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TROODONTID-LIKE PES IN THE DROMAEOSAURID *SINORNITHOSAURUS*

XING XU and XIAO-LIN WANG

Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, 100044, P. R. China

ABSTRACT-Previous studies suggest that there are fundamental differences in the pes of Dromaeosauridae and Troodontidae. *Sinornithosaurus*, a recently reported basal dromaeosaurid, has a troodontid-like pes, however. Troodontid-like features in the pes of *Sinornithosaurus* include: long and slender metatarsus, proximally compressed metatarsal III, absence of trochalae in the distal end of metatarsal III, long and robust metatarsal IV, less abbreviated phalanx II-2, and smaller ungual of digit II. A troodontid-like pes in basal dromaeosaurid may provide a further evidence for a monophyletic Deinonychosauria which includes dromaeosaurids and troodontids, yet it has to be testified by a thorough phylogenetic analysis of coelurosaurian dinosaurs.

INTRODUCTION

Dromaeosauridae was erected to include *Dromaeosaurus*, *Deinonychus* and *Velociraptor* by Colbert and Russell (1969). In the same paper, these authors furthermore noticed the distinctness of dromaeosaurid dinosaurs among then-known theropods and designated an infraorder Deinonychosauria to include Dromaeosauridae. Ostrom (1969) assigned troodontid *Stenonychosaurus* and *Sauronithoides* to Deinonychosauria. The family Troodontidae was assigned by Barsbold (1976) to the infraorder Deinonychosauria.

The Deinonychosauria is often recognized as a monophyletic taxon (Ostrom, 1990), which includes the Dromaeosauridae and Troodontidae. The most salient feature of the monophyletic Deinonychosauria is the presence of the specialized second pedal digit. Monophyly of Deinonychosauria was, however, questioned by Osmolska (1981) and lately also by Gauthier (1986), and its monophyly has not been corroborated in some recent cladistic analyses (Holtz, 1994; Forster *et al.* 1998; Xu *et al.* 1999a) although supported by others (Makovicky and Sues 1998; Sereno 1999). The similarities of the second pedal digit of Dromaeosauridae to those of Troodontidae were considered as being convergently evolved because this specialized digit is associated with the very derived metatarsus in troodontids but with a primitive one in dromaeosaurids (Osmolska, 1990). Osmolska (1982) noticed the functional difference of the specialized second pedal digit in Dromaeosauridae and Troodontidae. Currie and Peng (1994) has showed that there are fundamental differences in the pes of Dromaeosauridae and Troodontidae when studying a well preserved troodontid hindlimb.

During the 1997 and 1998 expedition by the IVPP (Institute of Vertebrate Paleontology and

Paleoanthropology, Academia Sinica), many well preserved vertebrate fossils were collected at the famous dinosaur-fish-bird Sihetun locality, Beipiao, Liaoning, northeastern China (Xu and Wang, 1998; Xu *et al.*, 1999a, b; Dong and Wang, 1998; Wang *et al.*, 1998). Among them includes the beautifully preserved skeleton of the basal dromaeosaurid *Sinornithosaurus millenii* (Xu *et al.*, 1999a). *Sinornithosaurus* is extremely similar to *Archaeopteryx* postcranially and its discovery greatly improves our understanding of the anatomy of dromaeosaurid dinosaurs, and of bird origin.

Surprisingly a troodontid-like pes is present in *Sinornithosaurus,* which is important to the understanding the evolution and character distribution of coelurosaurian dinosaurs, particularly of Deinonychosauria. In this paper, we will present a full description of the pes of *Sinornithosaurus* and compare it with those of other dromaeosaurids and troodontids.

The holotype of *Sinornithosaurus millenii* is of a nearly complete skeleton and was collected from the lacustrine deposits of the lower part of the Yixan Formation at Sihetun Locality (Fig.1). Unfortunately the slab of the fossil specimen was damaged, leading to the lack of the proximal end of the tibia, the proximal end of the fibula, and the distal end of the caudal series. Associated with *Sinornithosaurus* were also found numerous skeletons of *Psittacosaurus* and *Confuciusornis* among others.

