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A basal parvicursorine (Theropoda: Alvarezsauridae) from the Upper Cretaceous of China

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Abstract

A new alvarezsaurid theropod, *Xixianykus zhangi* **gen. et sp. nov.**, is described based on a partial postcranial skeleton collected from the Upper Cretaceous Majiacun Formation of Xixia County, Henan Province. The new taxon can be diagnosed by the following autapomorphies: sacral rib-transverse process complexes and zygapophyses fused to form separate anterior and posterior laminae; distinct fossa dorsal to antitrochanter on lateral surface of ilium; short ridge along posterior surface of pubic shaft near proximal end; distinct depression on lateral surface of ischium near proximal end; sharp groove along posterior surface of ischium; distal end of femur with transversely narrow ectocondylar tuber that extends considerable distance proximally as sharp ridge; transversely narrow tibial cnemial crest with sharp, ridge-like distal half; lateral margin of tibiotarsus forms step near distal end; fibula with substantial extension of proximal articular surface onto posterior face of posteriorly curving shaft; distal tarsals and metatarsals co-ossified to form tarsometatarsus; and sharp flange along anteromedial margin of metatarsal IV near proximal end. Cladistic analysis places this taxon as a basal parvicursorine within the Alvarezsauridae, a position consistent with the presence of several incipiently developed parvicursorine features in this taxon and also with its relatively early geological age. A brief analysis of vertebral functional morphology, together with data from the hindlimb, suggests that parvicursorines represent extreme cursors among non-avian dinosaurs.

Key words: Late Cretaceous, Majiacun Formation, Parvicursorinae, Theropoda, cursoriality

Introduction

Alvarezsaurids are a group of small maniraptoran theropod dinosaurs with highly modified forelimbs and elongate hindlimbs (Bonaparte 1991; Novas 1996, 1997; Chiappe *et al.* 2002), though a large-sized taxon has been recently referred to the group (Turner *et al.* 2009). Derived members of this group (Parvicursorinae, here defined as the most inclusive clade including *Parvicursor remotus* but not *Patagonykus puertai*) display many derived features that also occur in some birds, and were originally interpreted as very basal avians (Perle *et al.* 1993, 1994; Chiappe *et al.* 1996, 1998). However, most recent studies suggest that parvicursorines and other alvarezsaurids are non-avian coelurosaurs (Sereno 1999, 2001; Norell *et al.* 2001; Novas & Pol 2002; Xu 2002). Alvarezsaurid fossils have previously been recovered from the Upper Cretaceous of Inner Mongolia, but the known material is extremely fragmentary (Zhao X. J. personal communication). In the present paper, we describe the first diagnosable alvarezsaurid taxon from China based on a specimen collected from the Upper Cretaceous Majiacun Formation of Zhoujiagou, Xixia County, Henan Province (Wang *et al.* 2008). Previously, alvarezsaurid fossils have been recovered from only the northern part of Asia, so this new find extends the fossil record of the group a considerable distance southwards to a relatively low latitude part of the continent (Fig. 1).

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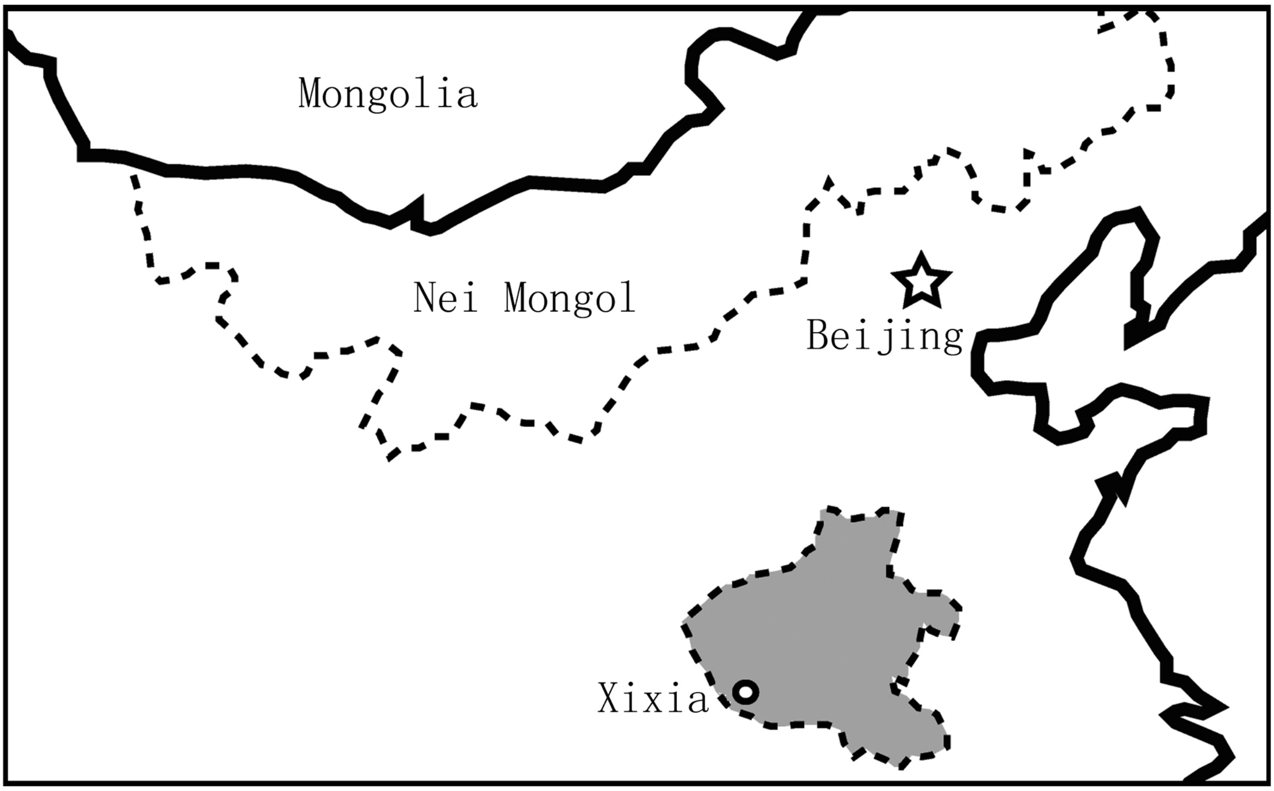

FIGURE 1. Geographic location of the *Xixianykus zhangi* type locality. Gray area: Henan Province. Circle: Xixia County, which includes the type locality.

Systematic paleontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Alvarezsauridae Bonaparte, 1991

Parvicursorinae Karhu & Rautian, 1996

Xixianykus zhangi gen. et sp. nov.

Etymology. Generic name from Xixia (area of origin), and *onyx* (Greek), claw; specific name is in honor of Prof. Zhang Wentang, who has contributed greatly to the study of paleontology in Henan Province. The taxon name is pronounced as 'SHEE-shya-nye-kus jong-eye'.

Holotype. XMDFEC V0011 (Xixia Museum of Dinosaur Fossil Eggs of China), a partial, articulated postcranial skeleton including five posterior dorsal vertebrae, a complete synsacrum, two anterior caudal vertebrae, a few dorsal ribs and gastralia, both ilia, the right pubis and ischium, and most of the right hindlimb (Figs 2, 3). A cast of the holotype is housed at the Institute of Vertebrate Paleontology & Paleoanthropology, Beijing (cast catalog number: IVPP FV1788)

Type locality and horizon. Zhoujiagou, Yangcheng, Xixia County, Henan Province. Majiacun Formation. The fossil-bearing beds are considered to be late Coniacian to Santonian in age based on invertebrate and plant fossils, including bivalves, gastropods, conchostracans, and ostracods (Wang *et al.* 2008).

Diagnosis. *Xixianykus zhangi* differs from other known alvarezsaurids in possessing the following autapomorphies: sacral rib-transverse process complexes and zygapophyses fused to form separate anterior and posterior laminae; distinct fossa dorsal to antitrochanter on lateral surface of ilium; short ridge along posterior surface of pubic shaft near proximal end; distinct depression on lateral surface of ischium near proximal end; sharp groove along posterior surface of ischium; distal end of femur with transversely narrow ectocondylar tuber that extends considerable distance proximally as sharp ridge; transversely narrow tibial cnemial crest with sharp, ridge-like distal half; lateral margin of tibiotarsus forms step near distal end; fibula with substantial extension of proximal articular surface onto posterior face of posteriorly curving shaft; distal tarsals and metatarsals co-ossified to form tarsometatarsus; and sharp flange along anteromedial margin of metatarsal IV near proximal end.

Description and comparisons. Some fusion features of this specimen suggest a relatively advanced ontogenetic stage. The sacral vertebrae are fused to form a synsacrum, the astragalus and calcaneum are coossified both to each other and to the tibia, and the distal tarsals are coossified with the metatarsals to form a tarsometatarsus. However, neurocentral sutures are visible on most of the adequately preserved vertebrae, indicating that the individual had not reached full skeletal maturity (Irmis 2007). With a femoral length of 70 mm (Table 1), XMDFEC V0011 is smaller than the vast majority of adult non-avian theropod specimens (Turner *et al.* 2007), but some further growth would have occurred if the animal had survived to reach adulthood.

