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New ornithomimosaurian (Dinosauria: Theropoda) pelvis from the Upper Cretaceous Erlian Formation of Nei Mongol, North China

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ABSTRACT

A newly identified ornithomimosaurian pelvis and sacrum from the Upper Cretaceous Erlian Formation of Nei Mongol, China is described in detail in this paper. This specimen is distinguished from previously described taxa by the presence of a combination of features that is unique among Ornithomimosauria: sacrum comprising five vertebrae with neural spines fused into a continuous plate, iliac posterior end rectangular, pubic shaft distally straight, ischial boot not broadened transversely, and ischial shaft proximally straight, distally curved, and 80 percent as long as the pubis. This specimen differs from at least some material assigned to the sympatric *Archaeornithomimus asiaticus*, showing that two distinct ornithomimosaurian taxa are present in this Upper Cretaceous fossiliferous rock unit. A phylogenetic analysis places LH-02-01 in a relatively early-diverging position within Ornithomimosauria, outside the two major clades Deinocheiridae and Ornithomimidae, but its relationships with other early-diverging ornithomimosaurs remain unresolved. The primitive nature of LH-02-01 adds to the evidence from fossil vertebrates that the Erlian Formation correlates with the Turonian Bissekty Formation of Uzebekistan, while the biostratigraphic evidence from non-vertebrates instead indicates a Campanian to Maastrichtian assignment for the Erlian Formation. This apparent contradiction remains unresolved, pending future research aimed at reconciling the seemingly incompatible lines of evidence.

1. Introduction

Ornithomimosauria is a clade of coelurosaurian dinosaurs classically described as having an ostrich-like appearance, given their small skulls, long necks, and long, slender limbs (Makovicky et al., 2004). Within this group, the two main clades Deinocheiridae and Ornithomimidae are mostly restricted to the Upper Cretaceous of Asia and North America, while the more primitive members are widely distributed in the Lower Cretaceous of Asia, North America and Europe (Makovicky et al., 2004; Serrano-Brañas et al., 2020). The Erlian Formation (formerly Iren Dabasu Formation, renamed by the Bureau of Geology and Mineral Resources of Nei Mongol Autonomous Region (1991)),

intermittently exposed in the Iren Nor region of Nei Mongol (Inner Mongolia), China, is composed of continental fluvial sediments including coarse-grained conglomerates and sands, fine-grained sand-, silt- and claystones, and paleosols (Currie and Eberth, 1993; Van Itterbeeck et al., 2005). Since first explored by the Central Asiatic Expeditions (CAE) of the American Museum of Natural History in the early 1920s (Granger and Berkey, 1922), this lithological unit has proven rich in the remains of dinosaurs such as hadrosauroids, titanosaurs, and various coelurosaurs, including tyrannosauroids, ornithomimids, oviraptorosaurs, therizinosauroids and troodontids (Gilmore, 1933; Currie and Dong, 2001; Ryan and Russell, 2001; Zhang et al., 2001; Xu et al., 2002, 2006, 2007; Yao et al., 2015; Funston et al., 2019). The Erlian Formation has also yielded isolated specimens tentatively referred to Ankylosauria and Dromaeosauridae (Currie and Eberth, 1993; Chiappe et al., 2002; but see Longrich and Currie, 2009). Currie and Eberth

(1993) also reported, but did not describe, a small number of "hypsilophodont" elements.

Only one ornithomimosaurian, the ornithomimid *Archaeornithomimus asiaticus*, has been reported from the Erlian Formation (Gilmore, 1933; Russell, 1972; Smith and Galton, 1990; Currie and Eberth, 1993). This species, originally assigned to *Ornithomimus* as *Ornithomimus asiaticus* before being moved to *Archaeornithomimus* (Russell, 1972), was erected on the basis of a collection of some 27 fragmentary specimens (Smith and Galton, 1990) collected by the CAE "from several localities in the Iren Dabasu basin" (Gilmore, 1933: p. 27). Thus, it is true only in a very geographically imprecise sense that the specimens making up the CAE sample of *Ornithomimus asiaticus* are "[a]ll from [the] same locality" (Smith and Galton, 1990: p. 256). Many of the specimens came from the "Kaisen Quarry" (AMNH field locality 140), situated about 13 km east of the former Iren Dabasu telegraph station (Gilmore, 1933). Of the two specimens designated as co-types, a nearly complete manus (AMNH 6569) and partial pes (AMNH 6565), the former was from the Kaisen Quarry and the latter from AMNH field locality 141, situated less than 1 km to the south (Gilmore, 1933: Fig. 1). AMNH 6565 was subsequently designated as the lectotype of *Archaeornithomimus asiaticus*, and AMNH 6569 as the paralectotype (Smith and Galton, 1990). Initially, this geographically dispersed material was not noted to be particularly variable, and indeed only minimal differences from North American ornithomimid specimens were discerned (Gilmore, 1933). Subsequent authors have identified distinctive features in the CAE sample that justify generic separation of *Archaeornithomimus* from *Ornithomimus* (Russell, 1972; Smith and Galton, 1990), but in some cases have also raised doubts about the original assumption that all the specimens really belonged to only a single species (Russell, 1972; Currie and Eberth, 1993), given the disassociated nature of the material and/or an impression that substantial morphological variability was present in the sample.

Here we report on a newly identified articulated ornithomimosaurian pelvis and sacrum (LH-02-01) from the Erlian Formation, which demonstrates the presence of a second definite ornithomimosaur within this fossiliferous rock unit. We discuss the phylogenetic position of this new material within Ornithomimosauria, and its implications for the age of the Erlian deposits during the Late Cretaceous.

2. Materials and methods

LH-02-01 was collected in 2002 by an expedition of the Long Hao Institute of Geology and Paleontology, Hohhot (also spelled Huhehaote) in the Iren Nor Region of Erenhot (also spelled Erlianhaote) (Fig. 1), but the precise location was not documented. LH-02-01 was undoubtedly recovered from the Erlian Formation, which is the only dinosaur-bearing unit in the vicinity. The specimen was most likely found in the southern part of the Iren Nor region, which is the predominant source of Erlian Formation vertebrates (Fig. 1). A phylogenetic analysis of the new specimen relative to other ornithomimosaurs was performed using the software Tree analysis using New Technology (TNT) version 1.1 (Goloboff et al., 2008).

Statements in this paper about the ilium and sacrum of *Archaeornithomimus asiaticus* refer to AMNH 21790, whereas statements about the pubis refer to AMNH 21799, and statements about the ischium refer to AMNH 21798. Statements about the proximal caudal vertebrae refer to AMNH 21790, 21791, 21802, and 21889. Although solid evidence for the presence of more than one ornithomimid in the Erlian Formation has been lacking (Currie and

Eberth, 1993), we do not consider it certain that all of these specimens are truly conspecific.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; IGM, Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbataar, Mongolia; LH, Long Hao Institute of Geology and Paleontology, Hohhot, China; MNA, Museum of Northern Arizona, Flagstaff, USA; ROM, Royal Ontario Museum, Toronto, Canada.

