungszustand. Andere Obere

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Jura Trampelpfade von Strandablagerungen in Frankreich und Polen sind auch klein (Fusslänge typischerweise 3–5 cm); viel grössere Abdrücke (Fusslänge 18 cm) sind nur bekannt an einem einzigen Ort in Asturien, Spanien. Es ist nicht klar, ob die meisten *Pteraichnus* die Kurzschwanzflugsaurier oder „Langschwanzflugsaurier“ vertreten, da die diagnostischen Abdrücke der Fusszehe V selten klar und unverwechselbar abgedrückt sind. Sechs *Pteraichnus* Ichnospezies der Unteren Kreide von mindestens zwölf Orten in Soria, Spanien, sind auch meist klein (Fussabdruckslänge 1–5 cm) und basieren auf noch unzulänglich beschriebenen, isolierten Fussabdrücken, nicht Trampelpfaden. Daher sind viele dieser Ichnospezies wahrscheinlich *nomina dubia*. Der zeitgleiche *Purbeckopus* aus England ist viel grösser (Fusslänge 19–22 cm). Obgleich sie klein sind, *Pteraichnus*-ähnliche Abdrücke von der post-Berriasian Kreide wurden gelegentlich gemeldet. Die meisten sind viel grösser (Fusslänge 10–20 cm) und, im Fall der *Haenamichnus* in Korea, 30–33 cm lang. Es ist nicht klar, ob *Agadirichnus* der Obere Kreide in Marokko (Fusslänge 10–12 cm) ein Pterosaurier ist. Die meisten Kreidefundorte stellen Lakustrine, und nicht Strandhabitate dar. Die Ansammlungen des sowohl Jura als auch der Kreide beinhalten oft eine sehr hohe Abdrucksdichte und eine Spanne von Abdrucksgrössen, die mit Spuren von wirbellosen Tieren in Verbindung gebracht werden. Das deutet darauf hin, dass verschiedene Schwärme von Flugsauriern in grossen Mengen hier zum Fressen zusammengekommen sind. Einige Ansammlungen zeigen Schwimmaabdrücke auf, die bedeuten, dass Flugsaurier sich haben treiben lassen im seichten Wasser, wobei sie das überschwemmte Substratum nur mit ihren Hinterfüssen berührt haben mussten. Diese Schwimmaabdrücke beinhalten auch mögliche Schnabelabdrücke, die auf Fressen hinweisen könnten.

Schlüsselwörter: Fährte, *Pteraichnus*, Paläoökologie, Verhalten

1. Introduction

More than 100 articles, reports and abstracts dealing with purported pterosaur tracks have been published since the 1860s, though the vast majority of these have been published since 1995. As outlined herein, the history of pterosaur ichnology has been controversial, especially in the 1980s and 1990s. Controversy revolved around arguments over whether pterosaurs were quadrupedal, as well-described trackways assigned to *Pteraichnus* (STOKES 1957) indicate, or bipedal, as inferred on theoretical grounds by PADIAN (1983a, 1983b) and PADIAN & OLSEN (1984). Although a few articles continue to dispute the pterosaurian affinity of *Pteraichnus* and *Pteraichnus*-like tracks (PADIAN, 2003), the vast majority of studies recognize the distinctive morphology of pterosaur ichnites as indicative of a pterosaurian origin.

Currently, pterosaur track occurrences span a wide distribution in space and time. As shown in Figure 1, Jurassic tracks are reported from at least 23 localities in North America and Europe (Fig. 1). Cretaceous tracks have also been reported from at least 27 localities distributed across all continents except Antarctica and Australia, although the single, additional African report is dubious. Based on the global distribution of

pterosaur body fossils, this distribution is not unexpected.

Only three well-documented pterosaurian ichnogenera have been described. These include: *Pteraichnus*, which primarily describes small- to medium-size Late Jurassic and Early Cretaceous tracks from multiple assemblages in North America and Europe; *Purbeckopus*, from a single earliest Cretaceous site in England; and *Haenamichnus*, from an Upper Cretaceous site in Korea. A possible fourth ichnogenus, *Agadirichnus*, is poorly known and its pterosaurian affinity remains uncertain.

Track evidence indicates that pterosaurs habitually progressed quadrupedally on the ground and often congregated in large numbers in shoreline habitats. A few tracksites indicate that they sometimes floated in shallow water. The primary purpose of this paper is to provide a brief review of the history of pterosaur track research, compile an updated bibliography, highlight the utility of the growing database, and draw attention to a few issues that are still controversial.

2. History of discovery and debate

The first reported purported pterosaur tracks, from the Solnhofen Limestone of Germany (OPPEL 1862), are probably the traces of limulids (MALZ 1964; WELLNHOFER 1991). The first convincing examples of pterosaurian tracks were reported much more recently from the Upper Jurassic of Arizona by STOKES (1957), who named them *Pteraichnus saltwashensis*. STOKES noted the distinctive shape of the manus impression, with an elongate, posteriorly-directed trace of what he (incorrectly) interpreted as the wing finger (digit IV). Similar tracks from the Upper Jurassic of Wyoming (LOGUE 1977) and Oklahoma (WEST 1978) were recognized not long after and, based on comparison to the Arizona tracks, also interpreted as pterosaurian. Thus, *Pteraichnus* was incorporated into the lexicon of vertebrate ichnology (KUHN 1958, 1964; HAUBOLD 1971, 1984) with no doubts voiced about the affinities of the track makers.

In a controversial and widely-cited paper, PADIAN & OLSEN (1984) proclaimed “The fossil trackway *Pteraichnus*: not pterosaurian, but crocodilian,” and promulgated the idea that pterosaurs were bipedal (PADIAN 1983a, 1983b, 1987). Because no specimens, other than the ichnogenotype, were the subject of this reassessment, the reinterpretation was widely accepted. As a result, known tracks of this type, including *Purbeckopus pentadactylus* from the Upper Jurassic-Lower Cretaceous of England (DELAIR 1963), which was not initially perceived as pterosaurian, were also assumed to be crocodylian (CONRAD et al. 1987; PRINCE & LOCKLEY 1989). During the “renaissance” in vertebrate ichnology in the 1980s, the debate was reviewed (UNWIN 1986, 1987, 1989) and vigorously discussed in the context of reports of “problematic” footprints of purported pterosaurian and/or crocodylian origin ranging in age from Early Jurassic (STOKES 1978; STOKES & MADSEN 1979) to late Early Cretaceous (GILLETTE & THOMAS 1989).

