

伤齿龙标本 IVPP V 10597 分类学重新讨论¹⁾

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摘要:保存部分后肢的标本 IVPP V 10597 最初被描述为蒙古蜥鸟龙 (*Saurornithoides mongoliensis*) 的幼年个体, 但存在一些疑问。近年来有关伤齿龙科 (Troodontidae) 的研究, 尤其是有关伤齿龙类分类学研究取得了重要进展, 因此有必要对该标本的分类学重新进行评估。通过细致的形态比较和数值化的系统发育分析, 确认相对于蒙古蜥鸟龙, V 10597 更加接近于同域的谭氏临河猎龙 (*Linhevenator tani*), 指示其有可能代表谭氏临河猎龙的幼年个体。但 V 10597 的许多后肢特征, 包括许多涉及后肢骨骼间比例的特征, 显示出与包括谭氏临河猎龙在内的其他伤齿龙类的明显区别。这些形态差异可能具有分类学意义, 表明 V 10597 代表一个新种。通过骨组织学分析, 确认该标本不可能代表谭氏临河猎龙或者其他大型伤齿龙类的幼年个体。基于已有的形态学和骨组织学信息, 将 V 10597 定为一新属、新种, 命名为柯瑞氏菲利猎龙 (*Philovenator curriei* gen. et sp. nov.)。这一发现增加了白垩纪晚期伤齿龙类的种群分异度和形态差异度。

关键词:内蒙古, 晚白垩世, 伤齿龙类, 后足形态, 骨组织学

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THE TAXONOMY OF THE TROODONTID IVPP V 10597 RECONSIDERED

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Abstract The partial troodontid hindlimb IVPP V 10597 was originally described as a juvenile *Saurornithoides mongoliensis*. The present study reconsiders the taxonomic placement of this interesting specimen, given the significant advances in understanding of the Troodontidae that have taken place since it was first described. Morphological comparisons and numerical phylogenetic analyses indicate that V 10597 is more closely related to the sympatric *Linhevenator tani* than to *Saurornithoides mongoliensis*, raising the possibility that V 10597 might be a juvenile *L. tani*. However, V 10597 differs significantly from other troodontids, including *L. tani*, in numerous hindlimb features and particularly in the proportions of various hindlimb elements. These differences are likely to be taxonomic, and suggest that V 10597 represents a new troodontid. Furthermore, histological analysis indicates that V 10597 is unlikely to be a juvenile of *L. tani* or any other large troodontid. Based on the available morphological and histological information,

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we propose the erection of a new taxon, *Philovenator curriei* gen. et sp. nov., based on V 10597. This new find increases the known taxonomic diversity and morphological disparity of Late Cretaceous troodontids.

Key words Nei Mongol, Late Cretaceous, Troodontidae, pedal morphology, histology

1 Introduction

In 1988, the China-Canada Dinosaur Project organized an expedition to Bayan Mandahu, Wulatehouqi (Urat Rear Banner), Nei Mongol (Inner Mongolia), which resulted in discoveries of many Late Cretaceous vertebrate fossils (Jerzykiewicz et al., 1993). Among these discoveries is a small, partial theropod hindlimb that displays an interesting combination of morphological features (Currie and Peng, 1994). Catalogued as IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing) V 10597, this specimen was referred to the troodontid *Saurornithoides mongoliensis* by Currie and Peng (1994). Although these authors did not adduce any unique feature shared by IVPP V 10597 and *S. mongoliensis*, the referral was reasonable at that time based on several lines of evidence: the general morphology of V 10597 is very similar to that of previously known Late Cretaceous troodontid hindlimbs (Wilson and Currie, 1985; Barsbold et al., 1987; Osmólska, 1987; Zanno et al., 2011); among previously known taxa, *S. mongoliensis* most closely resembles V 10597 in hindlimb morphology; and finally, the Bayan Mandahu fauna was then considered to be identical to the Djadokhta fauna from which *S. mongoliensis* was recovered (Jerzykiewicz and Russell, 1991; Jerzykiewicz et al., 1993). Currie and Peng (1994) did point out some significant differences between V 10597 and other troodontids, including *S. mongoliensis*. However, the fact that V 10597 is much smaller than the hindlimbs of the other troodontids that were known at the time, including *S. mongoliensis* (Osborn, 1924; Russell, 1969), prompted Currie and Peng (1994) to identify the specimen as a juvenile and attribute the differences to ontogenetic variation.

The recent discovery of the Bayan Mandahu troodontid *Linhevenator tani* raised the possibility that V 10597 might actually represent a juvenile individual of this species, given that V 10597 is more similar to *Linhevenator* than to *Saurornithoides* (Xu et al., 2011b). This prompted a re-examination of the morphology of V 10597, as well as an investigation of its histology. In this paper, we describe systematically and ontogenetically significant features preserved in V 10597, reconsider the taxonomy of this specimen, and discuss its possible implications for our understanding of troodontid evolution.