3. Results

3.1. Systematic paleontology

Dinosauria Owen, 1842
Theropoda Marsh, 1882
Ornithomimosauria Barsbold, 1976
Ornithomimosauria gen. et sp. indet.

Material. LH-02-01, a relatively complete, co-ossified pelvis and sacrum articulating with a caudal vertebra. This specimen is housed in the Collection of the Long Hao Institute of Geology and Paleontology, Hohhot, Nei Mongol Autonomous Region, China.
Locality and Horizon. Iren Nor region in Nei Mongol; Erlian Formation, uppermost Campanian to lower Maastrichtian (Van Itterbeeck et al., 2005; Bonnetti et al., 2014).

3.2. Description and comparisons

All of the preserved bones are articulated to form a relatively complete pelvis and sacrum, articulating with a caudal vertebra posteriorly. The anterior and dorsal portions of both ilia are damaged (Fig. 2). The neurocentral sutures of the caudal vertebra are still visible, suggesting that this specimen might represent an immature individual (Brochu, 1996). LH-02-01 is reasonably large for an ornithomimosaur specimen, and is more likely to be from a subadult than a juvenile.

The sacrum consists of five sacral vertebrae, which are sandwiched between the ilia. Among ornithomimosaurs in which the sacrum is known, only *Shenzhousaurus orientalis*, *Archaeornithomimus asiaticus* and *Gallimimus bullatus* possess five sacral vertebrae (Osmólska et al., 1972; Smith and Galton, 1990; Ji et al., 2003), rather than the typical number of six (Makovicky et al., 2004; Kobayashi and Barsbold, 2005a; Lee et al., 2014; McFeeters et al., 2016; Sues and Averianov, 2016a). The sacral centra are elongated and spool-shaped, having a constriction in the middle but expanding at their anterior and posterior ends. On the lateral surface, the first sacral centrum bears a distinct, anteroposteriorly aligned groove; the fourth bears an oblong depression; and the fifth appears to lack a groove or depression, but bears an irregular pit, probably resulting from damage. Lateral non-invasive depressions comparable to those on the first and fourth sacrals also occur in the sacral vertebrae of *Shenzhousaurus orientalis* and other ornithomimid taxa, including *Archaeornithomimus asiaticus*, *Sinornithomimus dongi*, *Gallimimus bullatus*, *Ornithomimus velox*, *Struthiomimus altus* and *Rativates evadens* (Osmólska et al., 1972; Smith and Galton, 1990; Ji et al., 2003; Kobayashi and Lü, 2003; Makovicky et al., 2004; McFeeters et al., 2016). The lateral surfaces of the second and third sacrals are concealed by the ilia. Their ventral surfaces are flattened, but bear anteroposteriorly extending sulci, which become gradually shallower posteriorly. Among ornithomimosaurs, shallow sulci on the ventral surfaces of the sacral vertebrae have only previously been documented in *Archaeornithomimus asiaticus*, and in the fourth sacral of *Sinornithomimus dongi* (Smith and Galton, 1990; Kobayashi and Lü, 2003). The anterior articular
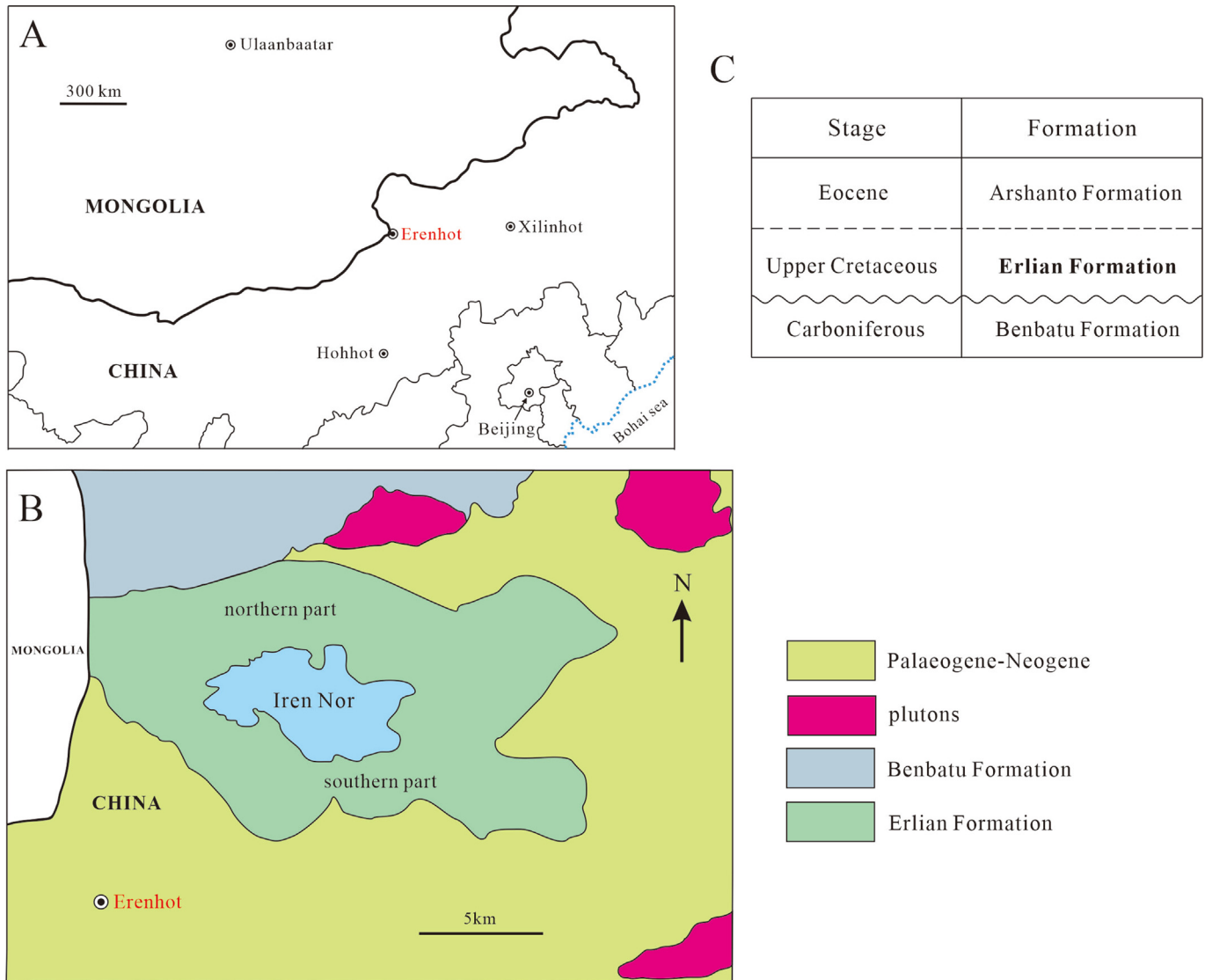
Fig. 1. Geographical and geological setting of the fossil locality of LH-02-01. Map showing the location of Erenhot in North China (A), a simplified geological map of the Iren Nor area modified from Van Itterbeeck et al. (2005) (B), and a simplified diagram showing the Erlian Formation within the regional stratigraphic succession (C).

surface of the first sacral is flattened and semi-elliptical, with a horizontal dorsal margin. The neural canal is elliptical, being dorsoventrally compressed, and the neurocentral sutures are visible.