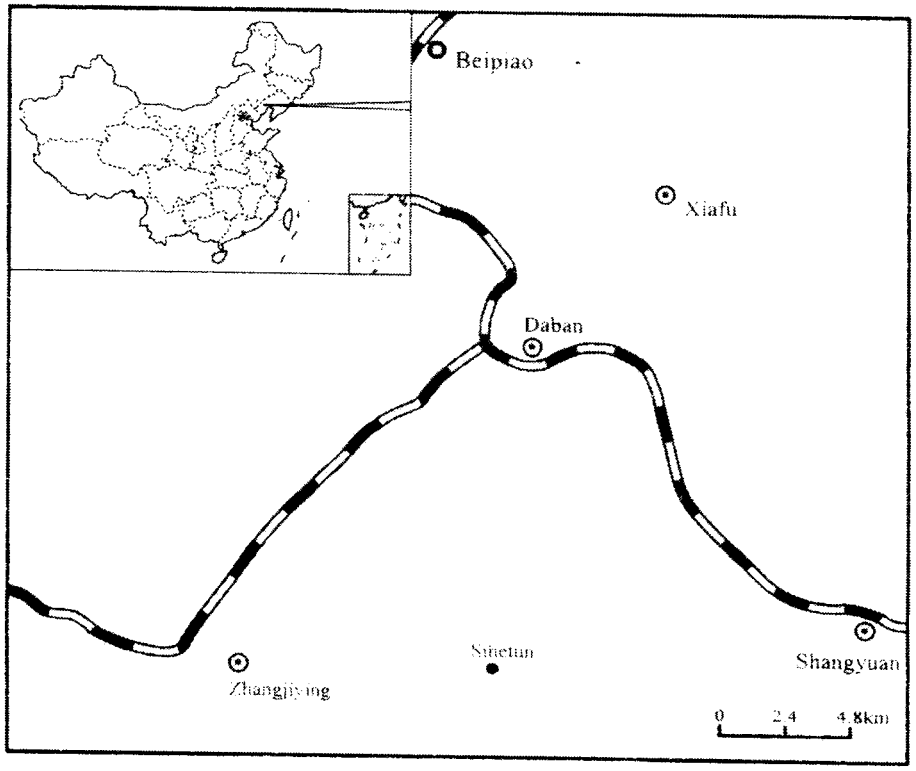

Figure 1. Sketch map showing the Sihetun locality, Beipiao City, western Liaoning, China (Modified from fig. 1 in Wang *et al.*, 1998).

Material--the right foot of the holotype of *Sinornithosaurus* (IVPP V12811), including distal tarsals III and IV, metatarsals I-V, and all phalanges (Fig. 2).

Abbreviations--**IGM**, Institute of Geology Mongolia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **YPM**, Peabody Museum of Natural History, Yale University, Vertebrate Paleontology Collection.

