PTEROSAURIANS AND ?AVIANS FROM THE MORRISON FORMATION (UPPER JURASSIC, WESTERN U.S.)

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Four taxa from the Morrison Formation appear to be validly assigned to pterosaurs: *Dermo-dactylus*, *Laopteryx*, *Comodactylus*, and *Mesadactylus*. The ichnotaxon *Pteraichnus* was not made by a pterosaur, but by a crocodilian; there are as yet no plausible pterosaur tracks reported from the Morrison Formation or anywhere else in the fossil record. "*Palaeopteryx thomsoni*" is an invalid name originally assigned to a specimen from the Morrison Formation identified as avian. Of this and other associated material, most is pterosaurian (*Mesadactylus*), and some is maniraptoran (avian, dromaeosaurian, troodontian) but nothing as yet has been identified as definitely avian. Footprints from horizons below and above the Morrison in the western U.S. have been assigned to birds, but the criteria for this assignment bear close scrutiny.

Keywords: Pterosaurs; Pterodactyloids; "Rhamphorhynchoids"; Avians?; Ichnofossil; Crocodilian

INTRODUCTION

Birds and pterosaurs are normally rare elements of any fossil fauna, because their bones are so thin, so small, and so easily fragmented. Large pterosaurs such as *Pteranodon* are known in some abundance from the shallow Cretaceous seas of the Western Interior, and smaller forms such as *Rhamphorhynchus* and *Pterodactylus* from the quiet lagoon waters of Solnhofen, Germany. These are the exceptions, however. The available fossil record of birds and pterosaurs can only be a small fraction of what lived, because so many kinds of environments in which they must have lived, such as forests, uplands, and open savanna, are poorly represented in the

fossil record, which is skewed towards environments and taxa associated with water (Padian and Clemens, 1985).

The Late Jurassic Morrison Formation of the western U.S. has a rich fauna known from several different types of sedimentary facies (Dodson and others, 1980; Chure and others, this volume), but few remains of pterosaurs or birds have been recovered. At present, there are four validly named genera of pterosaurs (though there is no evidence that three of them are not of the same taxon), and no diagnostic bird remains. The purpose of this note is to review briefly the available evidence and evaluate the condition of the fossil record of Morrison pterosaurs and birds.

PTEROSAURS

Osteological Remains

Marsh (1878) named *Dermodactylus montanus* based on a wing metacarpal from the Morrison Formation of Wyoming. No other remains were identified. The length of the wing metacarpal in relation to its diameter identifies it as pterodactyloid, but no more diagnostic features are present. Hence it would be difficult to refer any additional material to the genus, unless it were additional remains of the same skeleton or very similar bones from the same locality. Jensen and Ostrom (1977) described a proximal wing phalanx of a pterosaur from the Morrison, but more precise identification was frustrated by the incompleteness of the specimen. Galton (1981) identified a pterosaur wing metacarpal in two pieces in a box from Quarry 9, Como Bluff, Wyoming, among other small bones labeled as mammal remains, and named it *Comodactylus ostromi*. This metacarpal is relatively short compared to its diameter and about half as short as pterodactyloid metacarpals are, and its cross-section is more oblong than round (both primitive features of pterosaurs). Galton correctly inferred that it was not from a pterodactyloid, but from the paraphyletic group traditionally referred to as "rhamphorhynchoids." Its large size separates it from most other non-pterodactyloid taxa. *Nesodactylus hesperius* (Colbert, 1969), from the Late Jurassic of Cuba, is the only other known Late Jurassic pterosaur from North America and is very similar to the German *Rhamphorhynchus*. However, like *Dermodactylus*, it would be difficult to refer any additional material to *Comodactylus*.