The dorsal surfaces of the first four sacral vertebrae are obscured by matrix. On the fifth sacral, a robust supraradiapophysial lamina extends laterally to contact the medial surface of the ilium. The postzygapophyses are short and almost parallel to one another. As preserved, the articular facets of the postzygapophyses are not in natural contact with those of the prezygapophyses of the first caudal vertebra, probably due to taphonomic distortion (Fig. 2C). The well-preserved neural spines of the third and fourth sacrals are anteroposteriorly expanded and fused together, forming a continuous narrow plate. A similar condition occurs in the deinocheirids *Harpymimus okladnikovi*, *Garudimimus brevipes* and *Deinocheirus mirificus* (Kobayashi and Barsbold, 2005a, b; Lee et al., 2014), whereas in *Gallimimus bullatus* and *Rativates evadens* the sacral neural spines are separate (Osmólska et al., 1972; McFeeters et al., 2016), and in the Bissekty ornithomimid the neural spines are fused ventrally but separate near their dorsal ends (Sues and

Averianov, 2016a). The neural spines are very high and likely projected above the dorsal margin of the ilium in the intact specimen, so that the dorsalmost parts of the spines were exposed in lateral view. If so, this feature is peculiar. The neural spines are fully concealed by the ilium in most ornithomimosaurs, and extend far enough dorsally to be visible in lateral view only in *Harpymimus okladnikovi* and *Deinocheirus mirificus* (Kobayashi and Barsbold, 2005b; Lee et al., 2014).

The sole remaining caudal vertebra is preserved in articulation with the last sacral. Its robust centrum is spool-shaped, being gently constricted in the middle as in other ornithomimosaurs (Osmólska et al., 1972; Kobayashi and Barsbold, 2005a); by contrast, the first caudal of *Rativates evadens* has a straight ventral margin (McFeeters et al., 2016). The lateral surface of the caudal centrum is smooth, and there is no sign of pneumatization. The posterior articular surface is flat but rugose, and subquadrangular. The ventral surface is also flat. By contrast, proximal caudals of the sympatric *Archaeornithomimus asiaticus* are amphicoelous, with shallow ventral grooves (Smith and Galton, 1990). The broad transverse processes extend somewhat upward, taper distally, and
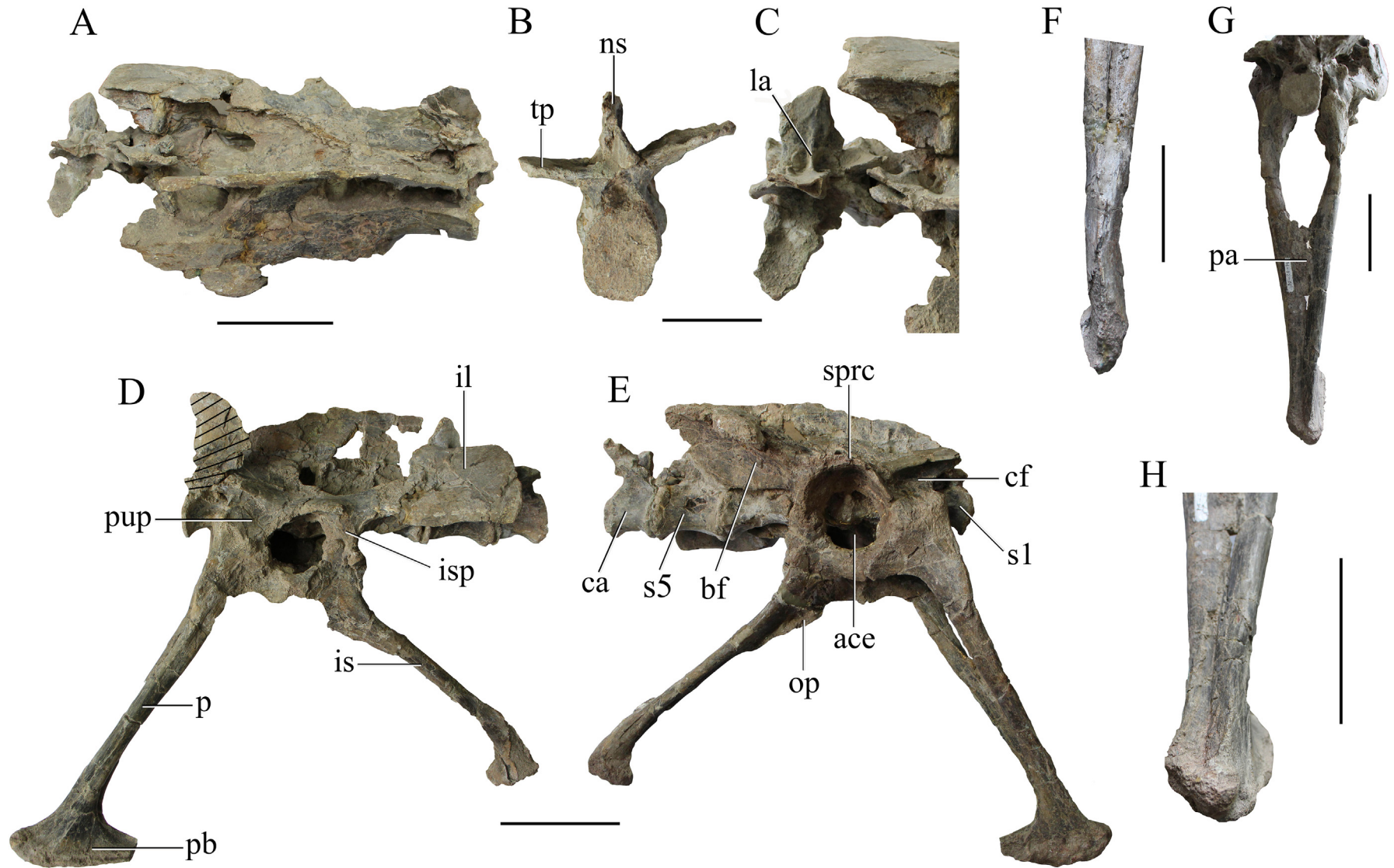
Fig. 2. LH-02-01, comprising an articulated pelvis, sacrum and first caudal. Specimen in dorsal view (A), first caudal in posterior (B) and dorsal views (C), specimen in left lateral (D) and right lateral views (E), ischia in posterior view (F), and pubes in anterior view (G, H). Abbreviations: ace, acetabulum, bf, brevis fossa, ca, caudal vertebra, cf, cuppedicus fossa, il, ilium, isp, ischial peduncle, is, ischium, la, lamina, ns, neural spine, s1 and s5, sacral vertebrae, sprc, supraacetabular crest, tp transverse process, op, obturator process, p, pubis, pa, pubic apron, pb, pubic boot, pup, pubic peduncle. Scale bar equals 10 cm.