It was not until the mid 1990s that a large number of new tracksites with distinctive *Pteraichnus* or *Pteraichnus*-like traces were reported (LOGUE 1994; LOCKLEY et al. 1995; LOCKLEY & HUNT 1995; MAZIN et al. 1995). This stimulated lively debate at the annual Society of Vertebrate Paleontology meeting (e.g., LOCKLEY & UNWIN 1996), and even made the pages of *Time*

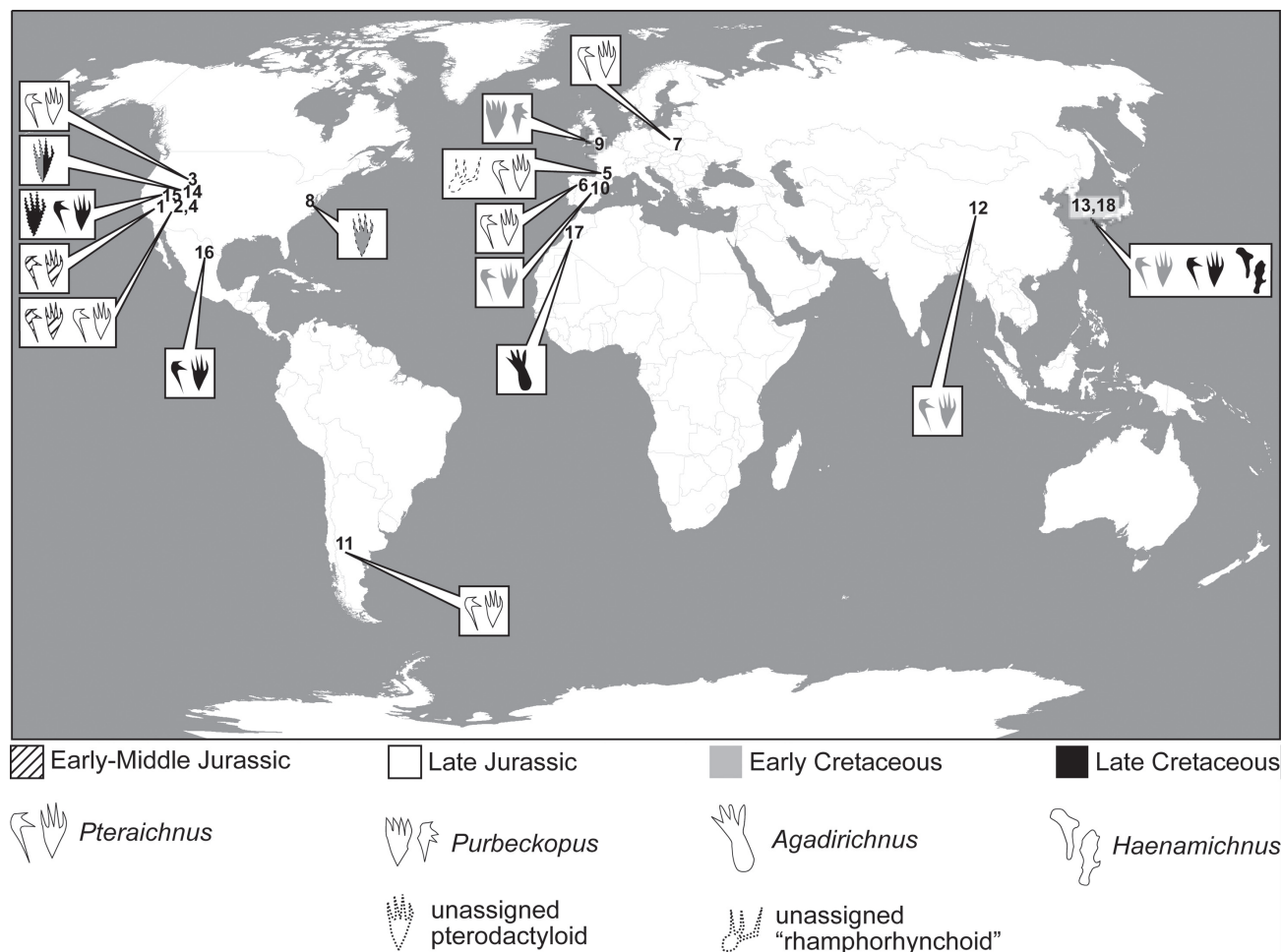


Figure 1: Locality map showing main reported pterosaur tracksites on all continents except Australia and Antarctica. 1 = Aztec Ss., California, USA; 2 = Navajo Ss., Arizona, USA; 3 = Sundance Fm., Wyoming, USA; 4 = Summerville & ?Bluff Ss. fms., Utah & Arizona, USA; 5 = unnamed unit, Crayssac, France; 6 = Lastres Fm., Asturias, Spain; 7 = unnamed unit, Wierzbica, Poland; 8 = Arundel Fm., Maryland, US; 9 = Purbeck Ls. Gp., Dorset, England; 10 = Oncala Gp., Soria + unnamed unit, La Rioja, Spain; 11 = Río Limay Gp., Neuquén, Argentina; 12 = Hekou Gp., Gansu, China; 13 = Haman Fm., Changseon & Sinsu, Korea; 14 = Dakota Gp., Colorado, USA; 15 = North Horn & Blackhawk fms., Utah, USA; 16 = Cerro del Pueblo Fm., Coahuila, Mexico; 17 = unnamed unit, Agadir, Morocco; 18 = Uhangri Fm., Uhangri, Korea. Several of these generalized map locations encompass numerous individual localities.

(NASH 1996) and *Earth* (MILLER, 1997) magazines. The result was a series of new publications on pterosaur tracks from North America (LOCKLEY et al. 1996; LOCKLEY & MICKELSON 1997; LOCKLEY 1998) and Europe (MORATALLA et al. 1994; MAZIN et al. 1997; WRIGHT et al. 1997), as well as the first reports to emerge from South America (CALVO & MORATALLA 1998) and Asia (LOCKLEY et al. 1997). Manus impressions were shown to include traces only of digits I–III (MAZIN et al. 1995), and several pterosaur experts (BENNETT 1997; UNWIN 1997) explicitly endorsed the conclusion that *Pteraichnus* and *Pteraichnus*-like tracks were pterosaurian, indicating quadrupedal progression on land. Such inferences had been reached independently by researchers studying skeletal anatomy and applying functional morphology principles (cf. WELLNHOFFER 1978, 1988, 1991; HAUBOLD 1984). Despite near-unanimous agreement on this subject, one set of morphologically different, purported pterosaurian tracks (GILLETTE & THOMAS 1989) was correctly reinterpreted as crocodylian in origin (UNWIN 1987; BENNETT 1992). PADIAN (1998) continued to defend the notion that *Pteraichnus* tracks pertained to crocodylians.