TABLE 1. Selected measurements (in mm) of the *Xixianykus zhangi* holotype.

Elements	
9th dorsal vertebra length (without condyle)	7.1
9th dorsal centrum height (posterior end)	4.4
10th dorsal vertebra length	8.5
10th dorsal centrum height (posterior end)	4.5
11th dorsal vertebra length	9.9
11th dorsal centrum height (posterior end)	5.0
12th dorsal vertebra length	11.0
12th dorsal centrum height (posterior end)	5.1
13th dorsal vertebra length	9.0
13th dorsal centrum height (posterior end)	*5.0
Synsacrum length	50.0
1st caudal vertebra length	9.0
1st caudal centrum height (posterior end)	4.4
Left ilium length	#39.0
Right ilium length	#47.5
Right pubis length	#53.0
Right ischium length	#47.0
Right femur length	70.1
Right tibiotarsus length	91.3
Right fibula length	*28.0
Right metatarsal II length	#58.0
Right metatarsal IV length	#68.4

* indicates the estimated complete length of a partial element
# indicates the preserved length of a partial element

FIGURE 2. Photographs of *Xixianykus zhangi* holotype in ventral (A) and dorsal (B) views. Scale bar = 10 mm.

The axial skeleton is represented by the five posteriormost dorsal vertebrae (identified as D9 through D13), a nearly complete synsacrum, and the two anteriormost caudal vertebrae. All but the most posterior of the preserved dorsal vertebrae are opisthocoelous, each bearing a convex, knob-like anterior projection that occupies only the central part of the articular surface (Fig. 4A–C). The last dorsal vertebra has a biconvex centrum as in *Mononykus* and *Shuvuuia* (Chiappe *et al*. 2002). The centra of all these dorsal vertebrae are considerably longer than either wide or tall (D9 has a centrum whose length is more than double either the height or width of the posterior end). All five dorsal centra are laterally compressed, but the degree of compression gradually decreases toward the posterior end of the dorsal series. The last dorsal centrum displays only marginal compression. The ninth dorsal centrum has a sharp ventral midline ridge, whereas the others each have a narrowly rounded ventral surface (Fig. 4D). Pleurocoels are not present in any of the preserved dorsal centra. The neural arches of D9 and D10 are centered on the centra, but those of the other dorsal vertebrae are shifted posteriorly. *Xixianykus* resembles other parvicursorines in that the parapophyses each sit at the end of a long stalk, and are level with the diapophyses (Chiappe *et al.* 2002). The parapophyseal and diapophyseal processes are merged into a horizontal lamina on the last dorsal vertebra, though the former process is distinctly shorter than the latter and the articular facets of the two processes remain separate. This suggests that the last dorsal rib was probably double-headed. Two additional features of the dorsal vertebrae are also typical of parvicursorines (Chiappe *et al.* 2002), but otherwise rare among theropods: the neural spines are low and relatively robust, and the zygapophyseal facets are strongly inclined, facing somewhat medially in the case of the prezygapophyses and somewhat laterally in the case of the postzygapophyses (Fig. 4A–C).

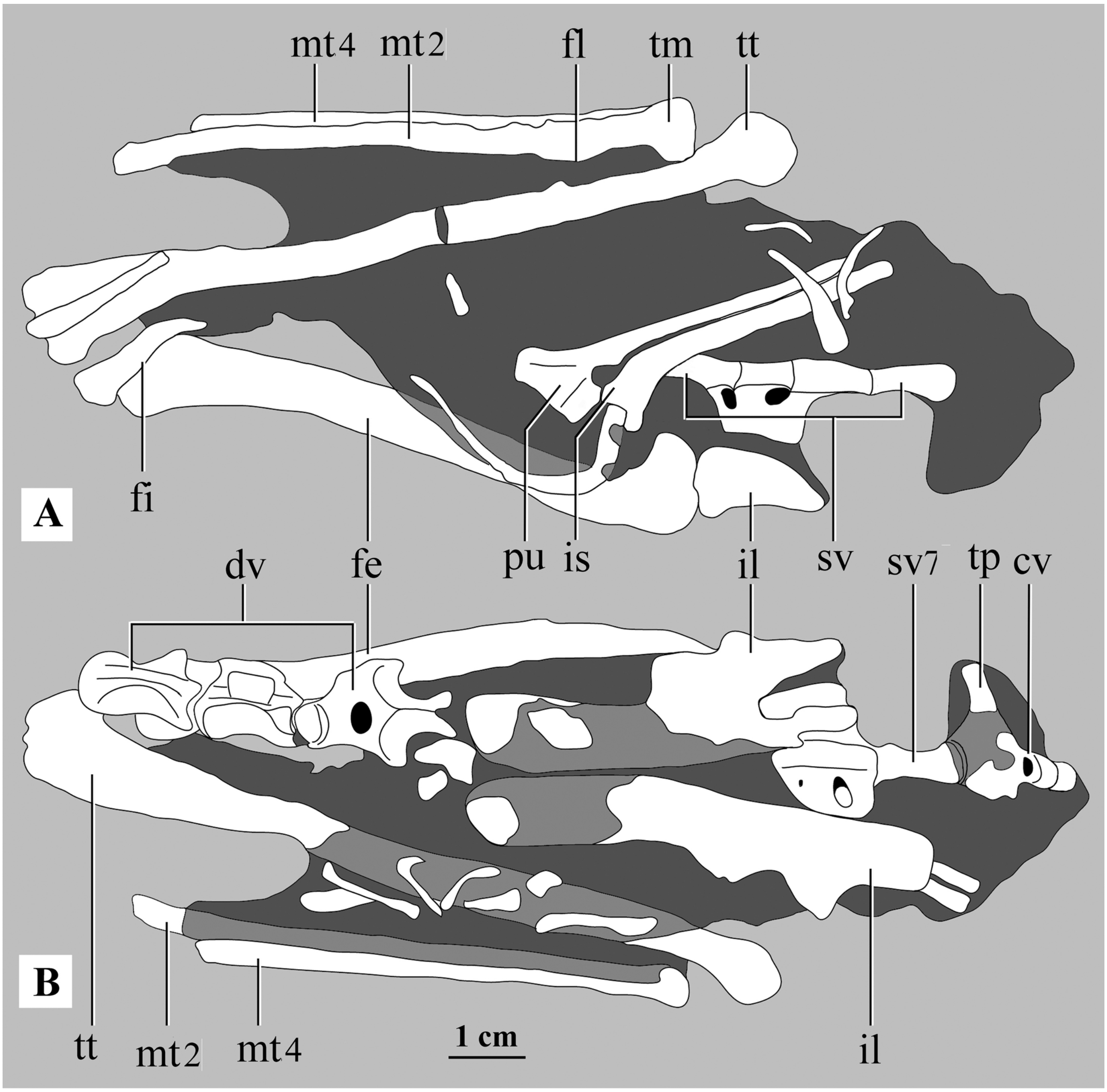

FIGURE 3. Line drawings of *Xixianykus zhangi* holotype in ventral (A) and dorsal (B) views. Abbreviations: cv, caudal vertebrae; dv, dorsal vertebrae; fe, femur; fi, fibula; fl, flange; il, ilium; is, ischium; mt2, metatarsal II; mt4, metatarsal IV; pu, pubis; sv, sacral vertebrae; sv7, seventh sacral vertebra; tm, tarsometatarsus; tp, transverse process; tt, tibiotarsus. Scale bar = 10 mm.

The synsacrum is formed by seven sacral vertebrae (S1–S7). The single most anterior and three most posterior ones are laterally compressed, but the second through fourth are considerably wider than tall. In contrast, all sacral vertebrae are laterally compressed in other alvarezsaurids (Chiappe *et al.* 2002). In S6 and S7 of *Xixianykus* the degree of lateral compression is extreme, pinching the ventral surfaces of the two successive centra into a prominent, laminar ventral keel that also extends onto the posterior portion of the fifth sacral centrum (Fig. 5). This ventral keel is probably a diagnostic feature for the Alvarezsauridae (Chiappe *et* *al.* 2002), but its ventral prominence and longitudinal extent vary among taxa. In *Patagonykus*, the ventral keel occupies only the two most posterior sacral vertebrae (Novas 1997), whereas in previously described Asian taxa the keel covers the three most posterior sacrals. In *Xixianykus* the ventral surface of the part of the synsacrum anterior to the keel is concave in lateral view (Fig. 5B–D), a feature also seen in other parvicursorines (Longrich & Currie 2009). The ventral surfaces of the first through fifth sacral centra also bear a shallow, wide longitudinal groove (Fig. 5B). A groove is also present in an unnamed alvarezsaurid from the Upper Cretaceous of Tugriken Shireh, Mongolia (referred to as the Tugriken Shireh alvarezsaur in Longrich & Currie 2009) and in *Alvarezsaurus* (Bonaparte 1991), but is shallower and shorter (covering fewer sacral vertebrae) in these taxa. *Xixianykus* also differs from the Tugriken Shireh alvarezsaur (Longrich & Currie 2009) in lacking a ventral keel on the first sacral centrum. The sacral rib-transverse process complexes and the zygapophyses of the anterior three sacral vertebrae, and of the fourth through sixth sacral vertebrae, are co-ossified with each other to form separate anterior and posterior horizontal laminae (Fig. 5A, B). The anterior lamina is transversely narrow but the posterior one is much wider, conforming to the posteriorly divergent ilia. Two small sacral fenestrae are present within the anterior lamina, and three more within the posterior. The third fenestra is located within an anterior extension of the large posterior lamina that is transversely very narrow and thus is barely visible in ventral view. Each fenestra is located near the transition between two sacral vertebrae. Lateral to the third fenestra is a much larger opening between the anterior and posterior laminae, which is roofed dorsally by the medially inclined iliac blade. The five fenestrae have smaller openings on the dorsal surfaces of the laminae than on the ventral surfaces. Although the dorsal surface of the synsacrum is obscured by the ilia anteriorly, it is clear that the neural spines of S4 through S6 are fused to each other, so that at least the posterior part of the synsacrum bears a median dorsal ridge.

