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SHORT COMMUNICATION

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A new maniraptoran dinosaur from China with long feathers on the metatarsus

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Abstract The unusual presence of long pennaceous feathers on the feet of basal dromaeosaurid dinosaurs has recently been presented as strong evidence in support of the arboreal–gliding hypothesis for the origin of bird flight, but it could be a unique feature of dromaeosaurids and thus irrelevant to the theropod–bird transition. Here, we report a new eumaniraptoran theropod from China, with avian affinities, which also has long pennaceous feathers on its feet. This suggests that such morphology might represent a primitive adaptation close to the theropod–bird transition. The long metatarsus feathers are likely primitive for Eumaniraptora and might have played an important role in the origin of avian flight.

Keywords *Pedopenna daohugouensis* · Dromaeosaurids · Theropod–bird transition · Arboreal–gliding hypothesis · Eumaniraptora

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Introduction

In the past few years dinosaur fossils (Zhang et al. 2002) as well as the earliest known crown-group salamanders and "rhamphorhynchoid" pterosaurs with beautifully preserved integumentary structures (Wang 2000; Wang et al. 2002; Gao and Shubin 2003) have been found near the village of Daohugou, Ningcheng, Nei Mongol, China. The Daohugou beds have been identified as Early Cretaceous on the basis of stratigraphic correlation (Wang et al. 2000) but the fauna are consistent with the Late or Middle Jurassic age (Ji and Yuan 2002; Ren et al. 2002; Zhang 2002; Shen et al. 2003). In 2002, a new feathered eumaniraptoran (Fig. 1) was discovered by a team from the Institute of Vertebrate Paleontology & Paleoanthropology, Beijing (IVPP) from the Daohugou location. Pending a precise radiometric date, this specimen might therefore represent the second known Jurassic taxon of the theropod–avian lineage, preserved with feathers (*Archaeopteryx* being the first). The specimen is preserved on a single slab as part and counterpart, which match exactly. Both part and counterpart are represented by a single block without any breakage. Much of the integumentary impression (including the metatarsal part) was prepared under the supervision of the authors.

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Systematic paleontology

- Theropoda Marsh, 1881
- Eumaniraptora Padian, Hutchinson & Holtz 1998
- *Pedopenna* gen. nov.
- *Pedopenna daohugouensis* sp. nov.

Etymology

The generic name refers to the long pennaceous feathers on the feet; the specific epithet refers to the locality that produced the holotype.

Holotype

IVPP V12721, partial right leg and associated integumentary structures preserved on a slab as part and counterpart.