2 Systematic paleontology

Theropoda Marsh, 1881
Coelurosauria Huene, 1920
Maniraptora Gauthier, 1986
Troodontidae Gilmore, 1924
***Philovenator curriei* gen. et sp. nov.**

Saurornithoides mongoliensis Currie & Peng, 1994

Etymology The name honors Dr. Philip J. (“Phil”) Currie for his contributions to the study of maniraptoran dinosaurs, including the initial description of IVPP V 10597. The genus name also recalls the combining form of the Greek φιλεῖν (*philein*), “to love”, and the Latin *venator*, “hunter”, suggesting a lover of the hunt.

Holotype IVPP V 10597, a nearly complete left hindlimb, including the following elements: nearly complete femur, partial tibia, partial fibula, astragalus-calcaneum complex, distal tarsals III and IV, metatarsals I, II, III, IV, and V, pedal phalanges I-1, II-1, II-2, II-3, III-1, III-2, IV-1, IV-2, IV-3, IV-4, and IV-5 (Fig. 1).



Fig. 1 Photographs of IVPP V 10597, left femur in proximal (A), anterior (B), posterior (C), medial (D) and lateral (E) views; proximal portion of left tibiotarsus in lateral view (F); distal portion of left tibiotarsus in anterior (G), posterior (H), medial (I), lateral (J) and distal (K) views; left pes in proximal (L), anterior (M), posterior (N), medial (O), and lateral (P) views

Locality and horizon Bayan Mandahu, “North Canyon” locality, Wulatehouqi, Nei Mongol; Wulansuhai Formation, Campanian, Upper Cretaceous (Jerzykiewicz et al., 1993).

Diagnosis A small troodontid that can be distinguished from other known members of the group by the presence of the following autapomorphies: a prominent process on the medial side of the femoral shaft slightly proximal to the distal end, a sheet-like tibial cnemial crest that expands significantly anteriorly, astragalo-calcaneal hemicondyles that are deep anteroposteriorly and separated by a deep and narrow groove, a proportionally extremely long and slender tarsometatarsus (tarsometatarsus/femur length ratio 1.25, tarsometatarsus length/width ratio 22.0), anteroposterior depth much greater than transverse width at the mid-shaft of the tarsometatarsus, and a prominent, elongate posterior flange that extends along most of the length of metatarsal IV and is about equal in depth to the metatarsal shaft.

3 Ontogenetic assessment

IVPP V 10597 is small for a Late Cretaceous troodontid, indicating that this specimen represents a juvenile and/or simply belongs to a species with small adult body size. In order to assess the ontogenetic status of V 10597, we took a thin section from the mid-shaft of the femur, where the diameter measures 5.40 mm (Fig. 2). This transverse section shows a very thin compacta (0.48 mm thick) surrounding an exceptionally large central medullary cavity (4.45 mm in diameter), attesting to the occurrence of substantial periosteal expansion. The cortex is fibrolamellar bone with predominantly longitudinal vascular canals. The degree of vascularization is low, and only primary osteons can be observed in the thin section. One line of arrested growth (LAG) is present in the inner region of the compacta. The bone tissue immediately preceding the LAG was deposited more slowly than the tissue beyond the LAG. Evidence for this is the lower density, smaller size, and somewhat more flattened morphology of the osteocyte lacunae in the tissue preceding the LAG, as well as the higher degree of organization of the bone apatite crystals. This tissue together with the LAG is best interpreted as an annulus recording a marked deceleration in growth, presumably representing the end of a yearly growth cycle. There is no external fundamental system (EFS) of closely packed peripheral growth lines.



Fig. 2 Histological section from the femoral shaft of IVPP V 10597

The presence of at least two growth cycles suggests that V 10597 was at least in its second year of life. The large size of the medullary cavity, which may have destroyed part of the growth record as it expanded, implies that the specimen may well have been even older.