Only two partial anterior caudal vertebrae are preserved and they represent the first and second caudal vertebrae (Ca1 and Ca2). They are procoelous, each bearing a prominent ball-like condyle on the posterior articular surface of the centrum. The centra are laterally compressed, and Ca1 bears a ventral midline ridge extending over all but the posterior end of the centrum (Fig. 5B). The neural arch is preserved only on Ca1 and is located on the anterior half of the centrum (Fig. 5C, D), as in other parvicursorines (Chiappe *et al.* 2002). The slightly anterolaterally oriented transverse processes of Ca1 are long (length of each process nearly three times width of centrum) and strap-like as in *Parvicursor* (Karhu & Rautian 1996) . They are anteriorly displaced on the centrum as in other alvarezsaurids, and their broad bases even extend slightly forward beyond the contact between the first caudal centrum and the synsacrum (Fig. 5A, B), a feature possibly also present in *P. remotus* (Karhu & Rautian 1996).

Both ilia are preserved, but neither is complete. As in other parvicursorines, the ilium is strongly inclined medially to contact the neural spines of the sacral vertebrae anteriorly, although the posterior end of the ilium diverges laterally away from the midline (Fig. 5A). The anterior margin of the iliac blade is slightly convex. The preacetabular process is relatively shallow compared to the more posterior portion of the iliac blade. The anteroventral corner of the iliac blade extends a significant distance ventrally, even protruding beyond the pubic peduncle. The posterior half of the ventral margin of the preacetabular process curves medially to slightly underlap the lateral margin of the anterior lamina of the synsacrum. The postacetabular process is largely broken away on each ilium. Immediately posterior and medial to the ischial peduncle of the ilium is a robust crest defining the brevis fossa, which tapers strongly toward the posterior end (Fig. 5B). The medial margin of the crest bears an articular facet for the large posterior lamina of the synsacrum. In lateral view, the ventral margin of the postacetabular process continues at nearly the same level onto the antitrochanter, not displaying the step-like configuration seen in most other non-avian theropods including basal alvarezsaurids. However, this feature is also seen in other parvicursorines in which the morphology of this region is known. The pubic peduncle extends anteroventrally from the acetabular region and has a sub-triangular lateral profile, as in other parvicursorines but in contrast to the sub-rectangular outline of the pubic peduncle in basal alvarezsaurids and most other non-avian coelurosaurs (Fig. 5C, D). The pubic peduncle is also unusual in being deflected medially relative to the iliac blade rather than lying in the same plane. It is difficult to assess whether this condition occurs in other alvarezsaurids, although it may be characteristic at least of parvicursorines. The articular surface of the pubic peduncle is composed of two facets: a small one oriented anterolaterally and a large, posteroventrally directed one that is transversely convex but much longer anteroposteriorly than wide transversely. The supracetabular crest originates midway along the length of the pubic peduncle and terminates over the anterior margin of the ischial peduncle (Fig. 5C, D). The anterior portion of the supracetabular crest extends farther laterally than the posterior portion, as in *Mononykus* (Chiappe *et al.* 2002), but in *Xixianykus* the crest terminates more posteriorly than in *Mononykus* and its lateral edge is convex in dorsal view. In more basal alvarezsaurids such as *Patagonykus* (Novas 1997), the supracetabular crest originates posterior to the pubic peduncle and its lateral edge is nearly straight in dorsal view (Fig. 5A). The small ischial peduncle is nearly transversely oriented and projects only slightly below the ventral edge of the postacetabular process. Lateral to the ischial articular facet is a large and robust antitrochanter, which is strongly expanded laterally as in *Mononykus* (Perle *et al.* 1994). However, the antitrochanter of *Xixianykus* seems to differ from that of *Mononykus* in that the contact surface for the femur faces almost straight anteriorly, rather than somewhat laterally. Accordingly, the antitrochanter of *Xixianykus* is nearly perpendicular to the edge of the supracetabular crest in dorsal view. There is a distinct fossa on the lateral surface of the iliac blade dorsal to the antitrochanter, a feature not previously reported in any alvarezsaurid. The acetabulum is partially closed by an extensive medial wall.

The right pubis is preserved, with only the distal end missing. The pubis is similar to that of other parvicursorines (Chiappe *et al.* 2002) in being closely appressed to the ischium throughout its entire length (Fig. 6). The proximal end is strongly laterally compressed, as in other alvarezsaurids (Hutchinson & Chiappe 1998), and forms a distinctive preacetabular tubercle like that seen in other parvicursorines (Hutchinson & Chiappe 1998). In *Xixianykus*, however, the tubercle is laterally compressed and anteroposteriorly short. The iliac peduncle is laterally concave and medially convex in proximal view as in other parvicursorines (Hutchinson & Chiappe 1998). The iliac articular facet is much longer anteroposteriorly than transversely, and is inclined slightly medially. The acetabular fossa of the pubis is sub-circular in proximal view, is inclined lateroventrally, and is bordered laterally by a distinct crest. The ischial peduncle is short and robust. Its sub-circular facet is similar in size to the acetabular fossa, as in basal alvarezsaurids (Novas 1997). In other parvicursorines, this facet is much smaller than the acetabular fossa (Hutchinson & Chiappe 1998). The orientation of the ischial facet relative to the long axis of the pubic shaft is intermediate between the conditions seen in basal alvarezsaurids and in other parvicursorines. In the former group, the facet is nearly parallel to the long axis of the pubic shaft, but in the latter group it forms a sharp angle with the pubic shaft. In *Xixianykus* the lateral surface of the proximal part of the pubis has two concavities, a large one occupying most of the available area and a small one on the lateral surface of the ischial peduncle. The medial surface of the proximal part of the pubis is slightly convex, but a proximodistally oriented shallow groove separates the ischial peduncle of the pubis from the rest of the surface. Immediately distal to the ischial peduncle is a distinct obturator notch (Fig. 6A, B). Distal to the notch is a sharp ridge along the posterior surface of the pubic shaft, close to the medial side, that is 4 mm in length. The shaft is mostly straight in lateral view except that the distal portion curves slightly anteriorly, a derived feature apparently also present in some other parvicursorines including *Shuvuuia* and the North American specimen described by Hutchinson & Chiappe (1998). In anterior or posterior view, the pubic shaft of *Xixianykus* is sigmoidal (Fig. 6C, D) as in *Patagonykus* (Novas 1997). The most proximal part of the pubic shaft is considerably laterally compressed, but most of the pubic shaft is sub-triangular in cross section, with flat posterior and medial surfaces and a convex lateral surface. However, the most distal portion is sub-circular in cross section as in *Shuvuuia* and *Patagonykus* (Chiappe *et al.* 2002). The pubis lacks a pubic apron, as in other parvicursorines.

The right ischium is mostly preserved, lacking only the distal end. The ischium has a transversely oriented iliac articular surface, which extends along the dorsal edge of an antitrochanteric flange that juts laterally from the posterior end of the proximal expansion of the ischium. Accordingly, the proximal end of the ischium is L-shaped in proximal view (Fig. 6E), a condition probably shared with other parvicursorines but poorly preserved in most known specimens. The iliac peduncle has a slightly concave anterior margin and a convex posterior margin in proximal view. The acetabular portion of the ischium is very narrow transversely, but is much longer anteroposteriorly than in other parvicursorines (Chiappe *et al.* 2002). As in other alvarezsaurids, the proximal portion of the ischial shaft has a considerable posterior curvature as it passes distally. The ischial shaft is laterally compressed and is considerably wider than the pubis in lateral view, a feature reminiscent of other maniraptorans. In more basal theropods and other parvicursorines the ischial shaft is sub-equal to or even narrower than the pubic shaft in lateral view, though the latter differ from the former in having an ischial shaft that is laterally compressed rather than rod-like. Immediately below the acetabular portion of the ischium is a fossa on the lateral surface. An eminence arising from the pubic peduncle separates this fossa from a second, more elongate fossa located further distally on the lateral surface. The Tugriken Shireh alvarezsaur also has a fossa bordered by a posterolateral ridge along the ischial shaft (N. R. Longrich pers. comm.). The posterior surface of most of the ischial shaft is somewhat flat and thus the ischial shaft is sub-rectangular in cross section, but the more distal portion is sub-triangular in cross section due to the ridged posterior surface. There is a distinct groove on the posterior surface of the flat middle portion, bounded by two ridges respectively located along the posteromedial and posterolateral edges of the ischial shaft (Fig. 6D). The medial ridge is sharp. The distal part of the ischial shaft also curves anteriorly, giving the shaft a sigmoidal appearance in lateral view; in anterior or posterior view, the shaft is also sigmoidal, with the proximal end curving laterally and the distal end medially.