have gentle troughs on their dorsal surfaces. A poorly developed vertical lamina is present on the dorsal surface of the left transverse process, separating an anterior fossa from a posterior one within the trough. A similar lamina and set of fossae have been reported only in the proximal caudals of *Garudimimus brevipes* among known ornithomimosaurians (Kobayashi and Barsbold, 2005a). Below the transverse process the caudal is smooth, lacking the centrodiapophyseal laminae seen in the Bissekty ornithomimids (Sues and Averianov, 2016a). Both sets of zygapophyses are inclined at about 30° from the sagittal plane, and bear rounded articular facets at their distal ends. Similar to *Garudimimus brevipes*, the neural spine is broad, nearly rectangular, and directed slightly posteriorly, whereas in *Archaeornithomimus asiaticus* the neural spine of the first caudal has an approximately vertical orientation (Smith and Galton, 1990; Kobayashi and Barsbold, 2005a).

Both ilia are preserved, although with damage to their dorsal portions. The total anteroposterior length of the preserved part of the left ilium is 342 mm, indicating that this specimen is much larger than the sympatric *Archaeornithomimus asiaticus* AMNH 21790, in which the single preserved ilium is only 114 mm long (Smith and Galton, 1990). As in other ornithomimosaurs, the ilia diverge laterally towards their posterior ends, and converge towards their anterior ones. The lateral surfaces of the ilia are anteroposteriorly broadly concave. The ventral portion of the preacetabular process flares laterally, forming a cuppedicus fossa in combination with the anteroventrally oriented pubic peduncle. The subcircular acetabulum has a diameter of about 64 mm, and is overhung by a robust, laterally projecting supraacetabular crest as in other ornithomimosaurs (Makovicky et al., 2004). The center of the acetabulum is approximately at the level of the junction between the second and third sacrals, whereas the anterior margin is aligned with the middle of the second sacral and the posterior margin with the middle of the third sacral. This placement of the acetabulum relative to the sacral series corresponds to the condition in *Archaeornithomimus asiaticus* and *Gallimimus bullatus* (Gilmore, 1933; Osmólska et al., 1972; Smith and Galton, 1990), whereas the acetabulum is positioned lateral to the third and fourth sacrals in *Harpymimus okladnikovi*, *Garudimimus bullatus*, *Deinocheirus mirificus*, *Sinornithomimus dongi* and *Rativates evadens* (Kobayashi and Lü, 2003; Kobayashi and Barsbold, 2005a, b; Lee et al., 2014; McFeeters et al., 2016). The pubic peduncle is wide in lateral view, its anteroventral margin measuring 61 mm. The articular surface for the pubis is triangular, with a wide posterior margin but a relatively narrow anterior end. The ischial peduncle is narrower and slightly longer than the pubic peduncle, and is convex ventrally, inserting into a concavity on the iliac peduncle of the ischium as in other ornithomimosaurs (Makovicky et al., 2004). The left ilium has a squared off posterior end as in other ornithomimosaurs, with the exception of *Shenzhousaurus orientalis* (Ji et al., 2003). The right brevis fossa is broad, and is formed by an arched shelf that extends across the medial surface of the ilium from the base of the ischial peduncle to the posterior end of the ilium. Due to distortion, the right brevis fossa is exposed in lateral view, while the left brevis fossa is concealed entirely by the iliac posterior end.

The pubis is the longest bone among the pelvic elements, measuring about 417 mm (Table 1), and is slender and straight with an expanded distal boot. The pubis has a similar appearance in most ornithomimosaurs, but in *Archaeornithomimus asiaticus* AMNH 21799 and *Ornithomimus* sp. MNA P1.1762A the distal part of the pubic shaft is sharply curved rather than straight (Decourten and Russell, 1985; Smith and Galton, 1990; Claessens and Loewen, 2015). The distal part of the pubis is also slightly curved in *Harpymimus okladnikovi*, *Garudimimus brevipes* and even *Shenzhousaurus orientalis*, but not nearly to the degree seen in *Archaeornithomimus asiaticus* (Smith and Galton, 1990; Ji et al., 2003; Kobayashi and

Table 1
Selected measurements of LH 02−01(in mm). * denotes preserved length of an incomplete element.

Element	Length	Width	Height
Ilium (L)	342.1*		
Pubis (L)	417.2		
Pubis(R)	434.0		
Pubic boot, anteroposterior length (L)	129.0		
Pubic boot, anteroposterior length (R)	116.2		
Ischium (L)	340.5		
Ischium (R)	357.8		
Obturator process, length parallel to ischium shaft	91.5		
Ischium distal end, anteroposterior length (L)	58.3		
Ischium distal end, anteroposterior length (R)	58.6		
Ischium distal end, transverse width		28.6	
Sacral 1 centrum	72.6	47.1	45.0
Sacral 2 centrum	61.8		
Sacral 3 centrum	68.7		
Sacral 4 centrum	83.6		
Sacral 5 centrum	80.9		
Caudal 1 centrum	65.2	43.8	58.6

Barsbold, 2005a, b). The pubis is transversely compressed at both its proximal and distal ends. Proximally, the iliac and ischial processes are both short, and are separated by a shallow concavity which constitutes the smallest of the three components of the acetabular boundary. The proximal margin of the expanded iliac process is straight in lateral view, whereas the ischial process has a convex caudal margin, which fits into a matching concavity on the pubic process of the ischium. The ischial process, and the curved suture between the pubis and ischium, resemble their counterparts in *Garudimimus brevipes*, *Archaeornithomimus asiaticus* and *Gallimimus bullatus* (Osmólska et al., 1972; Smith and Galton, 1990; Kobayashi and Barsbold, 2005a). This contact suture is zigzag in *Deinocheirus mirificus*, and straight in *Qiupalong henanensis* (Xu et al., 2011; Lee et al., 2014). The lateral surface of the iliac process is medially inclined from the sagittal plane at about 45°, facing dorsolaterally. A low but rugose swelling on the proximal part of the lateral surface extends from the posteroventral corner of the ischial process to the anterodorsal corner of the iliac process. Immediately ventral to the swelling, the proximal part of the lateral surface of the pubic shaft is depressed. The cross section of the pubic shaft is generally triangular. The anterior and posterior margins of the shaft are narrow but rounded, whereas the medial margin is sharp.