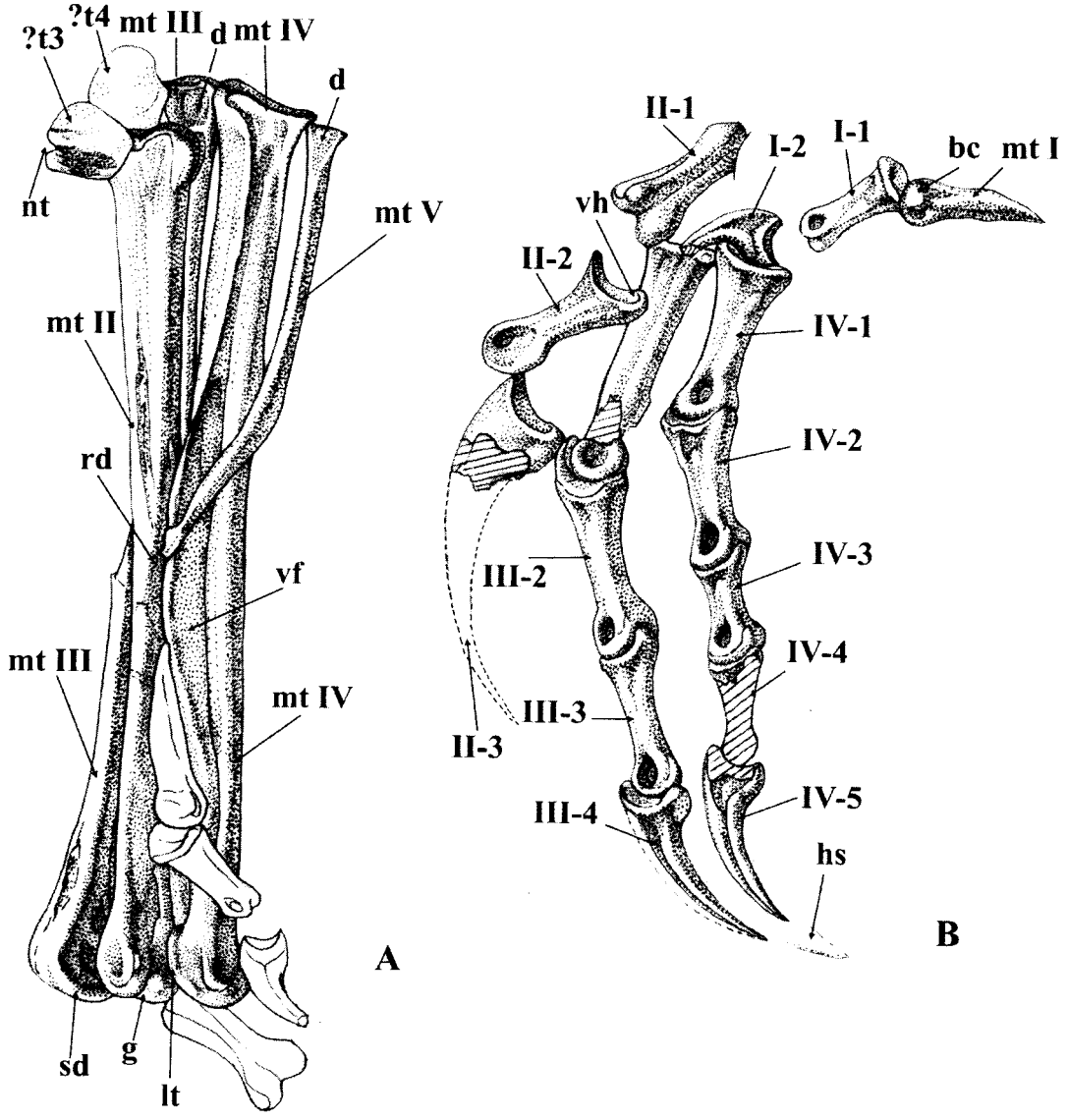

Figure 2. Right pes of *Sinornithosaurus millenii* (IVPP, V12811). **A**, Metatarsus in posterior view; **B**, Phalanges in medial view. **Abbreviations**: **bc**, ball-like condyle; **d**, depression; **g**, ginglymus; **hs**, horny sheath; **I-1 to IV-5**, phalanges I-1 to IV-5; **mt I-V**, metatarsals I-V; **rd**, ridge; **sd**, simple distal articulation; **?t3**, ?tarsal 3; **?t4**, ?tarsal 4; **vf**, ventral flange; **vh**, ventral heel. Scale bar equals 2 cm.

DESCRIPTION

The right foot of *Sinornithosaurus* is well preserved except for the overlapped distal end of phalanx II-3 by the tail. Most elements of the foot are exposed in their posteroventral views. The two tarsals were displaced slightly medially onto the proximal end of metatarsal II (Fig. 2A). The distal half of metatarsal III was moved medially to contact the medial side of the distal half of metatarsal II. Most other elements, including the phalanges, are still articulated except for phalanges I-2 and II-2 (Fig. 2).

In general, the metatarsus of *Sinornithosaurus* is comparatively gracile as in Arctometatarsalia (Holtz, 1994). The metatarsus is 93 mm in length, 18 mm wide proximally, 12.5 mm wide in the middle portion, and about 16 mm wide distally (Fig. 2A).

Two distal tarsals are neither fused to each other or to the metatarsals. Both tarsals are tabular, somewhat rounded triangular in outline. The medially located one bears a notch on probably its posterior border as in a Mongolian dromaeosaurid (IGM 100/985 in Norell and Makovicky, 1997).

Digit I is preserved on the posterior surface of the metatarsus and extends distally beyond the metatarsus (Fig. 2A). In most other non-avian theropods, the distal end of the digit I does not extend distally beyond the metatarsus. The metatarsal I is short, about 23% the length of metatarsal III. It is preserved on the posterior surface of metatarsal II, and its proximal end lies about two-thirds down the latter. The proximal end of metatarsal I tapers, and its shaft moderately compressed. The medial surface of the shaft is slightly convex. In medial view, the dorsal margin of the shaft is slightly concave and the ventral margin convex. The distal articulation of metatarsal I is ball-like and protruding medially (Fig. 2B). The ball-like condyle is more ventrally located. Dorsal to the ball-like condyle is a very shallow fossa. The ball-like distal articulation seems to bear no ginlymus as in typical theropods, including other dromaeosaurids and *Archaeopteryx*. Phalanx I-1 is slightly shorter than metatarsal I. Its proximal articulation is simple, with a moderately concave articular surface. The medial margin of the proximal articulation seems to be well developed, for articulating the ball-like distal articulation of metatarsal I. The shaft of phalanx I-1 is not constricted. Its distal articulation is ginglymoid, narrow dorsally and wide ventrally. The ungual of the first digit is as long as phalanx I-1, and is weakly curved and triangular in cross section.