The right femur is completely preserved (Fig. 7A–F). It is estimated to be about 55% of the trunk length (i.e., the estimated distance from the cervico-dorsal transition to the middle of the acetabulum). As in other alvarezsaurids, the proximal end of the femur is approximately L-shaped in proximal view, with the femoral head offset medially and slightly anteriorly (Fig. 7E). A well-developed trochanteric crest is formed by the completely fused greater and lesser trochanters. The anterior portion of the crest is much thinner than the posterior portion. The anterior margin of the lesser trochanter curves medially to border a large shallow fossa anterior to the femoral head on the medial surface of the femoral shaft. The femoral head is separated from the trochanteric crest by a distinct groove, but lacks the longitudinal posterior groove seen in many other theropods (Xu 2002). A ridge emanating from the proximal end of the femur runs along the posterolateral margin of the femoral shaft for nearly its entire length. The ridge is more prominent near the mid-length of the shaft. A second, much sharper ridge, emanating about 10 mm distal to the proximal end of the femur and running distally for a distance of 14 mm along the posteromedial margin, is probably a reduced fourth trochanter as in *Mononykus*, *Patagonykus*, and *Alvarezsaurus* (Chiappe *et al*. 2002). There is an elongate fossa lateral to the distal half of the fourth trochanter. The distal portion of the shaft is anteroposteriorly narrower than the proximal portion but transversely much wider. The medial distal condyle of the femur is transversely much wider than the lateral distal condyle. Unlike other parvicursorines, a distally closed popliteal fossa is absent; instead, the medial condyle extends laterally in the form of a small lateral tuber, partially closing the canal between the medial and lateral distal condyles (Fig. 7F). This represents the incipiently developed stage of a fully closed popliteal fossa. Distally the medial and lateral condyles are separated by an extremely shallow groove, which does not extend onto the anterior surface of the femur. The transversely very narrow lateral condyle projects considerably beyond the medial condyle as a distal peak, as in all alvarezsaurids (Chiappe *et al*. 2002). In *Xixianykus* this peak is strongly laterally compressed, though its lateral surface is damaged. The ectocondylar tuber of the lateral condyle is very narrow transversely and extends a considerable distance posteriorly, so that the tuber is about twice as high as transversely wide. This contrasts with the condition in most other theropods, including other alvarezsaurids, in which the tuber is about as high as it is wide. The ectocondylar tuber is sub-hemispherical, with the medial surface convex and the lateral surface flat. The lateral surface of the ectocondylar tuber also appears to be relatively flat in some other parvicursorines such as *Mononykus*, in contrast to the convex lateral surface seen in most other non-avian theropods. The tuber sends a high and sharp ridge proximally along the lateral margin of the popliteal fossa for about 10 mm.

The astragalus and calcaneum are coossified with the distal end of the tibia to form a tibiotarsus (Fig. 7G–L). The preserved right tibiotarsus is complete, and measures about 130% of the femoral length. The medial condyle projects proximally to the same level as the cnemial crest. In other parvicursorines, it projects even further proximally. The fibular condyle of *Xixianykus* is lower than the medial condyle and cnemial crest. In proximal view, the medial condyle is well defined by a sharp groove anteriorly (Fig. 7K), which extends onto the medial surface of the shaft for a short distance. The fibular condyle is cube-like, and is separated from the cnemial crest by a broad, smooth lateral indentation as in *Mononykus* (Perle *et al*. 1994). In *Patagonykus* and many other theropods (Novas 1997), there is a small accessory condyle anterior to the fibular condyle within the lateral indentation. Unlike in other parvicursorines, the cnemial crest of *Xixianykus* is transversely very narrow, and its distal half is sharply ridged (Fig. 7G, I). A shallow groove separates the cnemial crest from a small condyle at the anteromedial corner of the proximal end of the tibiotarsus. Distal to this small condyle is a distinct fossa. A 13-mm-long fibular crest fades off at both ends, and posterior to the crest is a weak parallel ridge. The crest and ridge together define a longitudinal groove, the distal end of which is pitted. The distal end of the tibiotarsus is transversely widened to a significant degree. As in *Mononykus* (Perle *et al.* 1994), the ascending process of the astragalus occupies only the lateral half of the anterior surface of the distal end of the tibiotarsus, and its base is distinctly depressed relative to the main body of the astragalocalcaneum. The medial half of the main body is distally excavated to form a distinct notch. Unusually, the lateral margin of the distal portion of the tibiotarsus is interrupted by an abrupt step due to a sudden lateral protrusion at the distal end (Fig. 7C, D).

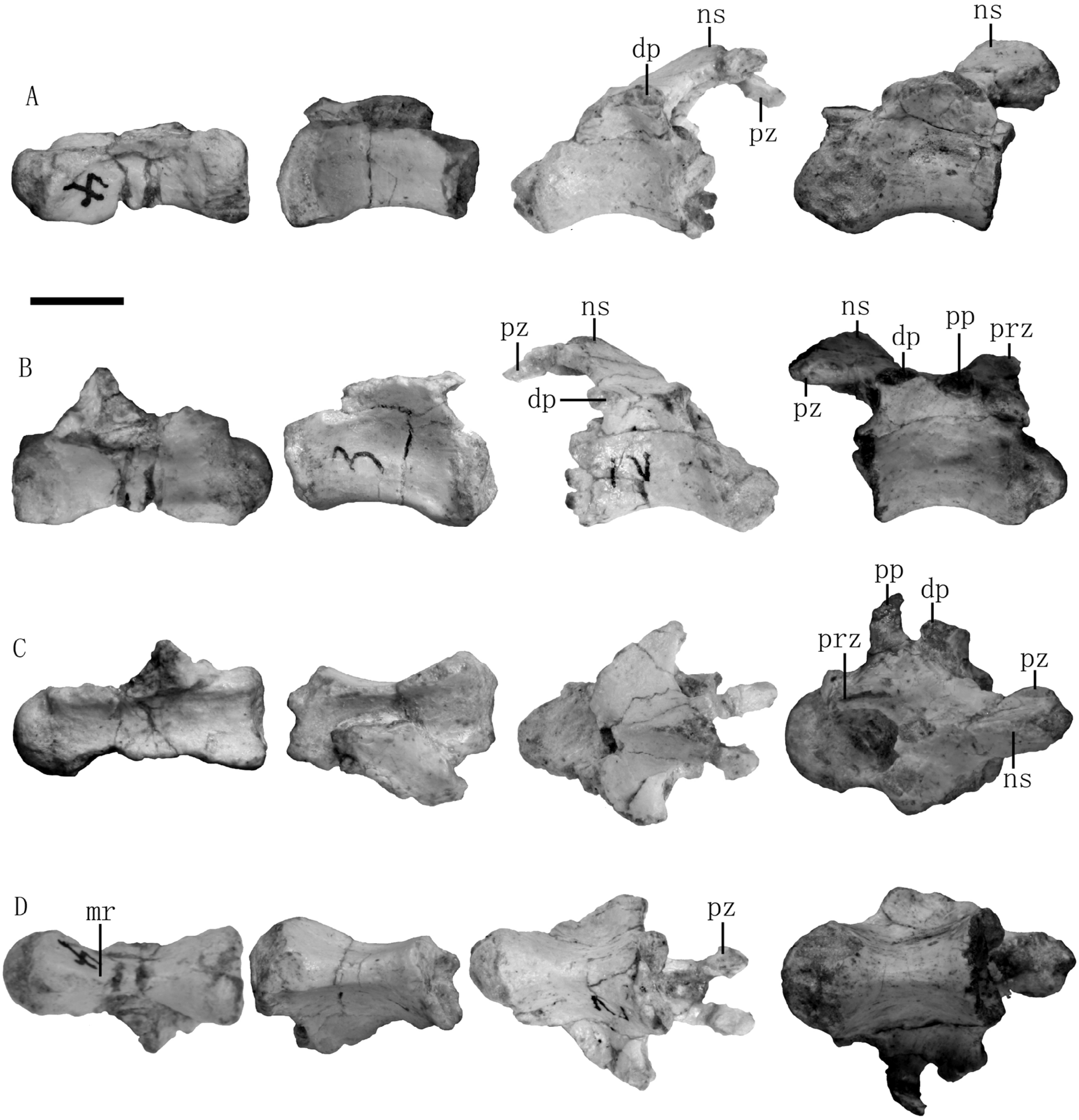

FIGURE 4. Dorsal vertebrae of *Xixianykus zhangi* holotype. Dorsal vertebrae 9 through 12 (from left to right) in left lateral (A), right lateral (B), dorsal (C), and ventral (D) views. Scale bar = 5 mm.