Some histological evidence might be taken to support the inference that V 10597 was a juvenile. The presence of fibro-lamellar bone tissue suggests a rapid rate of bone deposition. This type of bone tissue is characteristic of juveniles and, more generally, is deposited during periods of rapid growth in the life of an animal (Chinsamy, 1995). The absence of secondary osteons suggests that the observed tissue had not undergone any repair, adding to the impression of juvenile status. Some previous studies have suggested that small-bodied birds, non-avian dinosaurs and pterosaurs often lack secondary osteons in their long bones (Padian et al., 2004), but it must be noted that there are some exceptions: secondary osteons are present in sub-adult or adult *Confuciusornis* (Zhang et al., 1998), *Anchiornis* (Xu et al., 2009), *Orodromeus*, *Scutellosaurus* (Padian et al., 2004), and *Psittacosaurus* (unpublished data). In general, V 10597 is similar in many of its histological features to a previously described juvenile *Troodon formosus* (Varicchio, 1993). However, some contrary evidence weighs heavily against the interpretation that V 10597 represents a juvenile rather than a subadult. Available data indicate that juvenile theropod dinosaurs of even moderately sized taxa, such as derived troodontids, tended to grow quickly (Erickson et al., 2004, 2007). V 10597 was small despite being at least in its second year of life, implying a relatively slow growth rate despite the presence of fibro-lamellar bone. This is corroborated to some extent by the low degree of vascularization of the bone cortex and the predominance of longitudinal vascular canals in the histological section. A recent comprehensive analysis on paravian histology shows that there is a scale dependent histological continuum in this clade (Erickson et al., 2009). V 10597 is histologically similar to species with adult femoral lengths of less than ~90 mm, whereas taxa close in size to the much larger *L. tani* (~260 mm femoral length) show plexiform vascularization. This suggests that V 10597 would not have grown substantially larger even had its ontogenetic trajectory been allowed to continue. Accordingly, it is unlikely that this specimen is a juvenile of *L. tani*, *S. mongoliensis* or any other similarly-sized troodontid.

Finally, the degree of skeletal fusion seen in V 10597 indicates a relatively late ontogenetic stage. The preserved articular surfaces of all elements of V 10597 are well defined. The astragalus and calcaneum are completely fused to each other, and this complex is partially fused to the tibia. Similarly, the distal tarsals are completely fused to each other and to the proximal ends of the metatarsals. In summary, the available information indicates that V 10597 was probably at a relatively late ontogenetic stage (probably subadult) at the time of death. It appears to represent a new small-bodied taxon, designated *Philovenator curriei* in this paper.

4 Description and comparisons

Because IVPP V 10597 has been well described in the past (Currie and Peng, 1994), we restrict ourselves to highlighting important morphological features that have implications for the taxonomic and/or ontogenetic status of the specimen (Fig. 1). V 10597 comprises a nearly complete left hindlimb, including the following elements: nearly complete femur, partial tibia, partial fibula, astragalus-calcaneum complex, distal tarsals III and IV, metatarsals I-V, and complete phalangeal series for digits II and IV as well as phalanges I-1, III-1 and III-2. As a living individual, V 10597 was estimated by Currie and Peng (1994) to have been 0.5~0.7 m long based on comparisons with other troodontids, and can be estimated to have weighed about 0.9 kg based on an empirical bivariate equation (Christiansen and Fariña, 2004).

The femur has fused greater and lesser trochanters that form an anteroposteriorly wide trochanteric crest (about twice as wide as the mid-shaft of the femur, making the crest proportion-

ally wider than in most other non-avian theropods) as in derived troodontids (Makovicky and Norell, 2004; Norell et al., 2009). The trochanteric crest extends further proximally than the femoral head, as in derived troodontids such as *Troodon*, and is separated from it by a groove (Fig. 1A-C). These are derived features present in some derived alvarezsauroids and oviraptorosaurs (Xu et al., 2007, 2010). The ridge-like posterior trochanter is proximodistally long and positioned centrally on the posterior surface (Fig. 1C), as in derived troodontids (Norell et al., 2009; Xu et al., 2011b) but in contrast to the shorter and more laterally located trochanter seen in many other paravians such as *Sinovenator* and *Rahonavis* (Forster et al., 1998; Xu et al., 2002). The lateral ridge is represented by a prominent tuberosity (Fig. 1E), which is proximally separated from the femoral shaft by a notch in anterior or posterior view (Fig. 1B) as in *Troodon*. Like that of *Troodon*, the lateral ridge of V 10597 is intermediate in position between those of some flying forms, such as the dromaeosaurid *Rahonavis* and the avialan *Sapeornis* (Zhou and Zhang, 2003), and those of most other non-avian theropods. In the former, the lateral ridge is centrally located on the lateral surface of the femoral shaft, whereas in the latter it is close to the posterior edge. A prominent process occurs on the medial side of the femoral shaft, just proximal to the distal end (Fig. 1D). This feature is not known in any other theropod except *Linhevenator*, in which a similarly positioned but much more weakly developed eminence is present (Currie and Peng, 1994; Xu et al., 2011b). A weak, short longitudinal ridge is present on the lateral side of the femoral shaft near the distal end, another feature also seen in *Linhevenator* but unknown in most other paravians. However, a similar ridge is also present in some other maniraptorans, such as basal alvarezsauroids. As in most troodontids, there is a wide longitudinal groove on the anterior surface of the distal end of the femur, suggesting the presence of a shallow patellar sulcus (Fig. 1B).