Digit II displays a number of diagnostic features of the Dromaeosauridae but also some similarities to Troodontidae. Metatarsal II is 95% the length of metatarsal III. The proximal end of metatarsal II slightly expanded transversely. Its lateral surface curves around and contacts the metatarsal III. Almost half way down the length of the shaft is present a longitudinal ridge, running laterally to medially (Fig. 2A) as in the Mongolian dromaeosaurid, *Deinonychus*, *Velociraptor* and the troodontid *Sinornithoides* (Norell and Makovicky, 1997). The distal end of metatarsal II has a moderately incised ginglymus (Fig. 2A). This feature is more similar to that of other dromaeosaurids, though in the latter group the distal ginglymus of metatarsal II is more deeply incised (Norell and Makovicky, 1997). Posteriorly the distal articulation has a more or less ridge-like medial condyle and a wider rounded lateral condyle. A shallow ligmental pit is present on the medial surface of the distal articulation. Phalanx II-1 is slightly shorter than phalanx II-2, different from the condition in most non-avian theropods. It is wider than other phalanges. Distally it is transversely expanded, and deeply incised with a narrower medial condyle and a wider lateral condyle. Phalanx II-2 is morphologically more similar to that of troodontids than other dromaeosaurids. A proximoventral heel is present (Fig. 2B)

as in Dromaeosauridae and Troodontidae, however, this heel is not as significant as in other dromaeosaurids (Norell and Makovicky, 1997). Also different from other dromaeosaurids (Norell and makovicky, 1997), phalanx II-2 does not have a sharp constriction of its shaft between the articular facets. Its distal articular end extends moderately below and above the shaft. In other dromaeosaurids, it extends well above as well as below the shaft (Ostrom, 1969). A deep and large ligament pit is present dorsally on the lateral surface of the distal articular end. The ungual of digit II is missing its middle portion, but its distal portion is visible under CT scan. A precise size of the second pedal ungual could be therefore reliably reconstructed (Fig. 2B). It is strongly curved, and much larger than the other phalanges of digit II. This shows an intermediate condition between Troodontidae and Dromaeosauridae (Ostrom, 1969).

Metatarsal III is strongly compressed proximally (Fig. 2A), suggesting an arctometatarsalian condition as seen in Troodontidae, Ornithomimidae and a number of other theropods (Holtz, 1994). Proximally on the medial surface of metatarsal III is a triangular depression (Fig. 2A), for contacting the proximally curved lateral surface of metatarsal II. The strongly compressed proximal half of the shaft of metatarsal III is somewhat strap-like. Distally the shaft is triangular in cross section, with the posterior margin strongly compressed, thus forming a flat anterior surface and probably a ridge-like posterior margin. The distal end of metatarsal III is anteriorly about 4.5 mm in mediolateral width and posteriorly strongly compressed transversely. The distal articulation of metatarsal III lacks a ginglymus as in other dromaeosaurids (Norell and Makovicky, 1997). Its narrow posterior margin seems to bear a tongue-like structure as in troodontids (Currie and Peng, 1994). The four phalanges of digit III are well articulated, exposing their medial sides. These grade from larger to smaller distally except the ungual. Phalanx III-1 is long and seems to be bowed medially. The distal phalanx has more dorsally located ligament pit when compared to the proximal phalanges. The ungual has a relatively developed flexor tubercle.