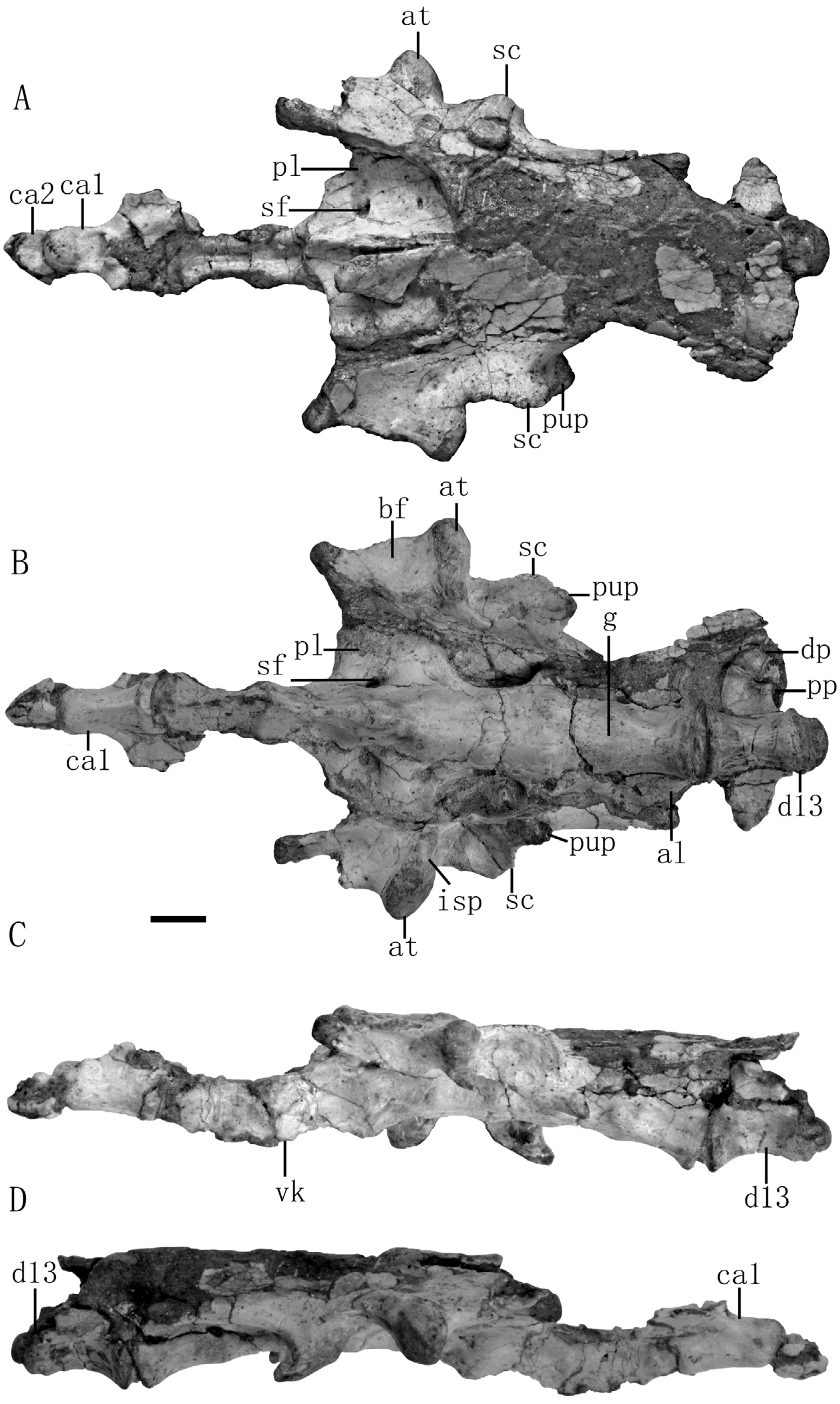

FIGURE 5. Ilia and associated vertebrae of *Xixianykus zhangi* holotype. Ilia and associated vertebrae in dorsal (A), ventral (B), right lateral (C) and left lateral (D) views. Abbreviations: al, anterior lamina; at, antitrochanter; bf, brevis fossa; ca1, first caudal vertebra; ca2, second caudal vertebra; d13, 13th dorsal vertebra; dp, diapophysis; g, groove; isp, ischial peduncle; pl, posterior lamina; pp, parapophysis; pup, pubic peduncle; sc, supracetabular crest; sf, sacral fenestra; vk, ventral keel. Scale bar = 5 mm.

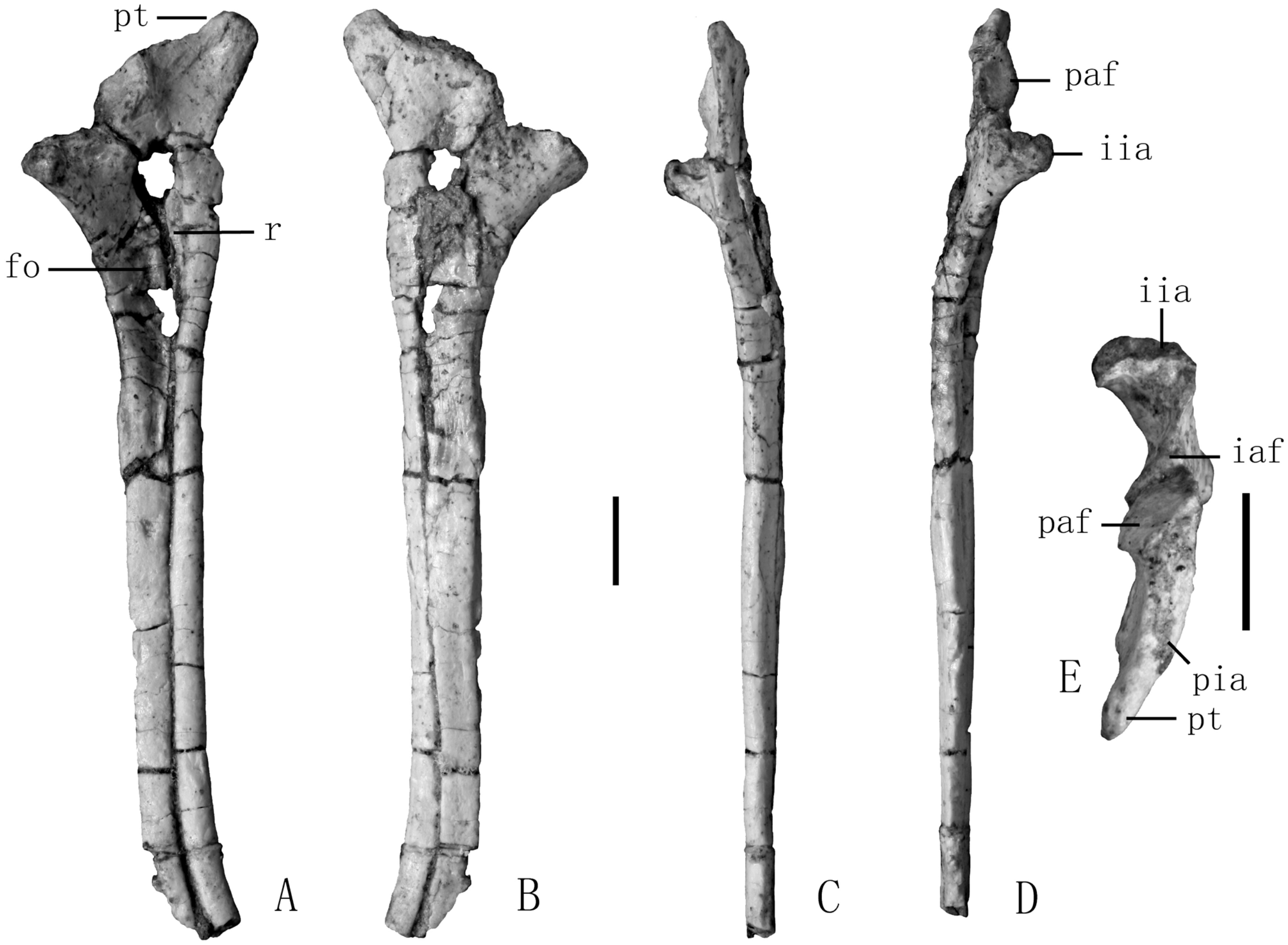

FIGURE 6. Right pubis and ischium of *Xixianykus zhangi* holotype. Right pubis and ischium in lateral (A), medial (B), anterior (C) and posterior (D) views. Close-up of proximal ends of right pubis and ischium in proximal view (E). Abbreviations: fo, fossa; iaf, acetabular fossa on ischium; iia, iliac articulation on ischium; paf, acetabular fossa on pubis; pia, iliac articulation on pubis; pt, prepubic tubercle; r, ridge. Scale bar = 5 mm.

The right fibula is nearly complete. The fibula curves strongly in the posterior direction as it extends distally (Fig. 7M–P). The posterior edge of the proximal end is wider than the anterior edge. The proximal articular surface has a large extension onto the posterior margin of the shaft, where it forms a shallow fossa (Fig. 7P). The medial and posterior surfaces of the shaft are flat, and the lateral and anterior ones convex, near the proximal end. A 5-mm-long tubercle for M. iliofibularis is present along the lateral surface of the fibular shaft. The tubercle is somewhat step-wise at both ends, and its outer edge curves posteriorly to help define a shallow, wide groove on the posterior fibular surface. The fibula thins significantly in the distal direction and seems to taper off immediately distal to the tubercle, suggesting that it was much shorter than the tibiotarsus even when intact. A significantly shortened fibula appears to characterize the Parvicursorinae (Chiappe *et al.* 2002).