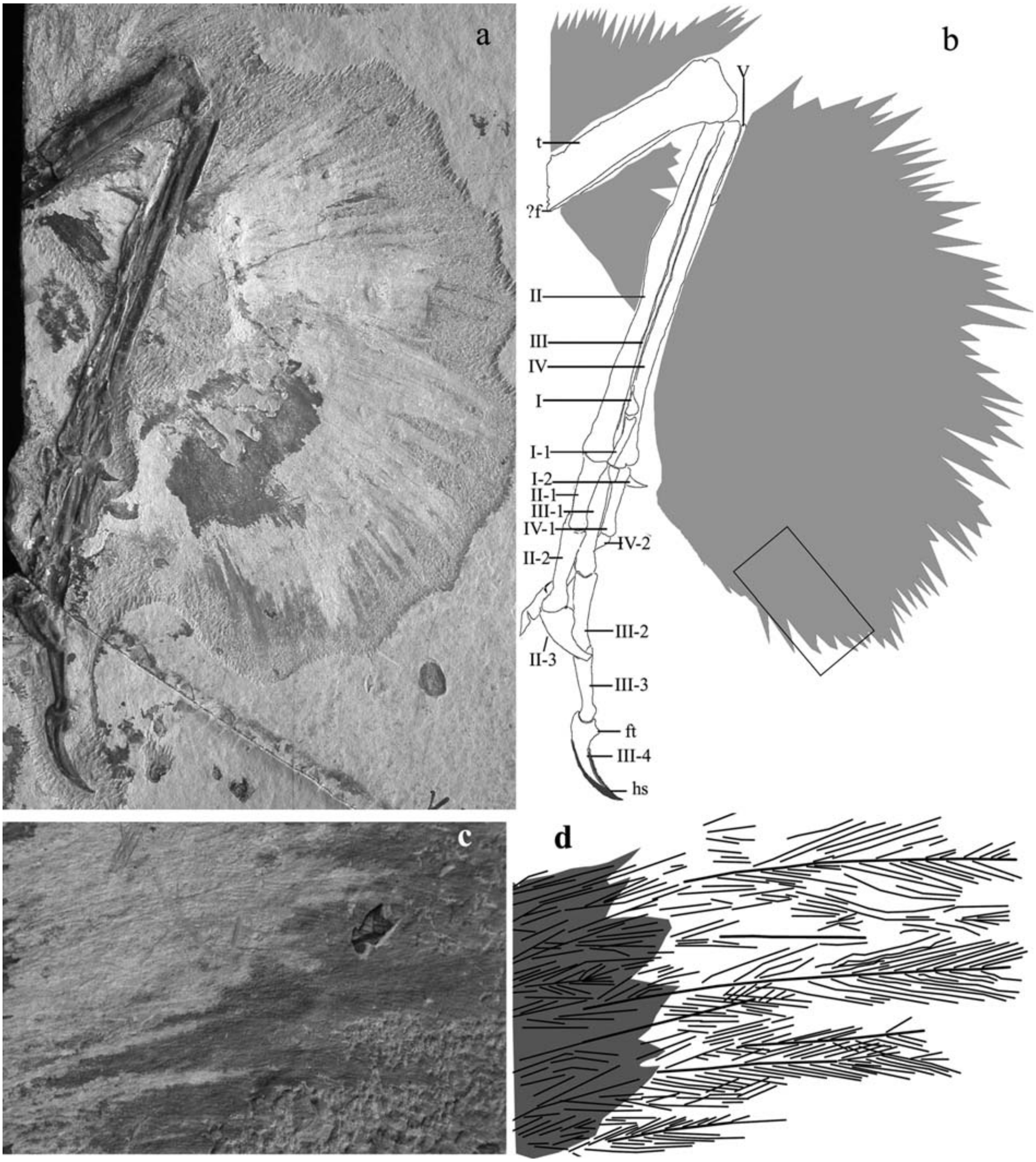

Fig. 1 The holotype of *Pedopenna daohugouensis* (Institute of Vertebrate Paleontology & Paleoanthropology, Beijing V12721): photograph (**a**) and line-drawing (**b**) of the partial leg and associated feathers, photograph (**c**) and line-drawing (**d**) of the feathers attached to the distal metatarsals showing the rachis and the parallel barbs. *Inset* in **b** indicates the positions of **c** and **d**. *Scale bar*=10 mm. *?f* Fibula, *ft* flexor tubercle, *hs* horny sheath, *I–V* metatarsal I–V, *I-1 to IV-2* pedal phalanx I-1 to IV-2, *t* tibia

Locality and horizon

Daohugou locality, Nei Mongol, northern China. Daohugou beds, the available palaeontological evidence consistent with a Late or Middle Jurassic age.

Diagnosis

A small eumaniraptoran apomorphically has a very slender pedal phalanx I-1 (length/mid-shaft-diameter ratio about 7.2). It differs from the dromaeosaurids and troodontids in having a less specialized pedal digit II and pedal phalanx II-2 longer than II-1, from the dromaeosaurids in having a short metatarsal V and lacking a postomedial flange on metatarsal IV, from the Aves including *Epidendrosaurus* in having a hallux which is not reversed and a pedal phalangeal portion shorter than the metatarsus.

Description

IVPP V12721 represents an individual that is estimated to be <1 m in length (see S1 for measurements of IVPP V12721). The tibia is partially fused to the proximal tarsals. The three middle metatarsals are subequal in length, a feature also seen in *Microraptor* (Xu et al. 2000) and *Epidendrosaurus*. Phalanx I-1 is a very slender bone, extending distally level with the distal end of the metatarsus. This is similar to the situation in *M. zhaoianus*, *Archaeopteryx* and *Confuciusornis*, but is different from that of most non-avian theropods and ground birds in which pedal digit I is more proximally positioned (Xu 2002). Phalanx II-2 is considerably longer than phalanx II-1, with a weak proximoventral heel. Phalanx II-3, the ungual, is considerably larger than the other unguals, but not to the degree seen in dromaeosaurids and troodontids (Xu 2002). Phalanx III-3 is elongate, subequal in length to phalanx III-2, but it is much shorter than phalanx III-1. Phalanx III-4, the ungual, is slender, and moderately curved. The articular surfaces on the penultimate phalanges are shifted onto the ventral margin as in *Microraptor* (IVPP V13476), a feature that might permit the unguals to flex ventrally more than in most other non-avian theropods. The horny sheath covers most of the ungual, reaching nearly to the flexor tubercle that is separated from the proximal articular end of the ungual by a distinct, small notch. Metatarsal V is a short bone, different from the much longer one in dromaeosaurids but similar to that of troodontids and *Archaeopteryx* (Xu 2002; Norell and Makovicky 1997).