The tibiotarsus has a strongly expanded proximal end, with a maximum anteroposterior depth measuring more than 1.5 times that of the distal end. The great depth of the proximal end is mostly due to the prominence of the anteriorly expanded cnemial crest, which is a thin sheet (Fig. 1F) rather than a robust crest as seen in most other non-avian theropods. Distally, the proximal tarsals are partially fused to the distal end of the tibia to form an integrated tibiotarsus (Fig. 1G-K). A short flange is present on the lateral edge of the posterior surface of the distal end as in many maniraptorans, including other troodontids; however, it is more lateral and less obliquely oriented in V 10597 than in other maniraptorans in which the flange is present. The posterior surface of the distal end is slightly concave transversely, and lacks the longitudinal central eminence seen in many maniraptorans including other troodontids.

The astragalus and calcaneum are completely fused to each other without any sign of a suture, and the astragalus-calcaneum complex is identical in overall shape to those of other troodontids (Xu, 2002). Nevertheless, the astragalus-calcaneum complex shows some differences from those of most non-avian theropods, including other troodontids. The two hemicondyles of the main body of the astragalus-calcaneum complex are prominent and are particularly deep anteroposteriorly (the anteroposterior depth/proximodistal length ratio for the medial hemicondyle is 1.6, a much greater value than in other troodontids). As a result, the intercondylar groove is narrow and deep in distal view. The base of the ascending process has a considerable transverse convexity and partially wraps around the medial margin of the tibial shaft, in contrast to the flat morphology seen in most other theropods. The ascending process extends to the lateral edge of the main body of the complex, preventing the formation of a notch for articulation with the fibula as in most other non-avian theropods. Rather than articulating with the astragalus-calcaneum complex, the fibula forms a tapering distal end that seems to terminate about 1 cm proximal to the main body of the complex (Fig. 1H and J).

The distal tarsals are fused to each other and to the proximal ends of the metatarsals, forming a tarsometatarsus (Fig. 1L-P) as in *Sinusonasus* (Xu and Wang, 2004) and probably

Zanabazar (Norell et al., 2009). The proximal surface of the fused distal tarsals bears two shallow concavities (Fig. 1L), which are separated by a large central eminence and represent articular surfaces for the two hemicondyles of the main body of the astragalus-calcaneum complex.

The tarsometatarsus is significantly longer than the femur (measuring about 125% of femoral length), a feature unknown in other non-avian theropods. In some derived alvarezsauroids, the tarsometatarsus is slightly longer than the femur (Chiappe et al., 2002; Xu et al., 2010, 2011a). In anterior view, the tarsometatarsus is extremely slender, with a length to midshaft width ratio of about 22.0. This ratio is significantly greater than in other troodontids (the ratio is about 9.0 in *Sinovenator*, 12.0 in *Sinusonasus*, and 6.5 in *Troodon*). The tarsometatarsus is also significantly deeper anteroposteriorly than wide transversely, with a depth/width ratio (measured at mid-length) of 1.6. This stands in stark contrast to other non-avian theropods, in which the tarsometatarsus is wider than deep. A deep longitudinal groove is present between the dorsal surfaces of metatarsal II and IV near proximal end of the tarsometatarsus, a feature also seen in some derived troodontids (Russell, 1969; Xu et al., 2011b).

Metatarsal II is short and slender, as in other troodontids (Makovicky and Norell, 2004). V 10597 differs from basal troodontids (Xu, 2002), but resembles some derived troodontids (Russell, 1969; Xu et al., 2011b), in that the distal fifth of metatarsal II is strongly compressed transversely. The anterior surface of this part of the metatarsal is thus ridge-like, and almost invisible in anterior view. Metatarsal III has very limited anterior exposure (only the distal half is visible in anterior view, in contrast to about two-thirds or even more in other troodontids) and even more limited posterior exposure (only the proximalmost and distalmost portions are visible in posterior view). A weak longitudinal groove occurs on the anterior surface of metatarsal III near the distal end. In *Linhevenator*, metatarsal III bears a groove that is similarly positioned, but is deeper and extends farther distally (Xu et al., 2011b). In V 10597, a distinct extensor fossa is seen immediately proximal to the distal end of metatarsal III as in some other troodontids. The distal end of metatarsal III is similar in size to that of metatarsal IV, whereas in more basal troodontids such as *Sinovenator* the distal end of metatarsal III is considerably larger than that of metatarsal IV (Xu, 2002). Metatarsal IV is much wider and considerably longer than metatarsal II. An extremely large posterior flange extends along most of the length of metatarsal IV, whereas in other troodontids this flange is shorter. The prominent posterior flange is about as deep as the shaft. The ratio of the anteroposterior depth of metatarsal IV (including the flange) to its transverse width is about 3.3, measured one-third of the way from the proximal end of the bone. Such a high value of the depth/width ratio is otherwise unknown among non-avian theropods, although metatarsal IV is anteroposteriorly deep in troodontids in general. The anterior surface of the distalmost part of metatarsal IV is very narrow, but metatarsal IV lacks the abrupt narrowing near the distal end seen in some derived troodontids (Russell, 1969; Xu et al., 2011b). Metatarsal V is short (about one-fifth of the length of metatarsal III) as in derived troodontids (Russell, 1969; Xu et al., 2011b), but in contrast to basal troodontids in which metatarsal V is typically longer (Xu, 2002).