The distal tarsals and the proximal ends of the right metatarsals II and IV are co-ossified to form a tarsometatarsus, and the co-ossification extends distally for a distance of at least 5 mm (Fig. 7Q–U). In *Patagonykus*, distal tarsal 3 and the proximal ends of metatarsals II and III have been suggested to be partially fused, but sutures are clearly present between the elements (Novas 1997). The tarsometatarsus of *Xixianykus* is clearly longer than the femur although the distal end is broken away. The preserved length of the tarsometatarsus is 68.4 mm, slightly shorter than the femur, but comparisons to other parvicursorines suggest that its length when complete was probably about 74 mm. The tarsometatarsus is a slender element, its minimum transverse width being less than 7% of its estimated length. The proximal articular surface is sub-rectangular in outline, and is slightly less than twice as transversely wide as anteroposteriorly deep (Fig. 7Q).

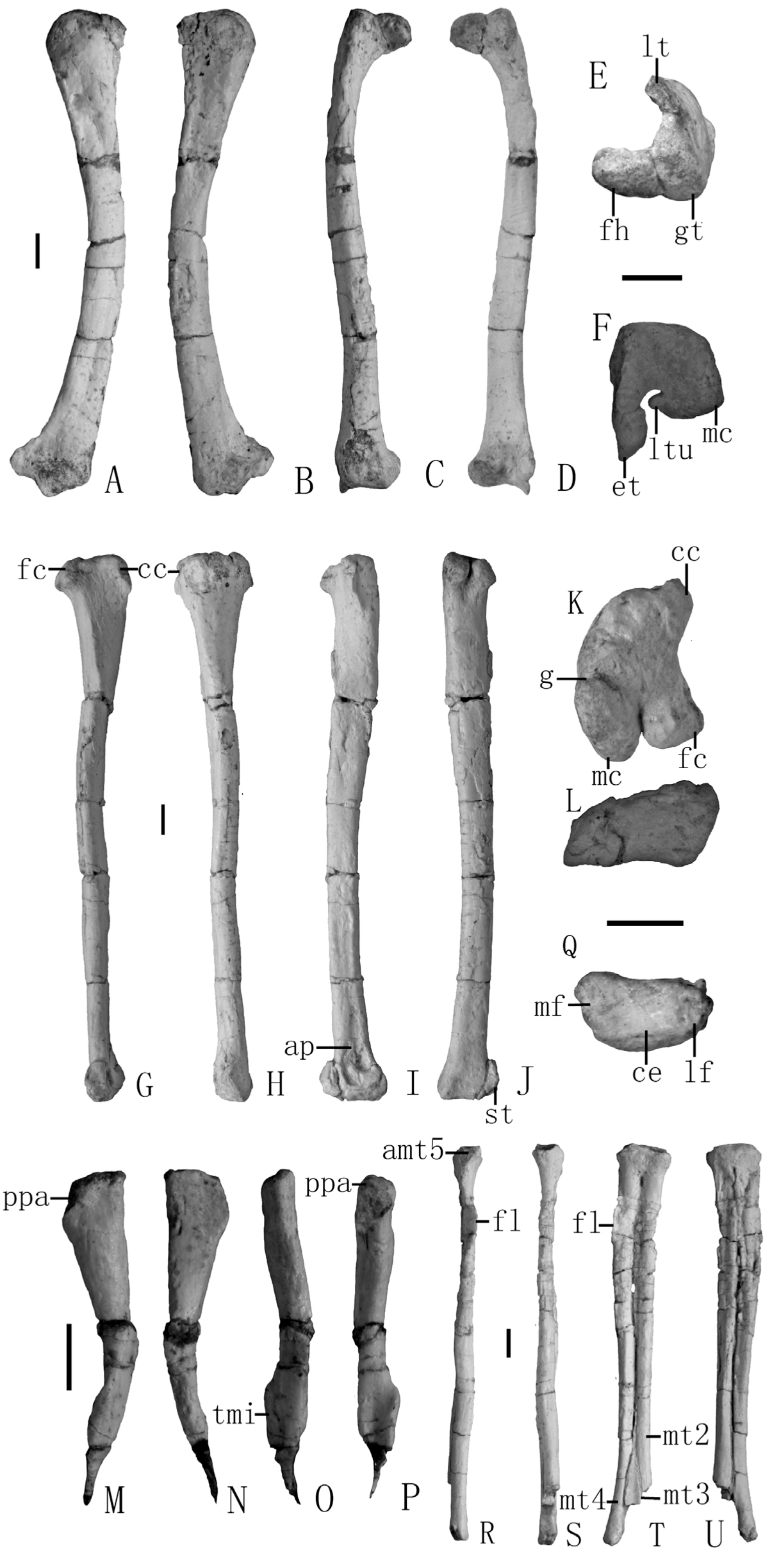

FIGURE 7. Right hindlimb of *Xixianykus zhangi* holotype. Right femur in lateral (A), medial (B), anterior (C), posterior (D), proximal (E), and distal (F) views. Right tibiotatarsus in lateral (G), medial (H), anterior (I), posterior (J), proximal (K), and distal (L) views. Right fibula in lateral (M), medial (N), anterior (O) and posterior (P) views. Right tarsometatarsus in proximal (Q), lateral (R), medial (S), anterior (T), and posterior (U) views. Abbreviations: amt5, articular surface for metatarsal V; ap, ascending process; cc, cnemial crest; ce, central eminence; et, ectocondylar tuber; fc, fibular condyle; fh, femoral head; fl, flange; g, groove; gt, greater trochanter; lf, lateral fossa; lt, lesser trochanter; ltu, lateral tuber; mc, medial condyle; mf, medial fossa; mt2–4: metatarsals II–IV; ppa, proximal articular surface on posterior margin; st, step; tmi, tubercle for M. iliofibularis. Scale bar = 5 mm.

The proximal end of the tarsometatarsus is only slightly wider transversely than the more distal portion, but is about twice as deep anteroposteriorly. In proximal view, the proximal articular surface has a sub-linear anterior margin and a markedly convex posterior margin. The proximal articular surface of the tarsometatarsus bears adjacent medial and lateral fossae, the medial one being larger and deeper than the lateral one (Fig. 7Q). They are separated by a low, wide eminence. This morphology somewhat resembles the condition in relatively derived birds (e.g., specimen of *Crossoptilon auritum*, IVPP collection) but differs from that in some non-avian theropods, in which the proximally fused tarsometatarsus has a flat proximal articular surface (e.g., IVPP V14009). There is a distinct sub-triangular articular facet on the posterolateral margin of the tarsometatarsus, situated near the proximal end and probably representing the articular facet for metatarsal V. The tarsometatarsus displays a modified arctometatarsal condition (metatarsal III fails to reach the proximal end of the metatarsus), as in other parvicursorines (Longrich & Currie 2009). A groove between the shafts of the second and fourth metatarsals extends over most of the length of the anterior surface of the tarsometatarsus, but terminates distally at the sharply pointed proximal end of the third metatarsal. By contrast, the posterior surface is mostly flat. The second and fourth metatarsals define only a short posterior midline groove extending over less than the middle third of the length of the metatarsus, in contrast to the many other theropods in which the metatarsus has a long, conspicuous groove along the posterior surface.

The transverse width of the proximal half of metatarsal II is considerably greater than its anteroposterior depth. The distal part of this metatarsal bears a weak flange on the anterior surface, and a ridge near the medial margin of the posterior surface. The distal portion of the shaft is deeper anteroposteriorly than wide transversely, and its posterior surface is flat. Metatarsal III is estimated to be less than half as long as metatarsals II and IV, and its tapering proximal end intrudes between the other two metatarsals. Most of metatarsal III has no exposure on the posterior surface of the tarsometatarsus. The preserved proximal portion is triangular in cross section, with a slightly transversely concave anterior surface as in other Asian parvicursorines and a sharply ridged posterior surface as in the North American alvarezsaurids (Longrich & Currie, 2009). As with metatarsal II, the proximal half of metatarsal IV is anteroposteriorly compressed. About 10 mm distal to the proximal end is a 6-mm-long sharp ridge along the anterolateral margin (Fig. 7R, T, U). The distal half of the shaft of metatarsal IV is anteroposteriorly deeper than transversely wide. A distinct ridge arises near the mid-length of the shaft and runs distally along the anterior surface. Along the posterior surface an oblique ridge arises more proximally, close to the medial margin of the shaft, and reaches the lateral margin as it passes distally. The distal portion of metatarsal IV diverges laterally, and bears a shallow notch on the medial margin in posterior view.

Discussion

Because *Xixianykus zhangi* is clearly a derived alvarezsaurid, we investigated its systematic position by adding it to a preexisting dataset specifically designed to illuminate alvarezsaurid interrelationships (Longrich & Currie 2009). The data matrix was analyzed using the NONA (ver 2.0) software package (Goloboff 1993), and matrix formatting and character exploration were performed in WinClada (Nixon 1999). The analysis was run with the following search parameters: 1000 replications, 10 starting trees per replication, and Multiple TBR+TBR (mult*max*) search strategy. Other settings, including character ordering, follow Longrich & Currie (2009). The analysis resulted in 2 most parsimonious trees, the strict consensus of which is shown in Figure 8.