Nonetheless, explicit and near-unanimous claims for a pterosaurian origin for such tracks, on the basis of morphological, paleoenvironmental (habitat), and paleoecological (ichnofacies) evidence, have appeared in a steady stream of reports published in the last decade (MEIJIDE CALVO & FUENTES VIDARTE 1999; LOCKLEY 1999a, 1999b, 2001, 2002; HUH et al. 2000; LOCKLEY & MEYER 2000; LOCKLEY et al. 2001; CALVO & LOCKLEY 2001; GARCIA RAMOS et al. 2000, 2001, 2002, 2007; PETERS 2001; HAYDEN 2002; HWANG et al. 2002; LOCKLEY & RAINFORTH 2002; PASCUAL ARRIBAS & SANZ PEREZ 2000; FUENTES VIDARTE 2001; MEIJIDE CALVO 2001a, 2001b; MAZIN et al. 2001a, 2001b, 2003; RODRIGUEZ DE LA ROSA 2001, 2003; STANFORD et al. 2002, 2007; BILLON-BRUYAT et al. 2003, 2004; LOCKLEY & WRIGHT 2003; BILBEY et al. 2004, 2005; FUENTES VIDARTE et al. 2004a, 2004b; MICKELSON et al. 2004, 2006; PIENKOWSKI & NIEDZWIEDSKI 2005; CHATTERJEE & TEMPLIN 2006; CONNELLY 2006; KIM et al. 2006; LEE & LEE 2006; LUCAS et al. 2006; ZHANG et al. 2006; LOGUE 2007). Despite this landslide of pterosaur track reports, PADIAN (2003) continued to resist the pterosaurian interpretation in most cases.



Figure 2: Photograph of rubber mold of manus pes set of *Pteraichnus stokesi* holotype from Upper Jurassic of Wyoming (see LOCKLEY et al. 1995: figs 1 and 2). Manus 7 cm long.

In an historically-interesting paper, BILLON-BRUYAT & MAZIN (2003) made the radical suggestion that the African Cretaceous ichnogenus *Agadirichnus*, which AMBROGGI & LAPPARENT (1954) described as possibly having been made by a lizard, may constitute a subjective senior synonym of *Pteraichnus*. As discussed below, although this paper has the merit of encouraging caution in the evaluation of pterosaur ichnology, it is too radical in suggesting that all pterosaur tracks belong to a single ichnogenus or ichnospecies and that ichnotaxa should be named in such a way as to reflect the “identity of the trackmaker.”

3. Current state of knowledge

Presumed pterosaurian tracks are now reported from at about 50 localities in Upper Jurassic through Upper Cretaceous deposits from North and South America, Europe, and Asia (see Appendix). To date, all Late Jurassic, and some Cretaceous, tracks have been assigned to the ichnogenus *Pteraichnus*. In contrast, at least two large Cretaceous forms have been assigned



Figure 3: Photograph of *Pteraichnus* manus-pes set (UCM 81961) from the Upper Jurassic of Colorado.

ned to the ichnogenera *Purbeckopus* (WRIGHT et al. 1997) and *Haenamichnus* (HWANG et al. 2002). The latter is the largest pterosaur track type currently known. BILLON-BRUYAT & MAZIN (2003) proposed that the poorly defined ichnospecies *Agadirichnus* AMBROGGI & LAPPARENT (1954), from the Upper Cretaceous of Morocco, might also be pterosaurian in origin.

Most pterosaur tracks assigned to the ichnogenus *Pteraichnus* are small (footprint length less than ~10 cm) and, with rare exceptions as noted below, show relatively little morphological variation. Localities with abundant *Pteraichnus* specimens reported from multiple sites in Arizona, Utah, Colorado, Wyoming, and Oklahoma (Figs 2–4) can be considered part of a large complex of assemblages that yield tracks similar or identical to the “type” material from Arizona. These assemblages all occur at stratigraphic levels that are more or less equivalent to the “type” stratigraphic horizon. As a result, these assemblages are amenable to the paleoecological and paleobiogeographical interpretations outlined below. Similar footprint size ranges are reported for Late Jurassic *Pteraichnus* from France (MAZIN et al. 1995, 1997, 2003) and Poland (PIENKOWSKI & NIEDZWIEDZKI 2005), as well as basal Cretaceous sites from Spain (FUENTES VIDARTE 2001; FUENTES VIDARTE et al. 2004a, 2004b). As discussed below, the ichnotaxonomy of basal Cretaceous *Pteraichnus* tracks from Spain is problematic and under revision at the present time (SÁNCHEZ-HERNÁNDEZ et al. in press; M. BENTON personal communication 2007).

In contrast to *Pteraichnus*, all other presumed or purported pterosaurian ichnogenera (*Purbeckopus*, *Haenamichnus* and *Agadirichnus*) are based on occurrences of large (footprint length ~11–33 cm) tracks from single localities. Ostensibly, if only three localities yield tracks that cannot be assigned to *Pteraichnus*, it appears that there is little discernable variati-



Figure 4: Photograph of multiple *Pteraichnus* tracks (UCM 81962) from the Upper Jurassic of Colorado.

on in the morphology of pterosaurian footprints that is not obviously attributable to extramorphological factors. This inference is consistent with the generally conservative nature of pterosaur postcranial (particularly manual and pedal) morphology, although, as noted below, there are important differences between the pedes of pterodactyloid and “rhamphorhynchoid” pterosaurs that may or may not be evident in footprint morphology. Footprint evidence suggests that the pterosaur footprint is generally conservative and that calls for caution (cf. BILLON-BRUYAT & MAZIN 2003) in the naming of pterosaur tracks should be heeded.