The second pedal digit displays two features reminiscent of dromaeosaurids and some derived troodontids (Ostrom, 1969; Xu et al., 2011b): pedal phalanx II-1 has a proximoventral heel, although this structure is only weakly developed, and pedal phalanx II-2 bears a large proximoventral heel and strongly skewed hemicondyles in lateral view. Pedal phalanx II-2 is less than half as long as II-1, a condition seen in other derived troodontids. As in *Linhevenator* (Xu et al., 2011b) and *Sinusonasus*, pedal phalanx IV-1 is relatively long (slightly longer than II-1, rather than considerably shorter than II-1 as in most other maniraptorans).

5 Phylogenetic analysis

Although much smaller than derived troodontids such as *Troodon*, *Saurornithoides*, *Zanabazar*, and *L. tani* (Russell, 1969; Norell et al., 2009; Xu et al., 2011b), *Philovenator curriei* shares some unique features with these taxa: a ridge-like posterior trochanter centrally located on the posterior surface of the femoral shaft, a metatarsal II whose distal fifth is highly compressed and has a ridge-like dorsal surface, a transversely compressed metatarsal III with only limited exposure in both anterior and posterior views, and a very short pedal phalanx II-2. These features suggest that *P. curriei* is a derived troodontid closely related to *L. tani*, *Saurornithoides*, *Troodon* and *Zanabazar*.

In order to test this phylogenetic hypothesis, we conducted a numerical phylogenetic analysis by coding *P. curriei* into a recently published data matrix designed to analyze coelurosaurian relationships (Xu et al., 2011b) (see Appendix 1 for scorings). It should be noted that we did not include the derived small troodontid *Talos sampsoni* in the analysis because this taxon was described very recently (Zanno et al., 2011). The matrix was analyzed using the software package TNT (Goloboff et al., 2008), using a traditional search strategy with default settings except the following: 10000 maximum trees in memory and 1000 replications. The analysis found 36 most parsimonious trees, a simplified strict consensus of which is shown in Fig. 3A. *P. curriei* was placed in a derived troodontid clade that also includes *L. tani*, *Saurornithoides*, *Troodon* and *Zanabazar*. However, interrelationships within this clade could not be resolved. Because *P. curriei* is known only from the hindlimb, we ran an additional analysis on a reduced data matrix containing 10 paravian taxa and 20 hindlimb characters that are known to be informative with respect to troodontid interrelationships (Appendix 2). This analysis produced eight most parsimonious trees, the strict consensus of which is shown in Fig. 3B. *P. curriei* was placed as the sister taxon to *L. tani*.

6 Discussion

Philovenator curriei differs from other troodontids, including *L. tani*, in many features. The most unusual feature of *P. curriei* is that the anteroposterior depth of the tarsometatarsus greatly exceeds its transverse width. This stands in stark contrast to the situation in other known non-avian theropods, in which the transverse width of the tarsometatarsus (or metatarsus, in taxa without fused distal tarsals) is greater than the anteroposterior depth