Distally, the left and right pubes fuse into a single median, anteroposteriorly expanded boot. The fusion of the boot is complete posteriorly, whereas in the anterior portion the two components are discernible as in *Gallimimus bullatus* (Fig. 2H). In *Garudimimus brevipes* and *Qiupalong henanensis*, the two halves of the pubic boot are partially separated anteriorly (Osmólska et al., 1972; Kobayashi and Barsbold, 2005b; Xu et al., 2011). The pubic boot extends from the shaft both anteriorly and posteriorly, and the posterior process of the boot is much longer than the anterior one as in most ornithomimosaurs other than *Nqwebasaurus thwazi* (de Klerk et al., 2000; Makovicky et al., 2004; Sereno, 2017), in which the anterior process is either equal in extent to the posterior one or entirely absent. The rugose ventral surface of the pubic boot was presumably covered by cartilage in life, and is uneven, the ventral margin of the boot appearing convex in right lateral view but relatively flat in left lateral view. The pubic boot varies in ventral convexity among ornithomimosaurs, the ventral surface being relatively flat in *Garudimimus brevipes*, *Archaeornithomimus asiaticus* and *Anserimimus planinychus* (Smith and Galton, 1990; Kobayashi and Barsbold, 2005a; Xu et al., 2011), convex in *Shenzhousaurus orientalis*, *Gallimimus bullatus* and *Qiupalong henanensis* (Osmólska et al., 1972; Ji

et al., 2003; Xu et al., 2011), and strongly convex in *Ornithomimus edmontonicus* AMNH 5201, albeit less so in *Ornithomimus edmontonicus* ROM 851 (Xu et al., 2011; McFeeters et al., 2016). The dorsal edges of the anterior and posterior processes of the pubic boot are sharp, and the anterior process tapers to a bluntly rounded point, whereas the posterior process is truncated by damage. The angle between the shaft and the main axis of the pubic boot is about 64°, similar to late-diverging ornithomimisaurs like *Qiupalong henanensis*, *Ornithomimus edmontonicus* ROM 851, and *Dromiceiomimus brevitertius* ROM 797 (Xu et al., 2011). The transition between the anterior edge of the pubic shaft and the dorsal edge of the anterior process of the pubic boot of LH-02-01 occurs along a curve as in most other ornithomimosaurs, whereas in *Archaeornithomimus asiaticus*, *Qiupalong henanensis*, and a *Harpymimus*-grade ornithomimosaur from Mongolia (IGM 960910KD) the two edges form a sharp angle (Xu et al., 2011). The ventral surface of the boot is slightly expanded transversely.

In anterior view, the proximal halves of the two pubes diverge slightly laterally as they extend posterodorsally just above the apron, but then curve back medially at their proximal ends, as in other ornithomimosaurs. About 140 mm from their proximal ends, the pubes give rise to thin medial flanges that meet at the midline to form a pubic apron which extends along the midline for 274 mm, approximately 2/3 of total pubic length. A sharp ridge begins on the medial surface of the base of the ischial process, curves across the medial surface of the pubic shaft, and eventually forms the proximal edge of the pubic apron. Two narrow apertures pierce the apron on the midline, the more distally located of the two being the more proximodistally elongate, but both of them seem to be the result of weathering.

Both ischia are completely preserved. The ischium takes the form of a long, posteroventrally directed rod, with an anteriorly expanded distal boot as in most ornithomimosaurs. In *Archaeornithomimus asiaticus*, by contrast, the distal end of the ischium has a slight posterior expansion as well as the typical, and more pronounced, anterior expansion (Smith and Galton, 1990). The ischium is roughly 80% as long as the pubis (Table 1). Among ornithomimosaurs, the equivalent ratio is similar in *Ornithomimus edmontonicus*, *Struthiomimus altus* and *Dromiceiomimus brevitertius* (Nicholls and Russell, 1980; Macdonald and Currie, 2019), but only about 71% in *Sinornithomimus dongi* and *Gallimimus bullatus* (Osmólska et al., 1972; Kobayashi and Lü, 2003), and more than 90% in *Shenzhousaurus orientalis*, *Deinocheirus mirificus* and *Archaeornithomimus asiaticus*, although the relative lengths of the pubis and ischium may be subject to ontogenetic as well as taxonomic variation (Smith and Galton, 1990; Ji et al., 2003; Lee et al., 2014). In lateral view, the ischial shaft appears essentially straight, but its distal end curves slightly anteriorly as in most other ornithomimosaurs. The proximal end of the ischium is divided into two robust processes that contact the ilium and pubis, separated by a crescentic concavity that constitutes the posteroventral boundary of the acetabulum. The dorsoventral height of the iliac process is slightly less than the anteroposterior length of the pubic process in lateral view, and both processes bear concave articular surfaces. The medial surfaces of the two processes are flattened, but the lateral surfaces are broadly convex. The cross section of the ischial shaft is generally elliptical, although the anteromedial surface appears flattened, and the ischium is transversely compressed both proximally and distally. The two ischia fuse with each other distally, and also along the ventral edge of their obturator processes. The obturator process is a subtriangular flange, proximally situated and occupying roughly one quarter of the length of the ischial shaft. The distal expansion of the ischium has a sharp posterior edge, and occupies about the distal third of the bone. More proximally, a gap exists between the ischial shafts as in most ornithomimosaurs,

although in *Rativates evadens* the ischia are fully fused throughout their length (McFeeters et al., 2016). The anterior edge of the distal ischial expansion is convex and thick, and the dorsal edge that recedes into the shaft is sharp. The entire ventral surface of the expansion is rugose, transversely broad, but relatively flat. A similar condition is present in *Sinornithomimus dongi*, whereas the fused distal ends of the ischia are strongly broadened in *Gallimimus bullatus*, and mediolaterally narrow in *Rativates evadens* (Osmólska et al., 1972; Ji et al., 2003; McFeeters et al., 2016).