Xixianykus zhangi is placed within the Parvicursorinae based on the following parvicursorine synapomorphies (Chiappe *et al.* 2002; Kessler *et al.* 2005; Longrich & Currie 2009): dorsal vertebrae opisthocoelous; dorsal hyposphene-hypantrum articulations absent (Perle *et al.* 1993); parapophyses of dorsal vertebrae elevated to level of diapophyses (Perle *et al.* 1994); zygapophyses of dorsal vertebrae with nearly vertical articular facets; posterior sacral vertebrae bear hypertrophied ventral keel; transverse processes of anterior caudal vertebrae anteriorly displaced; pubic apron absent; pubic shaft and ischium with extensive distal contact; ascending process of astragalus restricted to lateral part of anterior surface of tibiotarsus; fibula much shorter than tibiotarsus; metatarsal III much shorter than metatarsals II and IV; and distal end of tibia with lateral malleolus anteroposteriorly expanded. Furthermore, *Xixianykus* is more closely related to other Asian parvicursorines than to North American ones based on the following synapomorphy: anterior surface of metatarsal III transversely concave (Longrich & Currie 2009).

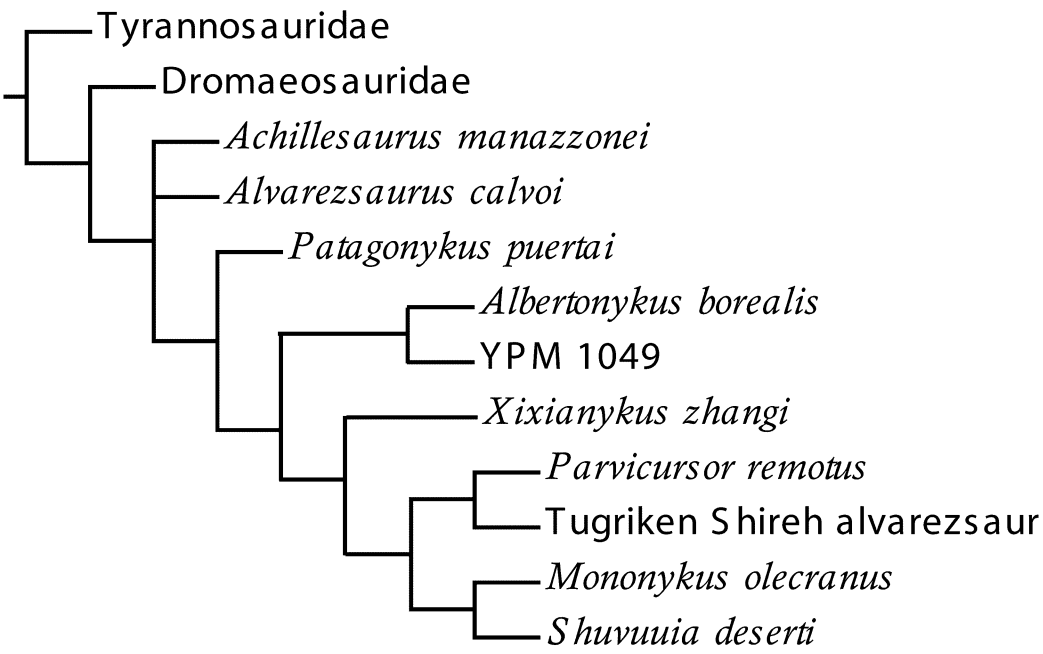

FIGURE 8. Strict consensus of 2 most parsimonious trees (tree length = 93, CI = 0.88, RI = 0.90) produced by analysis of a dataset from Longrich & Currie (2009) with *Xixianykus zhangi* added. The scorings for *Xixianykus zhangi* are: ?????????1111101102011????????????????????????110??111?10110100101111???????1.

Some plesiomorphic features suggest that *Xixianykus zhangi* is basal to other Asian parvicursorines. The first caudal vertebra of *Xixianykus zhangi* is not incorporated into the synsacrum as in other parvicursorines (Longrich & Currie 2009). *Xixianykus* has a preacetabular tubercle at the proximal end of the pubis, but it is small and laterally compressed rather than knob-like as in other parvicursorines (Hutchinson & Chiappe 1998). The pubic shaft is sigmoidal in anterior or posterior view as in *Patagonykus* (Novas 1997), rather than straight as in other parvicursorines (Hutchinson & Chiappe 1998). The pubis has an articular facet for the ischium that is similar in size to the acetabular fossa, as in basal alvarezsaurids (Novas 1997). This contrasts with other parvicursorines, in which this facet is much smaller (Hutchinson & Chiappe 1998). The ischial shaft is laterally compressed and is considerably wider than the pubis in lateral view, a feature reminiscent of other maniraptorans including basal alvarezsaurids (Novas 1997). These features suggest that *Xixianykus zhangi* is more basal than other parvicursorines. Furthermore, several other features are incipiently developed compared to the condition in other parvicursorines, providing more evidence that the position of *Xixianykus zhangi* is relatively basal. The ventral keel on the posterior sacral vertebrae is relatively low and longitudinally short (extending across the ventral surfaces of the posteriormost two sacral vertebrae and continuing only slightly onto the fifth sacral vertebra, rather than extending nearly across all three posteriormost sacral vertebrae as in other parvicursorines). A midline ridge extends across most of the length of the ventral surface of the first caudal but does not appear to continue onto the second caudal centrum, whereas in other parvicursorines the ridge traverses the ventral surfaces of the two anteriormost caudal centra in their entirety (Chiappe *et al.* 2002). The distal medial condyle of the femur is expanded transversely, but not to the degree seen in other parvicursorines (Chiappe *et al.* 2002). The popliteal fossa is not closed distally and the medial condyle of the proximal end of the tibia does not project proximally beyond the rest of the proximal surface. These features suggest that *Xixianykus zhangi* incipiently developed some parvicursorine features, but not to the fuller degree seen in other, perhaps more derived, parvicursorines.

The inferred relatively basal position of *Xixianykus* is also consistent with the stratigraphic distribution of the Parvicursorinae, as *Xixianykus* is the oldest known member of this clade. All previously known Asian parvicursorines are either Campanian or Maastrichtian in age (Chiappe *et al.* 2002; Alifanov & Barsbold 2009). *Xixianykus zhangi* is from the late Coniacian to Santonian (Wang *et al.* 2008), comparable to the parvicursorine sister taxon *Patagonykus* from Argentina (Novas 1997). Furthermore, North American parvicursorines and the possible parvicursorine material from Romania (Kessler *et al.* 2005) are all from the Maastrichtian, and are thus much younger than *Xixianykus*. Although our analysis places the North American parvicursorines at the base of the group, this result is most likely caused by a large amount of missing data for these taxa in the phylogenetic analysis. The Romanian alvarezsaurid *Elopteryx* is apparently more similar in femoral morphology to other parvicursorines (Kessler *et al.* 2005) than to *Xixianykus*, and is therefore likely to be a derived parvicursorine. If *Xixianykus* is basal to all other parvicursorines, the Parvicursorinae may have dispersed from Asia to North America, which appears to be true for many other dinosaur groups that occur on both continents (Xu *et al.* in press).

Derived alvarezsaurids (parvicursorines) are unique not only because of their bizarre sternal and forelimb morphologies, but also because they display a number of specialized vertebral and hindlimb features that are uncommon among non-avian theropods (Perle *et al.* 1994; Chiappe *et al.* 1998; Norell *et al.* 2001; Sereno 2001; Xu 2002). The holotype of *Xixianykus zhangi*, despite being incomplete, exemplifies many of these characteristics almost perfectly because of the high-quality three-dimensional preservation of the right pelvis and sacrum, the adjacent parts of the vertebral column, and the right hindlimb down to the level of the distal end of the tarsometatarsus. This specimen accordingly can be used as a basis for a functional evaluation of these portions of the parvicursorine skeleton, since the proportions of the hindlimb and the topologies of the various joint surfaces are generally clear. In particular, the *Xixianykus zhangi* holotype displays a number of characteristics that are strongly indicative of a cursorial locomotor habit, as has previously been suggested for alvarezsaurids in general on the basis of the wide pelvis, long hindlimbs, and short pedal digits (Chiappe *et al.* 2002).