4. Unresolved problems of pterosaur track interpretation

4.1 Identifying the track makers

Although pterosaurian ichnology is still in its relative infancy, known pterosaurian foot (manus and pes) skeletons fit well with the morphology of footprints. This “Cinderella syndrome” (sensu LOCKLEY 1998) encourages most authors to agree that *Pteraichnus*, *Purbeckopus*, and *Haenamichnus* truly represent pterosaurian track makers. Thus, the claim

that *Pteraichnus* is crocodylian (PADIAN & OLSEN 1984) now receives very little support (but see PADIAN 1998, 2003). However, it is important to note that variation in pterosaur track morphology is still poorly understood. This is in part due to perennial problems of preservation. For example, while the type specimens of *Pteraichnus saltwashensis* (STOKES 1957) and *P. stokesi* (LOCKLEY et al. 1995) are relatively well-preserved and based on well-defined trackways, including both manus and pes traces, all other ichnogenera (*Purbeckopus*, *Haenamichnus* and *Agadirichnus*) are based on relatively poorly preserved material that, in the cases of *Purbeckopus* (DELAIR 1963) and *Agadirichnus* (AMBROGGI & LAPPARENT 1954), were erected for isolated tracks (not trackways) by authors that assumed non-pterosaurian origins for the traces. Thus, only *Pteraichnus* and *Haenamichnus* were named by authors cognizant of probable pterosaurian affinities of the ichnites. These were also the only two ichnogenera that were defined on the basis of complete trackway segments, as advocated by preferred ichnotaxonomic procedure (PEABODY 1955; SARJEANT 1989).

Despite the well-known differences in the morphology of the pedes of pterodactyloid and “rhamphorhynchoid” pterosaurs (e.g. WELLNHOFFER 1991), it remains unclear whether such differences, particularly the presence of the plesiomorphic elongate but very delicate digit V in the latter (paraphyletic) group, would register in footprints. Given the apparent role of this digit in supporting the “rhamphorhynchoid” cruropatagium (sensu UNWIN 2006: 300), it is unlikely that this digit normally made contact with the ground. If this was the case, then in the vast majority of circumstances, a terrestrially locomoting “rhamphorhynchoid” would create tracks that would be very difficult, if not impossible, to differentiate from tetradactyl pterodactyloid tracks. However, there are claims of a very few, as-yet undescribed tracks that preserve impressions of “rhamphorhynchoid” digit V traces (MAZIN et al. 2001b; HARRIS et al. 2007; LOCKLEY et al. 2007).

4.2 Lack of convincing, pre-Late Jurassic reports of pterosaurian tracks

Following the interpretations of STOKES (1957) regarding type *Pteraichnus* from the Late Jurassic, unusual tracks from the eolian sandstones of the Lower Jurassic Navajo Formation were also interpreted as pterosaurian (STOKES 1978; STOKES & MADSEN 1979). However, the justification for these interpretations was never detailed. Subsequently, the tracks, which are poorly-preserved and not found in recognizable trackway segments, have been considered most likely not pterosaurian, but instead likely were registered by other quadrupeds, possibly the same as the *Batrachopus* track maker(s) (LEONARDI 1987) or, more probably, synapsids (LOCKLEY & HUNT 1995). Despite this challenge to the “Stokesian” interpretation of pterosaur tracks in desert sand dunes, REYNOLDS & MICKELSON (2006) perpetuated this scenario by interpreting tracks from the roughly correlative eolian Aztec Sandstone of California as pterosaurian. Like the Navajo Sandstone specimens, the Aztec tracks are also very poorly preserved and, in our opinion, lack diagnostic morphological characteristics to support this inference. While a pterosaurian track maker cannot be absolutely ruled out for these tracks, parsimony does not favor that interpretation. We thus infer that despite the fact that the

pterosaur body fossil record extends into the Late Triassic, there are still no unambiguous pterosaur tracks that predate the early Late Jurassic (Summerville and Sundance formations and equivalent occurrences, which date from near the Middle-Late Jurassic boundary).

4.3 Important new finds that have yet to be studied

Among various recently discovered sites, many show great potential for further detailed investigation. These include *Pteraichnus*-like tracks from the Lower Cretaceous Arundel Formation of Maryland, U.S.A. which occur in an unusual geological context, having been twice reworked, once in the Cretaceous and again in the Holocene (STANFORD et al. 2002, 2007). Likewise, tracks reported by PARKER & BALSLEY (1989) from the Upper Cretaceous Blackhawk Formation of Utah may be of pterosaurian origin, but have never been studied in detail, perhaps because they occur in the roofs of coal mines that are dangerous to enter. Confirmation of the existence of Late Cretaceous pterosaur tracks from Utah (North Horn Formation) is given by LOCKLEY (1999b) based on a small collection whose context also requires further study. Recently LOCKLEY et al. (2007) reported the first known occurrence of pterosaur tracks from the mid Cretaceous Dakota Group of Colorado.

The same need for further study applies to tracks from the Upper Jurassic of Asturias, Spain, which occur at a minimum of four stratigraphic levels. One of these ichnofaunas merits special mention because of exceptional preservation (GARCIA RAMOS et al. 2000, 2001, 2002, 2007; PINUELA et al. 2007). Pterosaurian tracks from Lower Cretaceous strata of La Rioja and Cuenca, Spain (LOCKLEY et al. 1992, 1995; MORATALLA 1993; MORATALLA et al. 1995) are also in need of careful restudy to determine the significance of multiple sites (see Appendix) and to assess the ichnotaxonomic validity of the six purported *Pteraichnus* ichnospecies discussed below.

As observed directly by one of us (M.G.L.), conjectural reports about giant pterosaurian tracks from the Upper Cretaceous Cerro del Pueblo Formation of Mexico (MEYER et al. 2005; KLEEMAN 2005) appear to have been based on incorrect interpretations of poorly preserved dinosaur tracks.

4.4 Preservation and implications for ichnotaxonomy

4.4.1 Exceptional preservation

Recent discoveries at one of four pterosaur tracksites from the Upper Jurassic of Asturias, Spain (GARCIA RAMOS et al. 2000, 2001, 2002, 2007) show that a large (footprint length ~18 cm) pterosaur species had well-developed interdigital webbing on the pes and a distinctive pattern of skin impressions (Fig. 5). Similar web traces were observed in much smaller pes prints from the Summerville Formation of Utah that are indistinguishable from typical *Pteraichnus* pes prints but that also possess very clear traces of pes digit V, strongly indicative of a “rhamphorhynchoid” track maker. Interdigital webbing is known from pterosaur body fossils (e.g. FREY et al. 2003), but has not been so clearly preserved in trace fossils before.