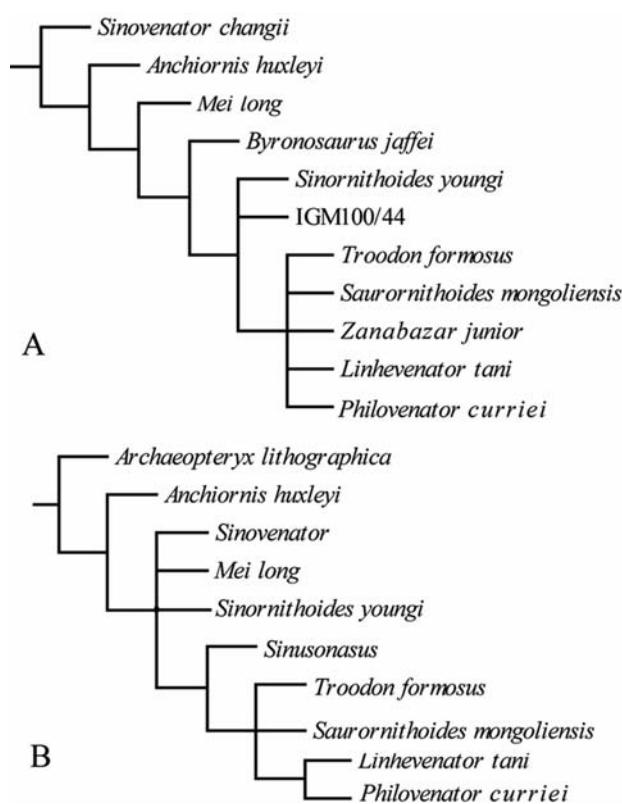


Fig. 3 Systematic position of *Philovenator curriei* gen. et sp. nov. within the Troodontidae

A. Simplified strict consensus of 36 most parsimonious trees (tree length = 1308 steps, CI = 0.33, and RI = 0.74); B. Strict consensus of 8 most parsimonious trees (tree length = 30 steps, CI = 0.80, and RI = 0.88)

(although in some non-avian theropods the discrepancy is slight). A tarsometatarsus whose anteroposterior depth significantly exceeds its transverse width is also known in some derived birds, mainly reflecting the presence of prominent crista hypotarsi. In *P. curriei* the low width/depth ratio results primarily from the prominence of the ventral flange on metatarsal IV. Other features that distinguish *P. curriei* include a prominent process on the medial side of the femoral shaft slightly proximal to the distal end (weakly developed in *L. tani*), a sheet-like tibial cnemial crest that expands significantly anteriorly (condition unknown in *L. tani*), astragalo-calcaneal hemicondyles that are deep anteroposteriorly and separated by a deep and narrow groove (condition unknown in *L. tani*), and a prominent, elongate posterior flange that extends along most of the length of metatarsal IV and is about equal in depth to the metatarsal shaft.

P. curriei also differs from the sympatric *L. tani* in the following aspects of its limb proportions: proportionally much longer and more slender metatarsus (metatarsal III/femoral length ratio 1.2, compared to 0.7 in *L. tani* holotype; metatarsus length/width ratio 22.0, compared to 7.3 in *L. tani* holotype), more limited dorsal exposure of metatarsal III (only distal third of metatarsal III visible in anterior view, compared to all but proximal portion visible in *L. tani* holotype), proportionally more slender metatarsal IV (metatarsal IV only slightly more robust than metatarsal II, whereas discrepancy is much greater in *L. tani* holotype), proportionally more slender pedal phalanx II-2 (phalanx II-2 length/height ratio 1.6, compared to 1.2 in *L. tani* holotype), and proportionally smaller pedal phalanx II-3 (phalanx II-3/II-1 length ratio about 1.3, compared to 1.8 in *L. tani* holotype). Although many of these proportional differences may be related to the sub-adult status of V 10597 (Holtz, 1994; Farlow et al., 2000; Currie, 2003), some of these differences are likely to be taxonomic in nature. For example, even juvenile deinonychosaurians show normally proportioned second pedal claws (G. Erickson, personal communication), suggesting that the relatively small second pedal claw in *P. curriei* might be a diagnostic feature for the taxon.

Although represented by limited material, *P. curriei* is significant in that it increases not only the known taxonomic diversity, but also the morphological disparity, of Late Cretaceous troodontid dinosaurs. Most obviously, *P. curriei* is much smaller than most other Late Cretaceous troodontids (Xu et al., 2011b; Zanno et al., 2011). This indicates significant size disparity among Late Cretaceous troodontids, resembling the situation in some other coelurosaurian groups such as the Dromaeosauridae. Furthermore, the hindlimbs, particularly the pes, of *P. curriei* are extremely specialized, as indicated by the proportionally extremely long, transversely slender, and anteroposteriorly deep tarsometatarsus. The new find indicates that morphological disparity among Late Cretaceous troodontids is greater than previously known.