Elongation of distal hindlimb segments relative to proximal ones is a classic indicator of cursoriality (Coombs 1978; Carrano 1999; Hildebrand & Goslow 2001). Because of fusion of the proximal and distal tarsals of *Xixianykus* to the tibia and metatarsus, respectively, ratios expressing limb proportions can only be calculated using tarsometatarsus and tibiotarsus lengths. These ratios are not strictly comparable to the values calculated from the tibia and metatarsus lengths that are often presented for theropods (e.g., Holtz 1994), but the small size of the tarsal elements implies that comparisons are still likely to be meaningful. In *Xixianykus* the distalmost part of the tarsometatarsus is broken away, but even the preserved length of 68.4 mm is equal to 0.75 times the length of the tibiotarsus. Calculations based on the large number of theropod hindlimb measurements given by Holtz (1994) show metatarsus/tibia length ratios equaling or exceeding this value only in two ornithomimid specimens: one of *Gallimimus* (0.75) and one of *Ornithomimus* (0.76). If our estimated length of 74 mm for the complete tarsometarsus of *Xixianykus* is correct, the ratio would be an even more exceptional 0.81. Similarly, the tibiotarsus/femur length ratio in *Xixianykus* is 1.30, a value equaled in Holtz's (1994) data set by one individual specimen of the ornithomimid *Struthiomimus* but exceeded among non-avialan theropods only by specimens of *Compsognathus* (1.31), of the ornithomimid *Dromiceiomimus* (1.36) and of the unusual oviraptorosaur *Avimimus* (1.37). Limb measurements published elsewhere for the troodontid *Sinornithoides* (Gatesy & Middleton 1997) imply a value of 1.41 and the value in the troodontid *Anchiornis* is about 1.50 (Xu *et al.* 2009). However, the tarsometatarsal/femur ratio of *Xixianykus* is 0.98 even under the unrealistically conservative assumption that the length of the tarsometatarsus was only the preserved 68.4 mm, indicating that the tarsometatarsus of *Xixianykus* is significantly longer in proportion to the femur than that of any non-avialan theropod specimen reported by previous studies (Holtz 1994; Gatesy & Middleton 1997). Our more realistic tarsometatarsal length estimate of 74 mm would lead to a tarsometatarsal/femur ratio of 1.06, well outside the ranges implied by these previously published measurements.

As an alternative means of expressing hindlimb proportions, ternary diagrams may be used to plot the percentage contributions of the femoral, tibial and metatarsal segments to the total length of the hindlimb excluding the phalanges (Gatesy & Middleton 1997). In *Xixianykus* the tarsometatarsus (considering only its preserved length) and femur respectively account for 29.8% and 30.5% of the total length, compared to 39.7% for the tibiotarsus. Although the tibiotarsal percentage falls well within the range encompassed by the non-avialan theropods in Gatesy & Middleton's (1997) study, *Xixianykus* falls slightly outside the morphospace occupied by the other non-avialan theropods because of its relatively long metatarsus and short femur. The ternary proportions of the hindlimb of *Xixianykus* are in fact similar to those of some neornithines (Gatesy & Middleton 1997), which might suggest that *Xixianykus* and other parvicursorines had adopted at least an incipient "knee-driven" mode of running similar to that of extant birds (Christiansen & Bonde 2002; Hutchinson & Allen 2009). However, parvicursorines do not display the gross anatomical modifications, particularly reduction of the tail and increased development of the anterior part of the body, that shift the avian center of gravity forward and are associated with knee-driven kinematics (Christiansen & Bonde 2002). It is more probable that the hindlimb proportions of *Xixianykus* reflect specialization for cursoriality.

Apart from hindlimb proportions, several other osteological features of *Xixianykus* and other parvicursorines also reflect morphological trends seen in extant cursors (Coombs 1978; Carrano 1999; Hildebrand & Goslow 2001). Consolidation and narrowing of the metapodium, as in the arctometatarsus of *Xixianykus*, is a common cursorial feature, and the arctometatarsal configuration may represent a specific adaptation for withstanding high locomotor stresses (Snively & Russell 2003). Most arctometatarsal theropods are characterized by relatively cursorial hindlimb proportions (Holtz 1994), and *Xixianykus* fits this pattern. It is also notable that reduction of metatarsal III has proceeded even further in parvicursorines than in other arctometatarsal taxa (Turner *et al*. 2009), with metatarsal III failing to extend to the proximal end of the tarsometatarsus.

Many typical features of cursors relate to the need to improve locomotor efficiency by reducing energy-wasting movements, such as lateral bending of the trunk and twisting of the distal parts of the limbs, and musculoskeletal structures that facilitate these movements but do not contribute to cursorial progression (Hildebrand & Goslow 2001). In connection with minimizing twisting, the fibula is often reduced in extant mammalian cursors, and the apparent loss or extreme reduction of the distal part of the fibula in *Xixianykus* is therefore consistent with cursoriality. Similarly, the steeply angled zygapophyseal facets of *Xixianykus* would have contributed to holding the trunk rigid and reducing the potential for lateral undulation. Such angulation is unusual among theropods, although alternative stabilizing mechanisms such as hyposphene-hypantrum articulations (e.g., *Sinraptor*, Currie & Zhao 1993) and transversely concavo-convex zygapophyseal articulations (e.g., *Deinonychus*, Ostrom 1969) have been reported in various taxa. In the case of *Xixianykus*, the functional interpretation of the angled zygapophyses is complicated by the fact that the parvicursorine forelimb shows probable adaptations for digging into insect nests (Senter 2005; Longrich & Currie 2009). It is possible that the primary selective value of the angled zygapophyses lay in stabilization of the trunk during digging, rather than during running. However, the existence of the angled zygapophyses would have subsequently made cursoriality more feasible, even if they originally evolved for another reason.

A particularly intriguing feature of *Xixianykus* and other parvicursorines is the lateral to slightly posterolateral orientation of the antitrochanter, which consequently articulates with nearly the entire posterior surface of the femoral head. This arrangement would have stabilized the hip against lateral rotation, as well as posterior displacement, of the femur. However, manipulation of the right hip joint demonstrates that the femur was still relatively free to protract and retract through a large range, and even to undergo considerable abduction and adduction, unless ligaments or other soft tissues greatly reduced the mobility of the hip in life. Similarly, the narrow distal prominence of the lateral femoral condyle of *Xixianykus* lies against the posteroproximal corner of the lateral surface of the tibia when the knee is placed in articulation, apparently falling posterior to the fibula. This arrangement would have helped to stabilize the knee against both medial rotation and lateral displacement of the tibia with respect to the femur. These apparent modifications for withstanding torsion at both the knee and ankle further support the inference that *Xixianykus*, and presumably other parvicursorines, were likely some of the most capable cursors among the non-avialan theropods. As with the angled zygapophyses of the trunk, the stabilizing features of the hindlimb may have been originally selected for their value in bracing the body when digging with the forelimbs, but they would nevertheless have been useful during running as well.

Measurement of limb proportions and qualitative identification of suggestive features cannot replace extensive biomechanical analysis as a means of testing hypotheses about locomotion (Hutchinson & Allen 2009), and drawing functional conclusions for parvicursorines on the basis of a single specimen is inevitably a tentative procedure. Furthermore, the immaturity of the *Xixianykus zhangi* holotype leaves open the possibility that its hindlimb proportions might have changed if further growth had taken place. Nevertheless, the hindlimb proportions of the *Xixianykus zhangi* holotype are so extreme among non-avialan theropods, and occur in combination with so many other likely indicators of cursoriality, that the inference of specialization for fast and/or efficient running is difficult to dismiss. Among other parvicursorines, the hindlimb proportions of *Mononykus* (Perle *et al.* 1994), *Parvicursor* (Karhu & Rautian 1996) and *Shuvuuia* (Suzuki *et al.* 2002) are broadly similar to those of *Xixianykus*, to the extent that they can be determined from material that has been described to date. A comprehensive biomechanical analysis involving all these taxa would be desirable in order to more definitively confirm or reject the interpretation of extreme cursorial specialization in parvicursorines, but at present we agree with previous authors (Chiappe *et al.* 2002) that a working hypothesis of cursoriality is warranted.

If the interpretation of parvicursorines as myrmecophages (Senter 2005; Longrich & Currie 2009) is indeed correct, the selective value of parvicursorine cursoriality may have lain in both the need to escape predators and the need to move efficiently among termite colonies. Individual giant anteaters (*Myrmecophaga tridactyla*) move regularly among ant or termite colonies and typically visit several per day in order to avoid over-exploitation of a limited resource, although their journeys are typically short (Dickman 1994). Aardvarks (*Orycteropus afer*) adopt a similar strategy (Aarde 1994), but apparently over greater distances. They have been recorded to move up to 5 km during a nocturnal activity cycle, but estimates of the maximum distance covered in a night range up to 30 km (Soshani *et al.* 1990). Although the lightly modified hyaenid body plan of aardwolves (*Proteles cristatus*) would suggest a greater degree of cursoriality than is present in either aardvarks or anteaters, aardwolves in fact cover only short distances within territories that may be as small as 1 km^2 for a mated pair (Koehler & Richardson 1990; Richardson & Bearder 1994).

Longrich & Currie (2009) noted that parvicursorines likely preyed specifically on various wood-nesting termites, based on the rarity of ants and mound-building termites in the Mesozoic. Wood-nesting termites may have essentially represented a patchy resource for these dinosaurs, forcing them to travel considerable distances between colonies and/or spend long periods searching for food as is apparently true of aardvarks and giant anteaters today. The cursorial adaptations exemplified by *Xixianykus* may then have permitted parvicursorines to forage over large tracts of land quickly and efficiently, a behavioral feature that might in turn have facilitated their dispersal and contributed to their wide geographical range. Alternatively, parvicursorines may have adopted a short-distance foraging strategy more similar to that of the aardwolf, in which case their cursorial adaptations were presumably valuable primarily as a means of escaping predators rather than improving foraging efficiency. While the emerging interpretation of parvicursorines as highly cursorial termite-eaters leaves them without any obvious living analogue, the inferences of both myrmecophagy (Senter 2005; Longrich & Currie 2009) and cursoriality are coming to rest on increasingly clear evidence.

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