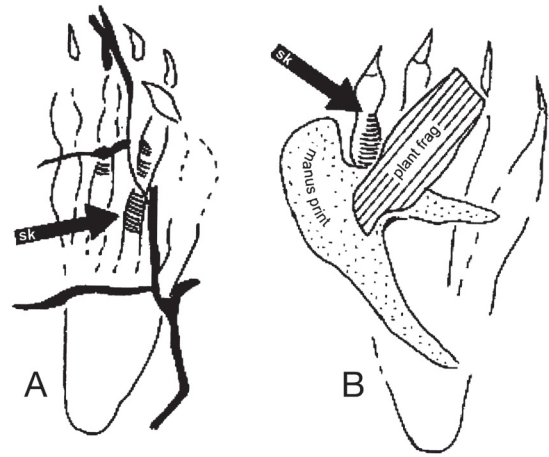


Figure 5: Line drawings of pterosaur tracks with skin impressions (sk). A shows pes, and B shows overprinted manus-pes set (with plant fossil). Modified from GARCIA RAMOS et al. (2001, 2002, 2007).

Such finds are very valuable in shedding light on the morphology of pterosaur pedes, and hold the promise for detailed ichnotaxonomic description. However, such material also creates dilemmas for the ichnotaxonomist: should one name a new ichnospecies on the basis of a track that has five digit impressions rather than four knowing that tetradactyl tracks may represent incompletely impressed pentadactyl pes prints? The dilemma permits two solutions, neither of which is ideal. The first option would be to name a new track based on the presence of fine and diagnostic detail such as webbing and skin traces (in, for example, the large Asturias tracks) not found in other tracks. In our opinion, such naming is justified in order to describe and distinguish new morphological details. This is not to say that this first approach *must* be adopted, and so authors should be cognizant of possible synonymy (or the desire of other ichnotaxonomists to synonymize: cf., BILLON-BRUYAT & MAZIN 2003). The second approach argues more cautiously that the tracks are just well-preserved examples of large *Pteraichnus*-like footprints, and so should not be named separately from existing ichnotaxa. The drawback of this approach is that it assumes that the morphologies of poorly-preserved tracks (including those already named) from one sample and stratigraphic unit, necessarily render them indistinguishable from well-preserved tracks (which merit naming if genuinely distinct) that come from quite different samples and/or stratigraphic units. It also encourages the questionable perception that the same track maker (or group of track makers) was responsible for all the tracks, and that differences between track specimens are wholly a function of substrate and/or locomotory differences. We consider the former “splitting” approach, which advocates naming distinct, observable morphologies, more fruitful than a “lumping approach” which assumes that newly-discovered, well-preserved material can be synonymized with existing ichnotaxa that are poorly preserved. This latter approach is particularly problematic if the naming of new ichnotaxa is predicated on correlation with the morphology of skeletal taxa (BILLON-BRUYAT & MAZIN 2003).

4.4.2 Poor preservation

We have already indicated that all pterosaurian ichnogenera except *Pteraichnus* are based on poorly preserved material, although *Haenamichnus* is at least based on extensive trackways. BILLON-BRUYAT & MAZIN (2003) suggest that Late Cretaceous *Agadirichnus* (AMBROGGI & LAPPARENT 1954) might be a senior subjective synonym of *Pteraichnus* (STOKES 1957). Nevertheless, BILLON-BRUYAT & MAZIN (2003) faced a dilemma at the ichnogenus level because it is hard to demonstrate the synonymy of *Agadirichnus* and *Pteraichnus* when the former is so poorly preserved and poorly documented.

LOCKLEY et al. (1995) faced a similar dilemma at the ichnospecies level. When erecting *Pteraichnus stokesi* as an ichnotaxon distinct from *P. saltwashensis*, they did so because the former was better preserved and showed morphological detail impossible to discern in the latter. In such cases, however, it may never be possible to demonstrate that the two ichnospecies are the same, though it is easy to show how they differ, even though the differences may be functions of preservation (substrate and/or locomotory variations, inducing extramorphological features in the resultant tracks). Ironically, while BILLON-BRUYAT & MAZIN, (2003) suggested synonymizing *Pteraichnus stokesi* with *P. saltwashensis*, they stated quite clearly (op cit., p. 315) that “ichnospecies should be defined on the print morphology and the relative position of the prints (including the variability due to the track maker’s dynamics).” These were precisely the criteria used by LOCKLEY et al. (1995) in erecting *Pteraichnus stokesi* as an ichnotaxon distinct from *P. saltwashensis*. We refute their proposed synonymy for these reasons (further discussed in the preceding section). To underscore this somewhat intractable problem, we again ask that ichnologists consider the description of actual tracks before making secondary inferences about track maker identity. Does one ignore discernable differences, thereby not formally addressing diagnostic morphological evidence by erecting a new ichnotaxon, or does one assume a pre-existing ichnotaxon (in this case, *P. saltwashensis*) would have shown the more diagnostic features (rendering them indistinguishable from *P. stokesi*) if better preserved? The latter inference requires untestable conjecture.

In the case of the six *Pteraichnus* ichnospecies named from the Lower Cretaceous of Spain (PASCUAL ARRIBAS & SANZ PEREZ 2000; MEJIDE CALVO 2001a, 2001b; FUENTES VIDARTE et al. 2004a, 2004b) (see Appendix), a strong case can be made that most of the ichnospecies are *nomina dubia* because they were not based on well-preserved tracks or trackway segments that were compared with type *Pteraichnus*. These ichnotaxa are currently being revised (SÁNCHEZ-HERNÁNDEZ et al. in press; M. BENTON personal communication 2007). In all cases, following the guidelines of PEABODY (1955) and SARJEANT (1989), it is prudent to remember that there is an important difference between “comparing up” from a poorly preserved type to a well preserved find, in which case naming a new ichnotaxon might be justified on morphological grounds, and “comparing down” from an existing ichnotaxon to a less well-preserved ichnite that might only differ on extramorphological grounds. In the latter case, the ichnite should not be considered diagnostic for the purposes of ichnotaxonomy.