Metatarsal IV is the most robust. It is 98% the length of metatarsal III. As in the Mongolian dromaeosaurid (Norell and Makovicky, 1997), metatarsal IV is widest at the proximal end and thinnest just proximal to the distal articulation. Posteriorly the medial surface of the proximal aritculation raises to form a somewhat tubercle-like structure, and down from this tubercle, a weakly developed, crest-like structure curves laterally and then medially. This crest becomes more pronounced and forms a large longitudinal ridge from half way down the shaft, as in other dromaeosaurids (Norell and Makovicky, 1997) and troodontids. This large ridge is more prominent in *Sinornithosaurus* than in other dromaeosaurids. The distal articulation is a simple one, without ginglymus. On the posterior surface of the bone, the articulation bears two tongues. The lateral one is shorter proxiodistally and the medial one extends further poximally. This is extremely similar to the situation in the Mongolian dromaeosaurid (IGM 100/985 in Norell and Makovicky, 1997). The lateral ligament pit is deep and extremely ventrally located. The five phalanges of digit IV are well articulated and expose their medial sides. Phalanx IV-1 is much longer than the other phalanges of the digit, and seems to be bowed toward the medial side distally. Phalanx IV-4 is longer than phalanx IV-3, which is different from the situation in most non-avian theropods, including *Deinonychus* (Ostrom, 1969) and the Mongolian dromaeosaurid. All of the medial ligament pits of these phalanges are moderately developed, and centered located. The ungual of digit IV is moderately curved. A medial ligament groove is deep, connecting the ligament fossa just distal to the proximal articulation of the ungual. The ungual bears a relatively prominent flextor tubercle. The distal portion of the horny sheath is preserved.

Metatarsal V is a slender, medially curved bone. It is about half the length of metatarsal III as in other dromaeosaurids (Norell and Makovicky, 1997). Its proximal end is somewhat mediolaterally compressed and anteroposteriorlly expanded. Proximally its medial surface has a depression, for contacting the posterolateral surface of the proximal end of metatarsal IV. Distally the proximal half of the shaft of metatarsal V is triangular in cross section, with a flat medial surface, which is appressed to the shaft of metatarsal IV. Further distally the shaft of metatarsal V is somewhat compressed anteroposteriorly and expanded lateromedially, and then tapers into a somewhat pointed distal end. The distal half of the shaft is subcrescent in cross section.

DISCUSSION

The specialized second pedal digit II is uniquely shared by dromaeosaurids, troodontids, and the basal bird *Rahonavis* (Forster *et al.*, 1998) among theropod dinosaurs, though detailed comparison reveals many differences between the pedal digit II of dromaeosaurids and troodontids (Currie and Peng, 1994). We believe that the following features of the pes of *Sinornithosaurus* are important and we will discuss them and compare them with those of other dromaeosaurids and troodontids.

1. Metatarsus relatively long and slender. The width/length ratio of the metatarsus of *Sinornithosaurus* is estimated as 0.16, which is equal to that of *Hulsanpes* (Osmolska, 1982), but less than that of other dromaeosaurids. It is 0.29 in the Mongolian dromaeosaurid (IGM 100/985), 0.28 in *Deinonychus* (YPM 5250), and 0.11 in the troodontid *Sinornithoides youngi* (IVPP V9612). The metatarsus/femur length ratio is about 0.63 in *Sinornithosaurus*, intermediate between about 0.50 in other dromaeosaurids and 0.75 in troodontids (Currie and Peng, 1994). In this character, *Sinornithosaurus* is more similar to troodontids than most other dromaeosaurids.

2. Ball-like distal articulation of metatarsal I. *Sinornithosaurus* has a ball-like distal articulation of metatarsal I, which has been reported in a juvenile specimen of troodontid *Sauronithoides mongoliensis* (Currie and Peng, 1994). In other dromaeosaurids and *Archaeopteryx*, the morphology of the distal articulation of metatarsal I is little different from that of most other non-avian theropods. In *Confuciusornis* and more derived birds, this ball-like distal articulation is well developed and medially extended (Chiappe *et al.*, 1999).

3. Moderately incised distal ginlymus of metatarsal II. Deeply incised distal ginglymus of metatarsal II is a unique feature for dromaeosaurids (Norell and Makovicky, 1997). The distal ginlymus of metatarsal II of *Sinornithosaurus* is not as deep as in other dromaeosaurids.

4. Moderately elevated ginglymus of phalanx II-1. The distal facet of phalanx II-1 extends moderately above the shaft in *Sinornithosaurus*. While in other dromaeosaurids, it extends significantly both above and below the shaft. In this feature, *Sinornithosaurus* is more similar to troodontids.

5. Prominent proximoventral heel of phalanx II-2. This feature is uniquely shared by *Sinornithosaurus*, other dromaeosaurids, troodontids, and *Rahonaivs* (Forster *et al.*, 1998). The proximoventral heel is less developed in *Sinornithosaurus* than in other dromaeosaurids, however.