Integumentary structures are preserved close to the tibia and the metatarsus (Fig. 1a, b). The integumentary structures close to the tibia are clearly branched, showing the presence of a rachis and barbs. Those attached to the metatarsus seem to be the pennaceous feathers: they have a stiff rachis and flat vanes formed by parallel barbs (Fig. 1c, d). The metatarsus feathers are generally 45 mm long and the distal ones are slightly longer than the proximal ones; the longest ones are >55 mm in length and are slightly shorter than the metatarsus. The exact number of metatarsus feathers is not known due to their preservation (overlapping of feathers and weak impressions of some individual feathers), but they are more numerous than in *M. gui* (Xu et al. 2003). They slightly curve toward the toes as indicated by the rachises (Fig. 1c, d). Although it is difficult to isolate a complete single feather, the metatarsus feathers seem to have nearly symmetrical vanes, which are proportionately narrower than in *M. gui* (Xu et al. 2003). There also appear to be some shorter feathers close to the metatarsus as indicated by the denser impression, analogous to the coverts in birds (Fig. 1d). Near phalanx III-3, some tuberculate impressions are also preserved.

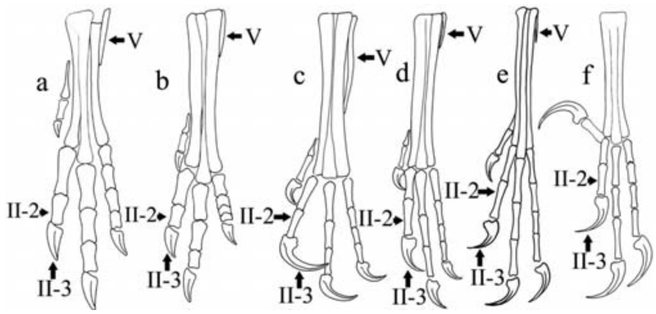

Fig. 2 Comparison of pedal morphology of *Syntarsus* (*a*), *Caudipteryx* (*b*), *Microraptor* (*c*), *Pedopenna* (*d*), *Archaeopteryx* (*e*), and *Sinornis* (*f*). Not to scale

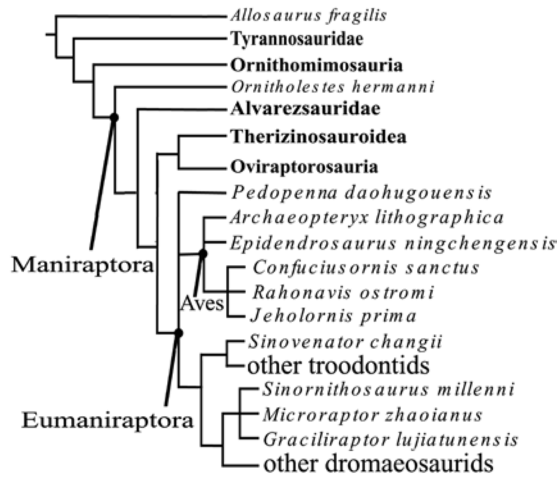

Fig. 3 A simplified cladogram representing a majority consensus of 1,616 most parsimonious trees showing the phylogenetic position of *P. daohugouensis* (see S1–S5 for detailed information)