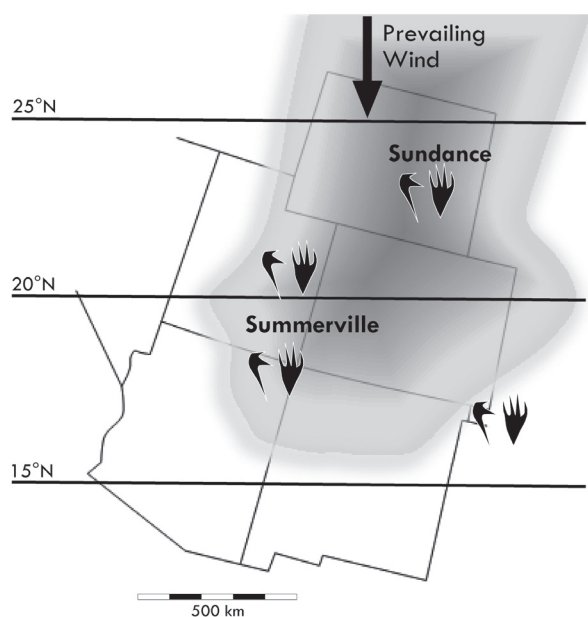


Figure 6: Distribution of *Pteraichnus* in the mid–upper Jurassic of the western U.S.A. is evidently strongly related to the paleogeography of a large marine embayment (after LOCKLEY et al. 1995, 2001, 2007). Compare with Fig. 7.

4.5 Tracks as indicators of pterosaur behavior and paleoecology

Almost all Late Jurassic pterosaur tracks (from North America, France and Poland) are associated with marginal marine deposits, whereas most, if not all, Cretaceous examples are associated with fresh water, fluvio-lacustrine settings (LOCKLEY et al. 1995; LOCKLEY 1998). This may reflect a shift, or at least expansion, of pterosaur paleoecological niches to encompass a broader range of facies and environments in the Cretaceous. This parallels the pterosaur body fossil record as well: Cretaceous pterosaurs occur in a broader range of body sizes, morphologies, and sedimentary environments than in the earlier Mesozoic, though this perception may be at least in part affected by the much larger number of discoveries in Cretaceous strata. The widespread appearance of pterosaur tracks in North America in the early Late Jurassic (probably Late Oxfordian–early Kimmeridgian) seems to coincide with the radiation of pterodactyloid pterosaurs (WELLNHOFFER 1991) although at least a few tracks with digit V traces represent “rhamphorhynchoids.”

Repeat occurrences of pterosaur tracks in similar facies gave rise to the recognition of “*Pteraichnus* ichnofacies,” defined as multiple ichnoassemblages (or ichnocoenoses) with similar ichnotaxonomic compositions (LOCKLEY & MEYER 2000). However, definitions in this field are currently the subject of debate. HUNT & LUCAS (2007) propose redefining most vertebrate ichnofacies as ichnocoenoses, and thus renaming the *Pteraichnus* ichnofacies (sensu LOCKLEY & MEYER 2000; LOCKLEY et al. 2001) as the *Pteraichnus* ichnocoenoses. In either case, there are at least two different facies associations, one carbonate and one clastic (LOCKLEY et al. 2001). Multiple

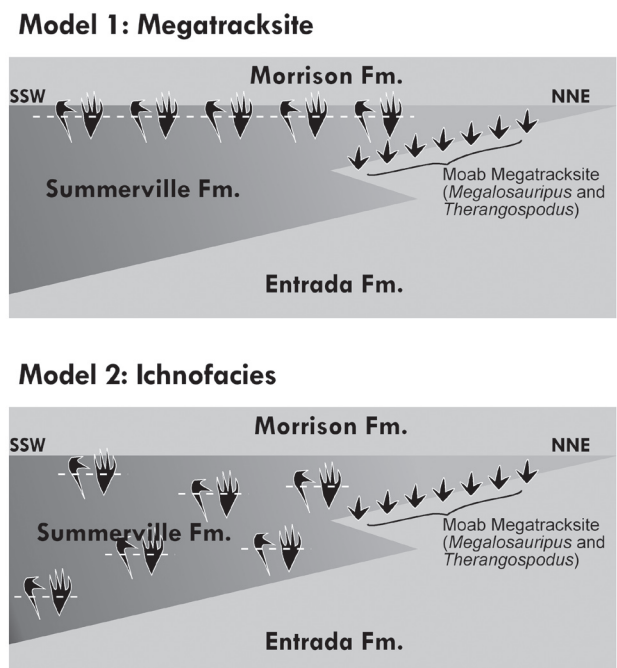


Figure 7: Two models for the stratigraphic distribution of *Pteraidhnus* in the mid-upper Jurassic of the western U.S.A., after MICKELSON et al. (2004). Model 1 suggests dominant stratigraphic control generating a sequence–stratigraphic megatracksite associated with coastal dynamics (aggradation). Model 2 suggests a distribution controlled by pterosaurian facies preference (ichnofacies model).

assemblages from France (MAZIN et al. 1995) also support a *Pteraidhnus* ichnofacies associated with carbonates (LOCKLEY & MEYER 2000), and a similar label may apply to multiple assemblages from Spain.

Ichnocoenosis distributions may have geological as well as paleobiogeographical and paleoecological explanations. For example, the *Pteraidhnus* ichnocoenosis may reflect rising sea-level and increased potential for preservation of track-bearing deposits as coastal sediments aggraded. For example, Late Jurassic *Pteraidhnus*-bearing deposits in the western USA are associated with a relatively narrow stratigraphic interval associated with a large marine embayment. (Fig. 6). This raises the question as to whether the distribution of tracks in space and time is the result of coastal dynamics and sequence stratigraphy, giving rise to a megatracksite (Fig. 7), the result of facies preference on the part of the pterosaurs (ichnofacies model), or a combination of both factors. Ichnofacies (or ichnocoenoses) also reflect evolutionary and paleoecological radiations of pterosaurs under favorable conditions. The majority of pterosaur track reports are consistent with the known distribution of skeletal remains and inferred paleoecology of the clade (i.e. preference for marginal marine lagoons, shallow epeiric seas, and lacustrine environments). Despite these inferences, we acknowledge that the pterosaur record is influenced by taphonomy, as shown by occurrences of fragmentary pterosaur remains in fluvial sediments. Nevertheless, while it is advisable to be cautious about drawing paleoecological conclusions from such a record, footprints represent an in situ record of the activity of track makers. Thus, we are confident in inferring