6. Phalanx II-2 moderately constricted. In other dromaeosaurids, the distal facet of pedal phalanx II-2 extends well above and below the shaft, and shaft significantly constricted. In this feature, *Sinornithosaurus* is more similar to troodontids.

7. Phalanx II-2 slightly longer than II-1. As in other dromaeosaurids, phalanx II-2 is slightly longer than phalanx II-1 in *Sinornithosaurus*. This is in contrast to the situation in troodontids and most

other non-avian theropods, in which phalanx II-1 is apparently longer than phalanx II-2.

8. Over-sized strongly recurved ungual of the digit II. Enlarged second ungual have been reported on in dromaeosaurids, troodontids, and *Rohanavis*. *Sinornithosaurus* seems to have a second ungual intermediate in size between troodontids and other dromaeosaurids. The ungual of the digit II is about 1.3, 1.7, about 2 times as large as that of the digit III in troodontid *Sinornithoides youngi* (Russell and Dong, 1994), *Sinornithosaurus*, and other dromaeosaurids, respectively.

9. Metatarsal III wedged between the adjacent ones. In *Sinornithosaurus*, the proximal portion of metatarsal III is strongly compressed, and so does most of the posterior margin of the metatarsal. This is apparently different from the situation in other dromaeosaurids. In this character, *Sinornithosaurus*

Table 1. Measurements of the right pes of *Sinornithosaurus millenii* (IVPP V 12811; in mm).

	Length	Proximal transverse width	Distal transverse width	Middle transverse width	Distal dorsoventral depth
Mt I	21	-	4	3.2	?
Mt II	88	8*	5	6*	6
Mt III	93	9	2.5	5	7.5
Mt IV	91	2.5	7	4	6.5
Mt V	47		-	2	-
Ph I-1	11		2.5		3
Ph I-2	11				
Ph II-1	15		6	4	-
Ph II-2	17				6
Ph II-3	35				
Ph III-1	25				6
Ph III-2	17.5				5
Ph III-3	16.5				4
Ph III-4	20				
Ph IV-1	20				6
Ph IV-2	14				5
Ph IV-3	10				4
Ph IV-4	12				4
Ph IV-5	18.5				

is similar to troodontids.

10. The distal articulation of metatarsal III not ginglymoid. In other dromaeosaurids, the distal articulation of metatarsal III has a ginglymus. In this character, *Sinornithosaurus* is more similar to troodontids and most other non-avian theropods.

11. Metatarsal III covering the anterior surfaces of both metatarsal II and IV distally. *Sinornithosaurus* has a arctometatarsal as in troodontids and many other coelurosaurians, as futher supported by that the metatarsal III overlaps the anterior surfaces of metatarsal II and IV distally (Holtz, 1994). While in other dromaeosaurids, all three metatarsals are more or less parallel in the same plane.

12. Metatarsal IV almost as long as metatarsal III and more robust than other metatarsals. In this feature, *Sinornithosaurus* is more similar to troodontids than other dromaeosaurids.

13. Metatarsal V half the length of metatarsal III. Dromaeosaurids have a long and slender metatarsal V, the length of which reaches half the length of metatarsal III. *Sinornithosaurus* shares this feature.

The above comparisons suggest the basal dromaeosaurid *Sinornithosaurus* has a somewhat troodontid-like pes. Previously the specialized pedal digit is associated with the derived metatarsus in troodontids but with a primitive one in dromaeosaurids, and was therefore considered as being convergently evolved (Osmolska, 1990). *Sinornithosaurus* has a troodontid-like pes in that its metatarsus is long, slender, and arctometatarsalian. Considering its basal position in Dromaeosauridae (Xu *et al.*, 1999a), the previously thought primitive metatarsus in other derived dromaeosaurids might actually represent the reversal to the primitive condition, and instead could be explained as synapomorphies for more derived dromaeosaurids. The discovery of a troodontid-like pes in a basal dromaeosaurid might also provide further evidence for a monophyletic Deinonychosauria (Makovicky and Sues, 1997; Sereno, 1999), yet it could be independently evolved as some recent analysis support a sister-group relationship of Dromaeosauridae and Avialae (Holtz, 1994; Forster *et al.*, 1998; Xu *et al.*, 1999a). A larger analysis on coelurosaurian phylogeny might be helpful to resolve this problem, which is beyond the scope of the present paper, however.

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