Discussion

The eumaniraptoran status of *Pedopenna daohugouensis* is indicated by the following synapomorphies to those of basal dromaeosaurids and basal birds (Xu 2002): slender pes with a long phalangeal portion, pedal digit I is relatively distally located; the second pedal ungual is hypertrophied; the penultimate phalanges are elongated; and the pedal unguals are slender and moderately recurved (Fig. 2). Unlike dromaeosaurids but as in basal birds, it has a less specialized second pedal digit, a short metatarsal V, and proportionately longer penultimate phalanges and lacks a ventral flange on metatarsal IV (Fig. 2). This phylogenetic hypothesis is supported by a numerical cladistic analysis, which suggests that *P. daohugouensis* is more closely related to the Aves than any other known non-avian theropods (Fig. 3; see S1–S5 for the phylogenetic analysis). The discovery of a basal member of the avian lineage from China has implications for understanding the biographical origin of birds. Early, primitive maniraptorans have been reported from the Late Jurassic and Early Cretaceous periods of North America (Jensen and Padian 1989; Kirkland et al. 1993). *Archaeopteryx*, the earliest known bird, is from the Late Jurassic of Europe, and a number of primitive maniraptoriform theropods are also known from the Early Cretaceous of Europe (Perez-Moreno et al. 1994; Hutt et al. 2001). However, unquestionably to date the oldest known and most basal representatives of the Troodontidae, Dromaeosauridae, Oviraptorosauria, and Therizinosauroidea are all from eastern Asia (Xu 2002), and *P. daohugouensis* represents the most basal member of the avian lineage. The available evidence thus strongly favors a Laurasian origin, and perhaps tentatively supports an Asian origin, of birds.

The most interesting feature of *P. daohugouensis* is the pennaceous feathers that are attached to the whole length of the metatarsus. These feathers are proportionally shorter than similar structures found in basal dromaeosaurids (Xu et al. 2003). Interestingly, some studies on *Archaeopteryx* specimens indicated long leg feathers on this earliest known bird (Beebe 1915; Longrich 2003; Christiansen and Bonde 2004). The available evidence thus suggests that long leg feathers, in particular long metatarsus feathers, is a common adaptation among basal eumaniraptorans; furthermore, it agrees with our earlier predictions that the highly specialized pennaceous feathers on the leg evolved in non-avian theropods and were later reduced and lost along the line to birds (Xu et al. 2003)

The leg feathers in basal dromaeosaurids display several striking features suggesting the presence of the functional hind wings (Xu et al. 2003). Comparatively the metatarsus feathers in *P. daohugouensis* show few aerodynamic features: they are proportionally shorter; the distal feathers are not significantly longer than the proximal ones; they seem to have nearly symmetrical leading and trailing vanes; and they are more numerous and appear to be less stiff than in basal dromaeosaurids. This suggests that the aerodynamic function, if there is any, of the metatarsus feathers in *Pedopenna daohugouensis* is much weaker than in basal dromaeosaurids. Feathered feet are present in some living birds such as many raptors (Weidensaul 1995). The feathers covering the raptors' feet are much shorter, fluffier, more proximally located on the leg, and less organized into a wing-shape than those in *P. daohugouensis* and might function in protecting the birds from their prey (Weidensaul 1995) or to keep them warm (Burton 1973). The other possible function of long metatarsal feathers might be ornamentation. Ornamental feathers are clearly present in the basal bird *Confuciusornis* (Chiappe et al. 1999). It is likely that large metatarsus feathers with asymmetrical vanes are primitive for eumaniraptorans and these structures function in flight or gliding; proto-birds evolved more powerful front-wings while reducing their hind-wings. *P. daohugouensis* might be in such as an evolutionary stage, and its metatarsus feathers reduced but still remained in some organizations of the hind-wings. A shift in function (from flight to ornamentation, protection or insulation) and/or relative importance in aerodynamics might explain the variation in leg feather morphology among eumaniraptorans including basal birds.

The presence of metatarsus feathers on non-avian theropods has been suggested to be inconsistent with a cursorial habit (Xu et al. 2003). Comparisons of feet in theropods (Fig. 1c) suggest a gradual adaptive modification towards the arboreal habit. In most non-avian theropods, the first pedal digit is positioned high, the pedal phalanges are robust, the penultimate phalanges are short, and the weakly curved pedal unguals are robust with a thick ventral margin. In some maniraptorans, the pes is modified in ways suggesting an arboreal habit: the pedal digits become longer relative to the metatarsus, the first pedal digit becomes larger and moves further down; the phalanges become more slender; the penultimate phalanges become longer, the articulations of the penultimate phalanges are more ventrally developed; the pedal unguals are laterally compressed, more slender and more curved. In enantiornithine birds, the pes show a fully adapted arboreal morphology in having well developed hallux and longer penultimate phalanges. Both the integumentary and osteological evidence suggest that the arboreal capabilities of birds might have been developed in primitive eumaniraptorans (Xu et al. 2000, 2003; Chatterjee 1997).

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