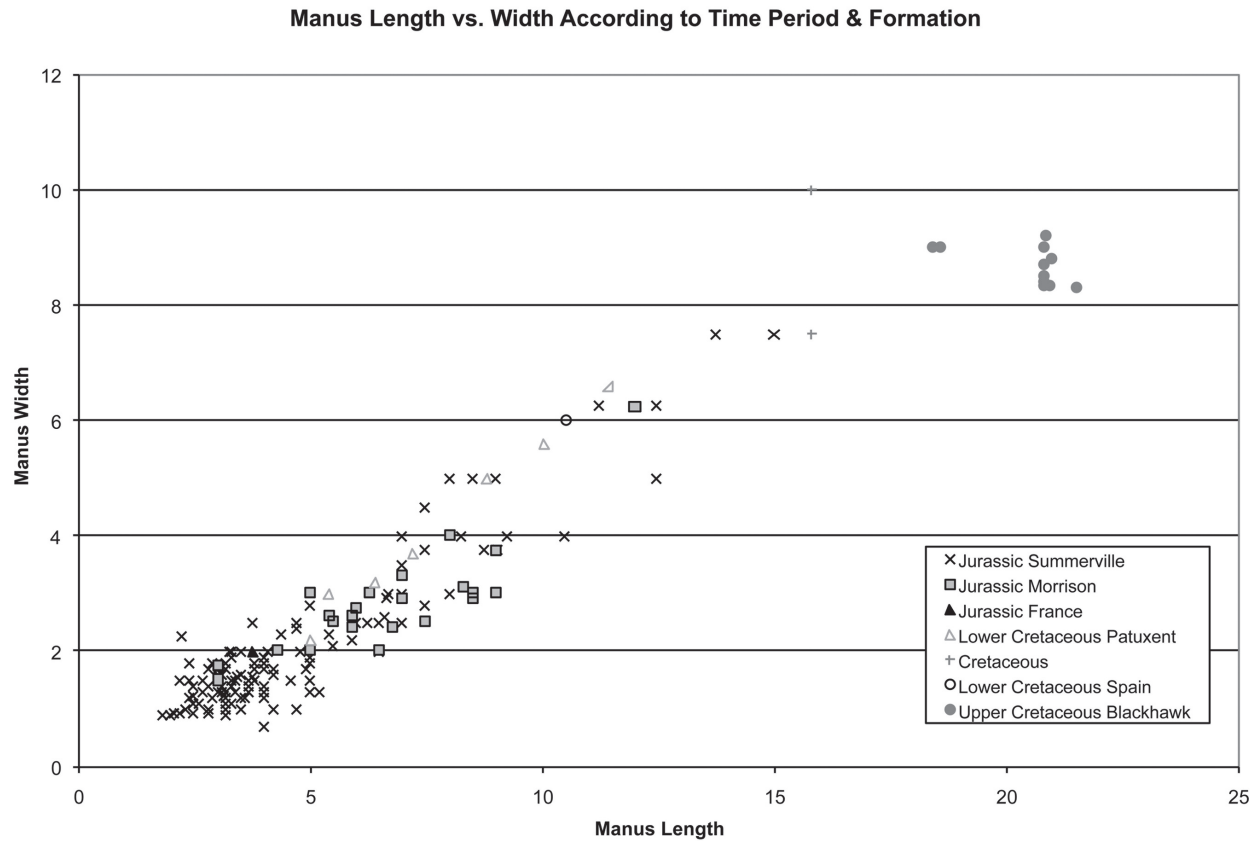


Figure 8: Size frequency distribution for pterosaur track manus size from selected Jurassic and Cretaceous samples.

that the track evidence supports the idea that pterosaurs were gregarious and attracted to broad, shallow water settings (lagoons, embayments, lake basins) where they walked on wet emergent surfaces and may, on occasion, have floated like sea birds in shallow water, probably while feeding (LOCKLEY & WRIGHT 2003; GARCIA-RAMOS et al. 2007).

Given the large size of samples available, there is ample opportunity for morphometric study to determine size ranges, evidence of allometric growth, and other factors. There is clearly a general trend toward increase in maximum track size from the Jurassic to Cretaceous (Fig. 8). However, some samples contain a significant range of track sizes. Some do not: one Asturias sample contains only large tracks, while another contains only small tracks. In contrast, the Maryland sample shows a considerable size range, presumably indicating multiple taxa. In addition to considering size frequency distributions, we can consider whether or not pterosaur tracks occur in “ichno-monospecific” assemblages. This is apparently the case in most Late Jurassic sites in the western USA. However, in other regions, they occur in association with tracks of dinosaurs, birds and other vertebrates, as in samples from Maryland, Korea, and China. Such differences indicate that track assemblages can provide valuable data for reconstructing faunas and establishing baseline paleoecological hypotheses especially in situations where body fossils are scarce or absent.

5. Conclusions

1) In recent years there has been a huge increase in the discoveries and documentation of purported pterosaur tracks. They are now known from four continents: North and South America, Europe, and Asia, and may also occur in Africa. This global distribution complements and corresponds to the known body fossil record.

2) Three definite and one possible ichnogenera are currently recognized: *Pteraichnus*, widely known from the Late Jurassic and Cretaceous, and *Purbeckopus*, *Haenamichnus* and possibly *Agadirichnus*, from restricted occurrences exclusively in the Cretaceous. All three of the later ichnogenera are significantly larger than type *Pteraichnus*. This indicates that increase in maximum size of pterosaurs is identifiable in the track record.

3) Multiple ichnospecies of *Pteraichnus* have been defined, but there is concern that the ichnogenus is over-split, especially with reference to Spanish ichnotaxa.

4) Late Jurassic *Pteraichnus* assemblages are associated with widespread, regionally-extensive facies, especially in marginal marine deposits in North America. Cretaceous pterosaur track occurrences are largely in non-marine facies, perhaps reflecting a shift in or expansion of pterosaur paleoecology. Some pterosaur tracks are associated with sedimentary facies in which their body fossils also occur, though this is not always the case. For example, no tracks are known from the Jehol Biota of northeastern China, although it yields abundant pterosaur body fossils. Therefore, more work is necessary to understand the degree of correspondence of the body and trace fossil records, and the implications for pterosaur paleoecology. Tracks also provide evidence of flock-like, gregarious behavior and swimming/floating/foraging in shallow water. Some assemblages are “monospecific” and indicate individuals that fall in

narrow size ranges.