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References

- Barsbold R, Osmólska H, Kurzanov S M, 1987. On a new troodontid (Dinosauria, Theropoda) from the Early Cretaceous of Mongolia. *Acta Palaeont Pol*, **32**: 121–132
- Chiappe L M, Norell M A, Clark J M, 2002. The Cretaceous, short-armed Alvarezsauridae: *Mononykus* and its kin. In: Chiappe L M, Witmer L M eds. Mesozoic Birds: Above the Heads of Dinosaurs. Berkeley: University of California Press. 87–120
- Chinsamy A, 1995. Ontogenetic changes in the bone histology of the Late Jurassic ornithopod *Dryosaurus lettowvorbecki*. *J Vert*

- Paleont., **15**: 96–104
- Christiansen P, Fariña R A, 2004. Mass prediction in theropod dinosaurs. *Hist Biol.*, **16**: 85–92
- Currie P, Peng J H, 1994. A juvenile specimen of *Saurornithoides mongoliensis* from the Upper Cretaceous of northern China. *Can J Earth Sci.*, **30**: 2224–2230
- Currie P J, 2003. Allometric growth in tyrannosaurids (Dinosauria: Theropoda) from the Upper Cretaceous of North America and Asia. *Can J Earth Sci.*, **40**: 651–665
- Erickson G M, Makovicky P J, Currie P J et al., 2004. Gigantism and comparative life-history parameters of tyrannosaurid dinosaurs. *Nature*, **430**: 772–775
- Erickson G M, Rauhut O W M, Zhou Z et al., 2009. Was dinosaurian physiology inherited by birds? reconciling slow growth in *Archaeopteryx*. *PLoS ONE*, **4**: e7390
- Erickson G M, Rogers K C, Varricchio D J, 2007. Growth patterns in brooding dinosaurs reveals the timing of sexual maturity in non-avian dinosaurs and genesis of the avian condition. *Biol Letters*, **3**: 558–561
- Farlow J O, Gatesy S M, Holtz T R et al., 2000. Theropod locomotion. *Am Zool.*, **40**: 640–663
- Forster C A, Sampson S D, Chiappe L M et al., 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science*, **279**: 1915–1919
- Goloboff P A, Farris J, Nixon K C, 2008. TNT, a free program for phylogenetic analysis. *Cladistics*, **24**: 774–786
- Holtz T R, 1994. The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). *J Vert Paleont.*, **14**: 480–519
- Jerzykiewicz T, Currie P J, Eberth D A et al., 1993. Djadokhta Formation correlative strata in Chinese Inner Mongolia: an overview of the stratigraphy, sedimentary geology, and paleontology and comparisons with the type locality in the pre-Altai Gobi. *Can J Earth Sci.*, **30**: 2180–2190
- Jerzykiewicz T, Russell D A, 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Res.*, **12**: 345–378
- Makovicky P J, Norell M A, 2004. Troodontidae. In: Weishampel D B, Dodson P, Osmólska H eds. *The Dinosauria*. 2nd ed. Berkeley: University of California Press. 184–195
- Norell M A, Makovicky P J, Bever G S et al., 2009. A review of the Mongolian Cretaceous dinosaur *Saurornithoides* (Troodontidae: Theropoda). *Am Mus Novit.*, (3654): 1–63
- Osborn H F, 1924. Three new Theropoda, *Protoceratops* zone, central Mongolia. *Am Mus Novit.*, (144): 1–12
- Osmólska H, 1987. *Borogovia gracilicrus* gen. et sp. n., a new troodontid dinosaur from the Late Cretaceous of Mongolia. *Acta Palaeont Pol.*, **32**: 133–150
- Ostrom J H, 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull Peabody Mus Nat Hist, Yale Univ.*, **30**: 1–165
- Padian K, Horner J R, De Ricqles A, 2004. Growth in small dinosaurs and pterosaurs: the evolution of archosaurian growth strategies. *J Vert Paleont.*, **24**: 555–571
- Russell D A, 1969. A new specimen of *Stenonychosaurus* from the Oldman Formation (Cretaceous) of Alberta. *Can J Earth Sci.*, **6**: 595–612
- Varricchio D J, 1993. Bone microstructure of the Upper Cretaceous theropod dinosaur *Troodon formosus*. *J Vert Paleont.*, **13**: 99–104
- Wilson M C, Currie P J, 1985. *Stenonychosaurus inequalis* (Saurischia: Theropoda) from the Judith River Oldman Formation of Alberta: new findings on metatarsal structure. *Can J Earth Sci.*, **22**: 1813–1817
- Xu X, 2002. Deinonychosaurian fossils from the Jehol Group of western Liaoning and the coelurosaurian evolution. Ph. D. Dissertation. Beijing: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. 1–322
- Xu X, Norell M A, Wang X L et al., 2002. A basal troodontid from the Early Cretaceous of China. *Nature*, **415**: 780–784
- Xu X, Sullivan C, Pittman M et al., 2011a. The first known monodactyl non-avian dinosaur and the complex evolution of the Alvarezsauroidea hand. *Proc Nat Acad Sci USA*, **108**: 2338–2342
- Xu X, Tan Q W, Sullivan C et al., 2011b. A short-armed troodontid dinosaur from the Upper Cretaceous of Inner Mongolia and its implications for troodontid evolution. *PLoS ONE*, **6**: 1–12
- Xu X, Tan Q W, Wang J M et al., 2007. A gigantic bird-like dinosaur from the late Cretaceous of China. *Nature*, **447**: 844–847
- Xu X, Wang D Y, Sullivan C et al., 2010. A basal parvursorine (Theropoda: Alvarezsauroidea) from the Upper Cretaceous of China. *Zootaxa*, (2413): 1–19
- Xu X, Wang X L, 2004. A new troodontid (Theropoda: Troodontidae) from the Lower Cretaceous Yixian Formation of western Liaoning, China. *Acta Geol Sin-Engl*, **78**: 22–26
- Xu X, Zhao Q, Norell M A et al., 2009. A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian

- origin. *Chin Sci Bull*, **54**: 430–435
- Zanno L E, Varricchio D J, O'Connor P M et al., 2011. A new troodontid theropod, *Talos sampsoni* gen. et sp. nov., from the Upper Cretaceous Western Interior Basin of North America. *PLoS ONE*, **6**: e24487
- Zhang F C (张福成), Hou L H (侯连海), Ouyang L (欧阳浪), 1998. Osteological microstructure of *Confuciusornis*: preliminary report. *Vert PalAsiat* (古脊椎动物学报), **36**(2): 126–135 (in Chinese with English summary)
- Zhou Z H, Zhang F C, 2003. Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China. *Can J Earth Sci*, **40**: 731–747

Appendix 1 Scorings for *Philovenator curriei* gen. et sp. nov.

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Appendix 2 Character list (all multi-state characters are ordered)

1. Femur, trochanteric crest, size (measured by anteroposterior width relative to the femoral mid-shaft): moderate (0) or large, about twice as wide (1)
2. Femur, the trochanteric crest higher than femoral head: absent (0) or present (1)
3. Femur, posterior trochanter, location in mediolateral direction: close to lateral edge (0) or centered on posterior surface (1)
4. Femur, a medial eminence near distal end: absent (0) or present (1)
5. Tarsometatarsus, transverse width relative to dorsoventral depth (measured at mid-length): much greater in transverse width (0), sub-equal in transverse width and dorsoventral depth (1) or much greater in dorsoventral depth (2)
6. Tarsometatarsus, longitudinal, deep groove between dorsal surfaces of metatarsal II and IV near proximal end: absent (0) or present (1)
7. Metatarsal II, dorsal surface of distal portion near distal end: wide and well exposed in anterior view (0) or ridge-like and invisible in anterior view (1).
8. Metatarsal II, length relative to metatarsal IV: slightly shorter (0) or considerably shorter (1)
9. Metatarsal III, dorsal exposure: along whole length (0) or extensive but not whole length (1) or limited (2)
10. Metatarsal III, ventral exposure: along whole length (0) or extensive but not whole length (1) or limited (2)
11. Metatarsal III, dorsal surface of distal portion, a longitudinal groove: absent (0) or present (1)
12. Metatarsal IV, size relative to metatarsal II (measured by transverse width): slightly greater (0) or much greater (1)
13. Metatarsal IV, dorsoventral depth relative to transverse width (measured at mid-length): considerably smaller (0) or slightly greater (1) or much greater (2)
14. Metatarsal IV, dorsal surface near distal end: wide (0) or substantially narrower than that of more proximal portion (1)
15. Pedal phalanx II-2, proximoventral heel, size: moderate (0) or enormous (1)
16. Pedal phalanx II-3, size relative to II-1 (measured by length ratio (tip to proximoventral end of the ungual): subequal or shorter (0) or considerably longer (1)
17. Pedal phalanx IV-1, length relative to II-1: considerably shorter (0) or sub-equal (1)
18. Femur, notch between lateral ridge and femoral shaft: absent (0) or present (1)
19. Metatarsal V, length relative to metatarsal III: relatively long (0) or very short (1)
20. Pedal II-1, length relative to II-2: less than (0) or more than twice as long as the latter (1)

Matrix

<i>Archaeopteryx lithographica</i>	000000000000?0000?00
<i>Anchiornis huxleyi</i>	?????000000000000?00
<i>Linhevenator tani</i>	1?11111121121111??1
<i>Philovenator</i>	11112111221120111111
<i>Sinusonasus</i>	01001001110010001000
<i>Sinovenator</i>	00001001000010000000
<i>Mei long</i>	00?00??100?11?000010
<i>Sinornithoides youngi</i>	000?1??1?0?11?000?00
<i>Troodon formosus</i>	11101111201?100?111
<i>Saurornithoides mongoliensis</i>	101?1?111?011110?0?1