Jensen and Padian (1989) erected a new genus and species of pterodactyloid, *Mesadactylus ornithosphyos*, based on a synsacrum and referred material from the Dry Mesa Quarry in the Brushy Basin Member of the

Morrison Formation in western Colorado (Miller and others, 1981). Diagnostic pterodactyloid characters include long metacarpals and short tail, as indicated by the reduction in the size of the posterior sacrals and proximal caudals, and the high number of sacrals. Referred material included cervical and dorsal vertebrae, scapulocoracoids, humeri, partial ulnae and radii, metacarpals, phalanges, and femora. Jensen (e.g., 1981a,b) previously identified some of this material as avian and referred it to the new taxon *Palaeopteryx thomsoni*, to the Jurassic bird *Archaeopteryx*, or to an indeterminate avian. Jensen and Padian (1989) showed that the type specimen of *Palaeopteryx* was misidentified by element and taxon; and because, as Molnar (1985) pointed out, this binomen had not been properly diagnosed, we advocated suppressing it in favor of the new taxon with diagnosed and referred material. A complete inventory and publication history of this material is provided in our 1989 paper.

Several years after the latter publication, Dr. Kenneth Carpenter and Mr. Matt Smith were examining the BYU small vertebrate collections from Dry Mesa when they came across the posterior portion of a skull, including a braincase with the skull roof missing, and some cervical vertebral remains, in a drawer labeled "Fishes." They recognized that it was pterosaurian and very kindly forwarded it to me for study. As Jensen and I noted in our 1989 paper, there seems to be only one pterosaurian taxon in the fauna from this locality, and it has clear pterodactyloid characters. If so, then it is possible that the newly discovered cranial and cervical material can also be referred to *Mesadactylus*.

Pterosaur remains from deposits elsewhere in the world that have often been treated as coeval with the Morrison Formation should be considered here for their bearing on biostratigraphy and paleobiogeography. In May 1983 and July 1986, I was fortunate enough to gain access to the collection of pterosaur material from the Tendaguru Beds of Tanzania in the Humboldt-Museum fur Naturkunde, Berlin, thanks to the late Dr. Hermann Jaeger. This material was described briefly by Reck (1931) as *Pterodactylus brancai*. Galton (1980) found a slender tibiotarsus in a box with bones of the ornithopod *Dryosaurus lettowvorbecki* in the Tendaguru collections of the British Museum (Natural History) and recognized it as very similar to Reck's material. But Galton disputed Reck's assignment to the genus *Pterodactylus* because he thought that the proximal tarsals were not fused to the tibia in that genus (whereas they were fused but retained a prominent suture in the genus *Rhamphorhynchus*). Galton found greater fusion of the tarsus in the Chinese pterodactyloid *Dsungaripterus* and the Argentinean pterodactyloid *Puntanipterus* (both from the Lower Cretaceous), so he

referred the Tendaguru material to the new combination *Dsungaripterus?* *brancai* and grouped these three species plus the type species *D. weii* in the Family Dsungaripteridae.

At the time, Galton did not realize that the character of tarsal fusion on which he based his taxonomy is primarily ontogenetic: as in birds, the proximal tarsals of pterosaurs fused to the tibia with adulthood. Preservational conditions can also affect the appearance of these bones. Accordingly, there is no diagnostic basis for his assignment of the Tendaguru material to *Dsungaripterus*, nor for his constitution of the Dsungaripteridae. However, Reck's assignment of the material to *Pterodactylus* in turn appears to be based more on stratigraphic proximity and taxonomic convenience, and a full revision of this material is in order. My own observations of the Tendaguru pterosaurs agree with Reck and Galton that there is only one taxon represented, and it is a pterodactyloid – but not *Pterodactylus*. There are several diagnostic pterodactyloid wing metacarpals, and long cervicals that have very low neural spines and prominent exapophyses, as seen in many pterodactyloids including *Quetzalcoatlus*. These observations have some bearing on the Morrison Formation fauna because the pterosaurs from both Tendaguru and Dry Mesa were collected from the matrix surrounding large dinosaur bones, and only one pterodactyloid seems to be present in both. Furthermore, both localities are high in the Jurassic, and presumably later than the Solnhofen localities, so it may be that "rhamphorhynchoids" had become extinct by that time. It is not possible at present to determine exactly how similar these two taxa may be, but it may turn out that this biostratigraphic datum, tenuous as it is, may support a latest Jurassic Tendaguru–Morrison correlation rather than the Early Cretaceous connections advocated by Galton (1980).