5) As the present rapid rate of discovery of pterosaur tracksites continues, few track occurrences remain controversial or ambiguous, despite previous controversy. Thus, few researchers doubt the pterosaurian origin of most *Pteraichnus* and *Pteraichnus*-like footprints, or dispute that they walked quadrupedally on land.

6) Despite the growing database, pterosaur ichnotaxonomy is still immature and there is little compelling evidence that large tracks assigned to *Purbeckopus*, *Haenamichnus*, and *Agadirichnus* are markedly different from *Pteraichnus* except in size. However, it would be conjectural and premature to synonymize all four ichnogenera without better evidence that all manifest indistinguishable (and not size-related) morphologies (compare with conclusion 7).

7) New finds of tracks with skin impressions, interdigital web traces, and impressions of digit V offer the possibility of refined ichnological and ichnotaxonomic description as well as recognition that not all tracks were necessarily made exclusively by pterodactyls (compare with conclusion 6).

8) There is still no compelling evidence of pterosaur tracks prior to the Late Jurassic. However, given that pterosaurs are known to have lived prior to the Late Jurassic, such evidence is likely to be found in future and will provide valuable tests of pterosaur behavior, ichnocoenoses/ichnofacies distributions, and paleoecological inferences.

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APPENDIX:

List of global pterosaur tracksites. CNUPH = Chonnam National University, Kwangju, South Korea, DORCM = Dorset County Museum, Dorchester, Dorset, England, KNUE = Korea National University of Education, Cheongwongun, South Korea, MNS = Museo Numantino, Soria, Spain, MP-Z KG = Museum of Przysucha, Geological Collection at Zapniów, Poland, MUCP = Museo de Ciencias Naturales de la Universidad Nacional del Comahue, MUJA = Jurassic Museum of Asturias, Spain, SEP CP = Secretaría de Educación Pública de Coahuila, Mexico, TATE = Tate Museum, Casper College, Casper, UCD = Dinosaur Tracks Museum, University of Colorado at Denver, UCM = University of Colorado Museum of Natural History (UC Boulder), UU = University of Utah, Salt Lake City, UW = University of Wyoming, Laramie; ? = repository (if any) unknown.

AGE	CONTINENT	COUNTRY/ STATE	LOCALITY	FORMATION	SPECIMEN REPOSITORY
JURASSIC	NORTH AMERICA	1 Arizona, USA	<i>Pterainchmus saltwashensis</i> type	Summerville (Morrison?) Fm.	UU
		2	Summerville	Summerville Fm.	UCD
		3 Colorado, USA	Cactus Park	Summerville Fm.	UCD
		4	Furnish Canyon	Summerville Fm.	UCD
		5	Unaweep Canyon	Morrison Fm.	UCM
		6	Colorado National Monument	Summerville Fm.	In field
		7 Oklahoma, USA	Kenton	Morrison Fm.	UCD
		8 Utah, USA	Delmonte Mines	Summerville Fm.	UCD
		9	Starr Springs	Summerville Fm.	UCD
		10	Flaming Gorge	Summerville Fm.	In field
		11	Ferron	Summerville Fm.	UCD, UU
		12	Moab	Summerville Fm.	UCD
		13	Duschene County	Summerville Fm.	UCM
		14 Wyoming, USA	Alcova/Grey Reef Reservoir	Sundance Fm.	TATE, UW
		15	<i>P. stokesi</i> type	Sundance Fm.	UW
		16	Seminole Reservoir	Sundance Fm.	UW
		17	Bighorn Canyon National Recreation Area	Sundance Fm.	?
	EUROPE	18 Spain	Asturias (Quintueles site)	Lastres Fm.	MUJA
		19	Asturias (Oles site)	Lastres Fm.	MUJA
		20	Asturias (Tazones site)	Lastres Fm.	MUJA
		21	Asturias (Luces site)	Lastres Fm.	In field
		22 Poland	Wierzbica, Holy Cross Mtns.	„Wierzbica Oolite and Platy Limestones“	MP-Z KG
		23 France	Crayssac	unnamed	?

AGE	CONTINENT	COUNTRY/ STATE	LOCALITY	FORMATION	SPECIMEN REPOSITORY
CRETACEOUS	NORTH AMERICA	24 Colorado, USA	John Martin Reservoir	Dakota Fm.	UCD
		25 Maryland USA	unnamed	Patuxent Fm., Potomac Gp.	UCD
		26 Utah, USA 27	near North Horn unnamed	Blackhawk Fm. North Horn Fm.	none UCD
		28 Mexico	Saltillo, Coahuila Province	Cerro del Pueblo Fm	SEP CP, UCD
	ASIA	29 Korea 30 31 32	<i>Haenamichnus</i> type Hasandong Sinsu Haman	Uhangri Fm. Hasandong Fm. Haman Fm. Haman Fm.	CNUPH, UCD ? ? KNUE
		33 China	Yanguoxia, Gansu Province	Hekou Gp.	UCD
	EUROPE	34 England	<i>Purbeckopus</i> type	Purbeck Limestone Fm.	DORCM
		35 Spain 36 37 38 39 40 41 42 43	Las Hoyas Santa Cruz de Yanguas Los Tormos (<i>P. palacieisaenzi</i>) type <i>Pteraichnus cidacoi</i> type los Cayos Oncala II Las Aldehuelas II Serrantes II Valdelavilla I (<i>P. vetustior</i> type)	Calizas de la Huérquina Fm. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp.	? ? none none ? ? ? ? none
		44 45 46 47 48 49	Valdelavilla II Valdelavilla III (<i>P. parvus</i> type) Valdelavilla IV Valloria Villar del Rio/Barranco de Serrantes (<i>P. manueli</i> type) Barranco de Serrantes (<i>P. longipodus</i> type)	Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp. Huerteles Allofm., Oncala Gp.	? MNS ? ? none MNS
	SOUTH AMERICA	50 Argentina	Lake Ezequiel Ramos Mexía	Candeleros Mbr., Río Limay Fm.	MUCP
	AFRICA	51 Morocco	<i>Agadirichnus elegans</i> type	unknown	none

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