4. Discussion

Pelvic material has rarely, in comparison to skull and limb bones, been considered as a basis for referring specimens to Ornithomimosauria (Makovicky et al., 2004; Choiniere et al., 2012; Serrano-Brañas et al., 2020). Sereno (1999) recovered only one pelvic synapomorphy for Ornithomimosauria: iliac blades deflected toward midline with partial contact along dorsal margin. The iliac blades of LH-02-01 indeed slope strongly dorsomedially (Fig 2A), and it is highly likely that they would have contacted each other dorsally when intact, although the dorsal portions of both ilia are missing in this specimen. Other systematic analyses involving ornithomimosaurians did not optimize any pelvic features as synapomorphies of Ornithomimosauria (Senter, 2007; Choiniere et al., 2012). However, a survey of ornithomimosaurian pelvic morphology indicates that the following combination of characters is sufficient to confidently refer LH-02-01 to Ornithomimosauria: ilia dorsomedially inclined, supraacetabular crest and cuppedicus fossa well developed, posterior process of pubic boot longer than anterior process, pubic boot only slightly expanded transversely, and ischial boot well developed. Within this group, the presence of only five rather than six sacral vertebrae distinguishes LH-02-01 from other ornithomimosaurs for which well-preserved sacra are known, with the exceptions of *Archaeornithomimus asiaticus*, *Gallimimus bullatus*, *Shenzhousaurus orientalis*, and possibly the Bissekty ornithomimid from Uzbekistan (Osmólska et al., 1972; Smith and Galton, 1990; Ji et al., 2003; Makovicky et al., 2004; Sues and Averianov, 2016a). Four sacrals are preserved in one specimen of the Bissekty ornithomimid, and there is an indication that another sacral was present posterior to those four, but Sues and Averianov (2016a) did not say why two additional sacrals could not have been present, for a total of six. LH-02-01 differs from *Shenzhousaurus orientalis* in that the iliac posterior end is squared off, the lateral surface of the pubis lacks a sinuous longitudinal ridge, and the ischium is only 80% as long as the pubis (Ji et al., 2003); from *Gallimimus bullatus* in that the neural spines are fused into a plate, and the ischial boot is not strongly broadened transversely (Osmólska et al., 1972); and from the Bissekty ornithomimid, in which the pelvis is poorly known, in that there are no centrodiapophyseal laminae on the anteriormost caudal vertebra, and ventral sulci are present on the sacrals (Sues and Averianov, 2016a).

Comparisons to the sympatric *Archaeornithomimus asiaticus* are more complex because of the possibility that not all of the material presently assigned to this species is in fact conspecific (Russell, 1972; Currie and Eberth, 1993). LH-02-01 exhibits minor differences in sacral and anterior caudal vertebral morphology from the previously described specimen AMNH 21790, which comprises a left ilium preserved in articulation with the five sacral and five anteriormost caudal vertebrae (Gilmore, 1933; Smith and Galton, 1990). Specifically, LH-02-01 differs from AMNH 21790 in that the shortest sacral centrum is the second rather than the third; the centrum of the first caudal is shorter than that of the fifth sacral, has a flat rather than concave posterior surface, and lacks a ventral groove; and the neural spine of the first caudal is inclined posteriorly. LH-02-01 shares with AMNH 21790 two features that are

unusual among ornithomimosaurians, namely a sacral series comprising five rather than six vertebrae and the presence of shallow ventral grooves on the sacral centra.

The pubis of LH-02-01 differs strikingly from the *Archaeornithomimus asiaticus* pubis AMNH 21799 in that the shaft is straight throughout its length, rather than curved in its distal portion. An additional minor difference is that the anterior margin of the boot of *Archaeornithomimus asiaticus* AMNH 21799 is illustrated by both Smith and Galton (1990) and Gilmore (1933) as quite bluntly rounded, whereas that of the boot of LH-02-01 comes to a sharper point. Similarly, the distal end of the ischium of LH-02-01 is expanded only in the anterior direction, whereas that of the *Archaeornithomimus asiaticus* ischium AMNH 21798 has both a sizeable anterior expansion and a smaller posterior one. Furthermore, the obturator process appears more prominent in AMNH 21798 than in LH-02-01.

The striking morphological differences between LH-02-01 on the one hand, and AMNH 21798 and 21799 on the other, indicate that LH-02-01 belongs to a different taxon than these two AMNH specimens. By contrast, the comparisons presented above between LH-02-01 and AMNH 21790 reveal two striking similarities alongside several minor differences, and imply two taxonomic possibilities. If LH-02-01 is not conspecific with AMNH 21790, then the latter specimen presumably belongs to the same species as AMNH 21798 and 21799, with LH-02-01 representing a separate taxon. Alternatively, LH-02−01 may indeed be conspecific with AMNH 21790, implying that AMNH 21790 is taxonomically distinct from AMNH 21798 and 21799. In either case, two different ornithomimosaurs are present in the Erlian Formation. A revision of the Erlian ornithomimosaur material is beyond the scope of this contribution, but we note that only material that is demonstrably likely to be conspecific with the lectotype of *Archaeornithomimus asiaticus* (AMNH 6565; Smith and Galton, 1990) should be referred to this species. Future discoveries may show that LH-02-01 belongs to *Archaeornithomimus asiaticus*, which would imply that AMNH 21798 and 21799 represent a different species, or may show that LH-02-01 belongs to a different species and AMNH 21798 and 21799 represent the ischium and pubis of *Archaeornithomimus asiaticus*.

No sacral material is known for the ornithomimosaurians *Nqwebasaurus thwazi*, *Beishanlong grandis*, *Qiupalong henanensis*, *Dromiceiomimus brevitertius*, *Paraxenisaurus normalensis* and *Tototlmimus packardensis* (Makovicky et al., 2010; Xu et al., 2011; Serrano-Brañas et al., 2016; Sereno, 2017; Macdonald and Currie, 2019; Serrano-Brañas et al., 2020; Cuesta et al., 2022). Furthermore, no pelvic material is known for *Paraxenisaurus normalensis* and *Tototlmimus packardensis*, taxa represented exclusively by fragmentary specimens (Serrano-Brañas et al., 2016, 2020). However, *Beishanlong grandis* differs from all other ornithomimosaurians in which the pelvis is known, including LH-02-01, in that the ischium has the sigmoid curvature typical of late-diverging taxa but lacks a strongly developed distal boot and obturator process (Makovicky et al., 2010); LH-02-01 differs from *Qiupalong henanensis* in that the right and left components of the pubic boot are fused anteriorly, and in that the ischial process of the pubis has a convex caudal margin and lacks a ventral tubercle (Xu et al., 2011); and LH-02-01 differs from *Dromiceiomimus brevitertius* in that the anteriormost caudal centrum is less than twice as long as wide, and in that the dorsal edge of the postacetabular process of the ilium, and the distal and the posterodorsal edges of the distal part of the ischium, are straight rather than convex (Macdonald and Currie, 2019). The only known specimen of *Nqwebasaurus thwazi* preserves partial pubes in which the distal boot is only incipiently developed, in marked contrast to the condition in LH-02-01 (de Klerk et al., 2000; Sereno, 2017). The pelvic elements of LH-02-01 show a suite of anatomical features not seen in any other known ornithomimosaurian pelvic material. Given the fragmentary nature of LH-02-01 and the lack of discernible autapomorphies, however, we refrain from erecting a new taxon based on this incomplete specimen.