Footprints

Footprints from the Morrison Formation have also been ascribed to pterosaurs, beginning with Stokes' (1957) identification of *Pteraichnus saltwashensis* from the Salt Wash Member of Apache County, Arizona, very low in the Morrison sequence. Similar tracks were later reported from the Navajo Sandstone of Utah (Stokes, 1978; Stokes and Madsen, 1979), and at the top of the Sundance Formation near Alcova, Wyoming (Logue, 1977), just below the Morrison. Padian and Olsen (1984) showed that *Pteraichnus* could not be the track of a pterosaur, for two reasons: first, the manus had five fingers (pterosaurs had four); and second, even if pterosaurs walked quadrupedally (which is unlikely on kinematic grounds: Padian,

1983a), they could not have brought the manus as close to the body as the pes while the forelimb was protracted (Padian, 1983b). Padian and Olsen concluded that the *Pteriachnus* tracks were most likely crocodilian, which we showed by running a small caiman along a muddy surface of clay under varying conditions. We also concluded that other footprints ascribed to pterosaurs on the basis of similarity to the tracks that Stokes (1957) described were also most likely crocodilian. The apparent similarity between crocodile and pterosaur feet is based principally on the four-toed foot, in which the second and third toes are slightly longer than the first and fourth. But there the superficial similarity ends, and unfortunately the original trackbed was too soggy to preserve important details of pha-langeal formula and pes structure that would have provided further infor-mation to determine the original assignment.

In May of 1986, we had a further opportunity to study the Navajo tracks reported by Stokes and Madsen during the field trip in conjunction with the "Dinosaur Tracks and Traces" symposium held in Albuquerque, New Mexico. The slab containing these tracks had been removed to the Moab Museum in Moab, Utah. As Stokes and Madsen (1979) reported, the lithology of the slab indicates deposition under saturated conditions. Again, there is little detail in the individual tracks because the mud slumped into the impressions. Curiously, however, it is possible to trace individual trackways on this slab that, in moving from less competent to more competent spots, resolve a digital pattern from allegedly "pterosaurian" to clearly crocodilian. (If taken at face value, this would qualify as the most rapid instance of macroevolution on record!) These "pterosaurian" trackways may be referable to the crocodilomorph ichnogenus *Batrachopus* (Olsen and Padian, 1986).

Gillette and Thomas (1989) described problematic traces from the Mesa Rica Sandstone (Dakota Group, probably Late Albian) in Clayton Lake State Park, New Mexico, and assigned them tentatively to a pterosaurian trackmaker. Unwin (1989) disagreed with the assignment, and it is admit-tedly difficult to find diagnostic points in its favor – although probably no trackmaker can be ruled out absolutely, given that we do not have com-plete knowledge of the behavior of any fossil animal (or most recent ones). However, there is no clear indication whether this track is of a manus or pes, nor of which three digits of a limb it might represent; and the spatial relations of the tracks to each other present a pattern unmatched by any kinematic process in known animals.

Given that pterosaur bones are found in the Morrison Formation (and have been reported from Late Triassic [e.g., Chatterjee, 1986] and Early

Jurassic [Padian, 1984] sites in western North America), their trackways might be expected in the Morrison as well. However, to date they have not been found. Unwin (1989) agreed with Padian and Olsen (1984) that no tracks reasonably referable to pterosaurs have been found anywhere in the fossil record. He attempted to reconstruct what these tracks would look like, both in a quadrupedal, plantigrade, sprawling position (his Fig. 27.10(A)) and in a bipedal, digitigrade, upright position (his Fig. 27.10(B)). Both reconstructions can be debated in some details, but the bipedal version is perhaps more appropriate to consider because, in my view, more evidence of phylogeny and functional morphology appears to support this position (Padian, 1983b), and no complete consideration of the structure and function of the *entire* pelvic girdle and hindlimb, and the rest of the skeleton, has yet been proposed to contradict it. Unwin (1989, Fig. 27.10(B)) reconstructed the hindfoot tracks as parasagittal, close to the body midline, and digitigrade, but two details may require modification in order to match the prediction of Padian and Olsen (1984: 182) that the tracks of pterosaurs would probably resemble those of birds and small bipedal dinosaurs. First, Unwin reconstructed the pterosaur foot with the fourth digit the longest, followed by the third, second, and first. This lizard-like formula is not typical of pterosaurs and the evidence for it is difficult to substantiate. Usually the third toe is the longest, followed by the second and fourth, which are generally subequal, with the first a bit shorter (Wellnhofer, 1978, Fig. 17, p. 25). This varies with the size of the animal and the phylogenetic position of the taxon. Second, the mesaxonic axis of the foot might as likely be expected to point not outward, but directly forward to slightly inward, as it does in birds and basal dinosaurs, the closest sister taxon to pterosaurs for which footprints are known. Figure 1 shows an approximation of what such pterosaur tracks could be expected to look like.

Finally, with regard to *Pteraichnus* and other Morrison Formation crocodiloid trackways, it is important to affirm with Gillette and Thomas (1989) that, just because this ichnofossil has been shown to be crocodiloid, not pterosaurian, it does not mean that all putative "pterosaurian" tracks are crocodiloid; each track type must be carefully analyzed. To this we should add that there are explicit ways of analyzing trackways in a more meaningful way than simple thought experiments that attempt to match possible morphologies of ichnites and bones. Padian and Olsen stressed Baird's (1957) maxim that a footprint is not a record of anatomy, but a record of behavior of a particular anatomical part under the constraints of kinematics and substrate condition. Analysis of poor tracks, as Baird pointed out, is unlikely to yield zoologically significant information, and the
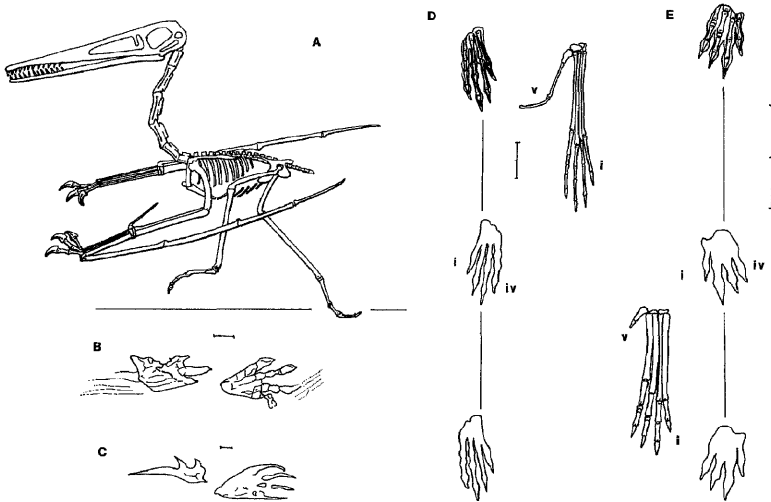
FIGURE 1 (A) Reconstruction of the Late Jurassic pterodactyloid *Pterodactylus* in a running pose; wingspan 20–60 cm. (B) and (C) Comparison of the left manus and pes prints of a small caiman (B) to those of the Morrison Formation crocodylomorph footprint *Pteraichnus* (C) (Stokes, 1957), originally identified as a pterosaur footprint; after Padian and Olsen (1984). *Pteraichnus* is probably a junior synonymof the ichnogenus *Batrachopus*, known from the Early Jurassic through Recent (living crocodilians, as shown in (B), make tracks quite comparable to *Batrachopus*: see Olsen and Padian, 1986). (D) and (E) Reconstructions of the foot skeletons and hypothetical trackways of *Rhamphorhynchus* (D) and *Pterodactylus* (E), in bipedal, parasagittal gait. In actual trackways, the distance between successive footfalls would be much greater, even at low speeds. Note that only the toes are impressed, reflecting a digitigrade stance; the first metatarso-phalangeal joints would not be expected to be impressed, and the smaller phalanges would probably not be individually distinct. In comparison to the tracks of birds and other dinosaurs, pterosaur footprints would be expected to be placed one in front of the other, and slightly toed inward (Padian and Olsen, 1984; cf. Unwin, 1989). In (A), the right forelimb is fully retracted, and the left is protracted forward; as this occurs, the manus is moved away from the body midline, so even if pterosaurs walked quadrupedally (which appears unlikely: Padian, 1983b), the manus would have touched the ground considerably lateral to the pes prints (Padian and Olsen, 1984), unlike the condition in *Pteraichnus*. All scale bars = 1 cm. Abbreviations: *i, iv, v* = first, fourth, and fifth digits.