Currie and Eberth (1993) suspected that some *Archaeornithomimus asiaticus* specimens from the Erlian Formation might belong to *Garudimimus bullatus*, and contended that the presence of only five vertebrae in the sacrum of *Archaeornithomimus asiaticus* AMNH 21790 might be attributed to its immaturity. However, this explanation cannot be applied to LH-02-01. The pubis measures 417 mm long in LH-02-01 and only 390 mm in the holotype of *Garudimimus bullatus* (Kobayashi and Barsbold, 2005a), indicating that LH-02-01 is the larger individual. This comparison, especially in combination with the presence of pubic curvature in *Garudimimus bullatus* but not in LH-02-01, shows that the latter cannot be considered an immature *Garudimimus bullatus* which would have gained an additional sacral vertebra with age.

This new discovery increases the known coelurosaurian diversity in the Erlian Formation, and more specifically demonstrates the presence of a second ornithomimosaur distinct from *Archaeornithomimus asiaticus* in the Iren Nor Region in the Late Cretaceous. Coexistence of multiple ornithomimosaur taxa in a single stratigraphic unit is not uncommon (Longrich, 2008; Sues and Averianov, 2016a). Given that both of the Erlian ornithomimosaurs are relatively poorly known, speculation regarding the palaeobiological factors that permitted them to maintain sympatry without one competitively excluding the other is difficult.

4.1. Phylogenetic relationships

To investigate the phylogenetic position of LH-02-01 among Ornithomimosauria, we added scorings for this specimen into a recent character-taxon matrix with broad sampling of theropod dinosaurs presented by Serrano-Brañas et al. (2020). This matrix was derived from one compiled by Choiniere et al. (2012), and incorporated subsequent modifications by Lee et al. (2014) and Sues and Averianov (2016a). Following the settings used in these previous studies, *Herrerasaurus* was chosen as the outgroup, and all characters were equally weighted and unordered. The search iterations were performed in TNT version 1.1 with heuristic tree search methods on 1000 Wagner tree replicates with random addition sequences, and then subjected to TBR (tree bisection-reconnection) swapping methods until all most parsimonious trees (MPTs) were obtained (Goloboff et al., 2008). Our analysis resulted in 3600 MPTs, each having a length of 2936 steps, a consistency index of 0.228, and a retention index of 0.613.

The results supported assignment of LH-02-01 to Ornithomimosauria, but placed it outside the two major clades Deinocheiridae or Ornithomimidae, as part of a polytomy with several other early-diverging ornithomimosaurian taxa (Fig. 3). No unambiguous synapomorphies were optimized for the node Ornithomimosauria. Deinocheiridae is supported by characters 302, six sacral vertebrae; 410, ratio of proximodistal length of phalanx I-1 to that of MC I between 1 and 1.5; 412, penultimate phalanx of the third finger longer than each of the more proximal phalanges of the same digit; and 557, MT III shaft rectangular in cross section. Ornithomimidae is supported by characters 263, anterior cervical centra length between two and three times transverse width; 517, shape of fibular crest quadrangular; and 554, MT III subequal in proximal width to MTs II and IV.

The inability of the analysis to resolve the interrelationships among LH-02-01 and other early-diverging ornithomimosaurians results in substantial part from the fact that the pelvis is poorly known among ornithomimosaurs, and in particular among early-diverging members of the group. The pelvis is unknown in
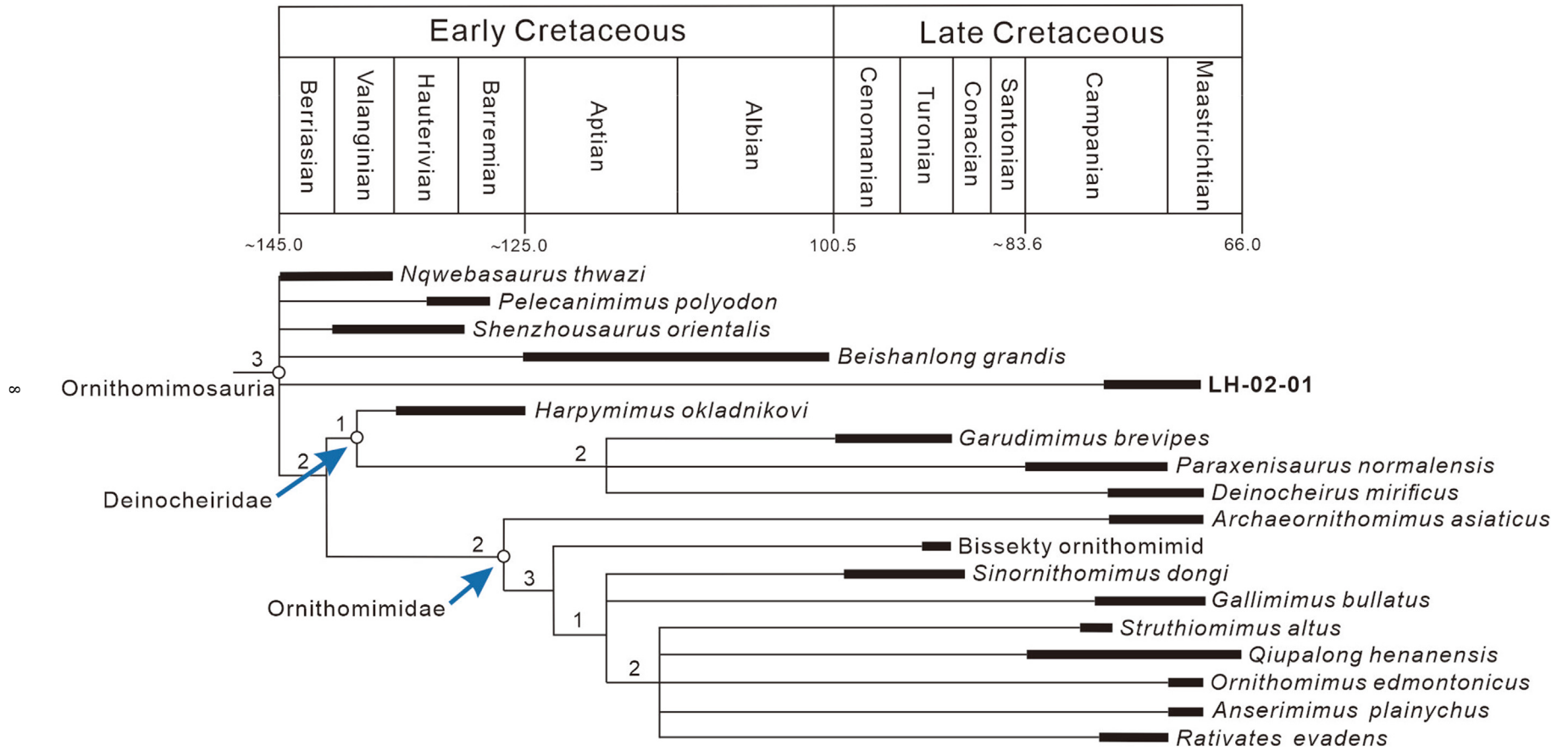
Fig. 3. Time-calibrated strict consensus of 3600 MPTs, showing the phylogenetic position of LH-02-01 among Ornithomimosauria. Numbers associated with nodes represent Bremer support values.