kinematics of the limbs and the conditions of the substrate must be considered in any attempt to interpret tracks. Recently there has been some resurgence in both kinds of consideration (Padian, 1986; Gillette and Lockley, 1989).

Dr. Martin Lockley and his co-workers (Lockley and others, 1995; see also Lockley *et al.*, this volume) have identified a number of sets of what they regard as pterosaur tracks, including some new occurrences in the Morrison Formation, and have also taken issue with the 1984 study of Padian and Olsen that concluded that *Pteraichnus* was a crocodilian track. Through the kindness of Dr. Lockley I was able to examine some of the

original prints and casts of prints that he and his co-workers regard as pterosaurian. I agree with them that they are very similar to (and probably referable to) *Pteraichnus*, but they appear to me to be crocodilian tracks, commensurate with the criteria that Olsen and I developed. I refer the reader to our original paper for a full explanation of the reasoning. Here it is important to note that Lockley and others (1) do not contest the conclusion of Padian and Olsen that *Pteraichnus* is a poorly preserved ichnofossil, influenced by both poor substrate competence and kinematics of the track-maker's step cycle; (2) do not analyze pterosaurian skeletal fossils biomechanically to determine potential degrees of movement and positions of limbs (see Padian, 1983b); (3) do not analyze the paleoenvironmental context of the tracks in question, or determine the effects of the first on the second; and (4) do not experimentally test or even compare living crocodilians and their trackways to *Pteraichnus*. Lockley and others say that *Pteraichnus* cannot be crocodilian because the pes print is in front of or on top of the manus print; this, however, is a function of the animal's speed. They also cite the presence of a tail drag mark in our caiman's tracks, which is not present in *Pteraichnus*, a fact that we attribute to differences in substrate competence and in stance and gait. Other more specific issues of difference in interpretation may be discussed elsewhere.

POSSIBLE AVIANS

Osteological Remains

Marsh (1881) described briefly a crushed partial occipital region of a small archosaur from Quarry 9 near Como Bluff as *Laopteryx priscum*, and assigned it without question to the birds. In the ensuing century little further attention was paid to it apart from the usual mentions in reviews of Mesozoic faunas and taxa (e.g., Simpson, 1926; Lambrecht, 1933; Brodkorb, 1971), although Brodkorb did amend the Latin declension to *prisca*. Ostrom (1986) reviewed the specimen in detail and concluded that it bore no unique avian features. This doubt had also been expressed to Ostrom by G.G. Simpson (personal communication), and was independently reached by other investigators, including Kenneth N. Whetstone, who examined the specimen with me in 1979.

Ostrom concluded that *Laopteryx* was a pterosaur, confirming Brodkorb's (1971) suggestion, on the basis of the form of the occipital condyle and its size, which is small compared to the foramen magnum. Ostrom was limited in his comparison to *Pteranodon*, but the features agreed in their particulars;

these proportions can also be seen in *Nyctosaurus* (Williston, 1902) and in *Rhamphinion* and *Rhamphorhynchus* (Padian, 1984). Unfortunately, the preserved features of *Laopteryx* do not permit a more precise assignment, either to pterodactyloid or non-pterodactyloid pterosaurs. Quarry 9 is near the middle of the Morrison section, and an undoubted non-pterodactyloid (*Comodactylus*) is already known from there.

Jensen (1981a,b) described what he identified as a proximal left tibiotarsus (BYU 2022) from the Dry Mesa fauna (Brushy Basin Member) and assigned it to a new taxon of bird, which he named *Palaeopteryx thomsoni*. As noted above, Molnar (1985) showed that Jensen did not diagnose the taxon, so it was a *nomen vanum*, and Jensen and Padian (1989) showed that the bone in question was not a tibiotarsus, but was a distal right radius of a maniraptoran. Jensen (1981b) also assigned to the earliest known bird, *Archaeopteryx*, a right femur lacking the distal end (BYU 2023); Jensen and Padian revised this assignment because the features of the femur also precluded a more specific assignment than Maniraptora (Gauthier, 1986). Jensen (1981b) called two other specimens "avian-like," without a more specific taxonomic referral. One of these, a synsacrum (BYU 2024), was re-identified as pterosaurian and became the holotype of the pterodactyloid *Mesadactylus ornithosphyos* of Jensen and Padian (1989); the other, a left femur (BYU 2024), was referred to the preceding taxon. No other specimens could be diagnostically referred to Maniraptora, and of the two that could, neither appears to show diagnostic features of birds at present. The size range is slightly larger than that known for *Archaeopteryx*, which appeared earlier than the Dry Mesa fauna.

Footprints

Recently, Lockley and others (1992) attempted to establish that birds may be represented in the fossil record as early as the Early Jurassic or even Late Triassic by their footprints. They defined ten criteria on which they based the identification of bird tracks. Unfortunately, none of the morphological features can be regarded as diagnostically avian, and three of the ten are based on paleoecological interpretations. The two that are most likely to pertain to true bird tracks appear to be "(ii) small size" and "(iv) wide divarication angle", but inasmuch as the pes divarication angles of small (including very young) non-avian theropod feet are entirely unknown, these features are not demonstrably unique to birds. Other features, such as "(i) similarity to extant bird tracks," "(v) posteriorly directed hallux", and "(vi) slender claws," are general to hierarchical levels within

theropods (Padian and Olsen, 1989); and others, such as "(iii) slender digit impressions, with indistinct differentiation of pad impressions," would appear to be more reflective of poor preservation than of systematic position. Among nearly 50 figures of (sometimes multiple) putative bird or bird-like tracks in Lockley and others' (1992) paper, none has distinct phalangeal impressions and none is restored in comparison to the tracks of living birds and of well-preserved non-avian dinosaurs. The authors do not identify any tracks from the Morrison Formation as "avian" or "birdlike," but they do apply these two designations (usually interchangeably) to tracks found in horizons both earlier and later in time than the Morrison. We can agree that some theropod tracks in the fossil record may well have been made by birds, and that these may even turn out to appear earlier in the record than osteological remains. However, at this point it is difficult to see how the criteria that Lockley and others advance for recognizing avian tracks can be regarded as diagnostic.

CONCLUSIONS

Comodactylus is a non-pterodactyloid pterosaur, *Dermodactylus* is a pterodactyloid, and *Laopteryx* is an indeterminate pterosaur. All three taxa are based on such fragmentary remains that assignment of further material is highly unlikely. *Mesadactylus* is better known and it is likely that further exploration of Brushy Basin deposits will turn up more material, as these bones were found in the matrix surrounding large sauropod bones. There are no definite pterosaur footprints from the Morrison Formation or anywhere else.

There are no diagnostic bones or footprints of birds from the Morrison Formation. Two bone specimens from Dry Mesa have been assigned to the more inclusive taxon Maniraptora, but bear no diagnostic avian features. Birds had evolved by Morrison times, and their remains may yet surface with further surveys and improved collection techniques.

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