Pelecanimimus polyodon and *Hexing qingyi* (Pérez-Moreno et al., 1994; Jin et al., 2012; Cuesta et al., 2022), and represented in the only known specimen of *Nqwebasaurus thwazi* merely by the partial pubes (de Klerk et al., 2000; Sereno, 2017), which display a pubic boot that is rudimentary relative to those of late-diverging ornithomimosaurs. *Shenzhousaurus orientalis* has a well-preserved pelvis, which appears less derived than that of LH-02-01 in having a rounded iliac posterior end, a pubic boot with only a weakly developed anterior process, and a straight ischial shaft (Ji et al., 2003). Makovicky et al. (2004) also pointed out that *Harpymimus okladnikovi* was united with other ornithomimosaurs in which the pelvis was known at the time, excluding *Shenzhousaurus orientalis*, by the fact that the ischium was rostroventrally concave rather than straight, in agreement with our observations. The ischium of LH-02-01 is distally curved, although not to the degree seen in late-diverging ornithomimosaurs. LH-02-01 and *Beishanlong grandis* both have a distally curved ischium, but other phylogenetically informative differences between them have not been observed (Makovicky et al., 2010).

LH-02-01 shares with deinocheirids one unique feature: the sacral neural spines are fused into a plate. This feature is poorly illustrated in other ornithomimosaurs, but in ornithomimids in which the sacrum has been well described, such as *Gallimimus bullatus* and *Rativates evadens*, the neural spines are separated, and in the Bissekty ornithomimid the sacral neural spines are only partially coalesced (Osmólska et al., 1972; McFeeters et al., 2016; Sues and Averianov, 2016a). As a matter of fact, full coalescence of the neural spines might ultimately prove to be a synapomorphy of deinocheirids or a slightly wider clade, and a close relationship between LH-02-01 and this group cannot be entirely ruled out until more information regarding variation in pelvic morphology within Ornithomimosauria has been obtained. Nonetheless, LH-02-01 also resembles some late-diverging ornithomimosaurs in having a straight pubis. Xu et al. (2011) stated that the pubic shaft is nearly straight in most ornithomimosaurs other than *Archaeornithomimus asiaticus*, which is generally true (Xu et al., 2011). Strictly speaking, however, the distal part of the pubic shaft is also curved in *Harpymimus*, *Garudimimus brevipes* and even *Shenzhousaurus orientalis*, although not to the extent seen in *Archaeornithomimus asiaticus* (Xu et al., 2011). The more fully straight pubis seen in LH-02-01, however, resembles the condition in late-diverging ornithomimosaurs, including *Gallimimus bullatus*, *Qiupalong henanensis*, and North American taxa. This distribution pattern indicates that a straight pubis independently evolved at least twice within Ornithomimosauria, whereas the curved pubis seen in some members of each clade represents the plesiomorphic condition. Finally, a sacrum comprising five vertebrae occurs only in the early-diverging ornithomimosaurs *Shenzhousaurus orientalis* and LH-02-01, and the ornithomimids *Archaeornithomimus asiaticus* and *Gallimimus bullatus*, suggesting this feature is likely plesiomorphic. Other ornithomimosaurians, which have six sacral vertebrae, probably increased the count by incorporating the last dorsal vertebra into the sacrum, given that the acetabulum is positioned further posteriorly relative to the sacrum in these taxa than in the few ornithomimosaurians with only five sacrals.

4.2. Age of the Erlian Formation

Numerous authors have considered the age of the Erlian Formation since paleontological exploration began in the 1920s. In a paper submitted from the field, Granger and Berkey (1922) recognized this unit (called by them, and many subsequent authors, the Iren Dabasu Formation) as Cretaceous on the basis of its fossil vertebrate content, but made no attempt to determine its age with greater precision. Osborn (1922) later republished their report with minor modifications, including a change in the inferred chronostratigraphic assignment of the formation from "Cretaceous" to "Upper Cretaceous" at one point in the text, but without giving any reason for the emendation. Berkey and Morris (1927) tentatively considered the Erlian Formation to be Lower Cretaceous, based on an assessment by William Diller Matthew of the fauna as "rather primitive" (Berkey and Morris, 1927, p. 355). Although they mentioned the presence of "iguanodonts", in the formation, which presumably factored heavily into Matthew's opinion, there is no indication that they "proposed a Lower Cretaceous age…based on the occurrence of the ornithopod dinosaur *Iguanodon*" (Van Itterbeeck et al., 2005: p. 702) in particular. Incidentally, and as a historical footnote, it has often been asserted (e.g. by Gilmore, 1933; Morris, 1936; and Currie and Eberth, 1993; although notably not by Berkey and Morris, 1927) that Granger and Berkey (1922) also assigned the Erlian Formation to the Lower Cretaceous in their original assessment. The basis for these statements appears to be a reference in an unnumbered table to "Lower or Dinosaur beds" within the Cretaceous strata (Granger and Berkey, 1922: p. 5), but the context implies that the word "Lower" was meant to designate the stratigraphically inferior portion of the putatively Cretaceous beds in what Granger and Berkey (1922) called the Iren Dabasu basin, rather than to suggest that the beds were assignable to the Lower Cretaceous Series. The "Lower or Dinosaur beds" are now considered to represent the entirety of the Erlian Formation, as Granger and Berkey's (1922) supposedly Cretaceous "Upper barren members" were recognized by Berkey and Morris (1927) and later authors as being Cenozoic in age.

Morris (1936) regarded the assignment of the Erlian Formation within the Cretaceous as uncertain, and highlighted the divergent opinions of earlier authors, but was impressed by similarities between the dinosaur faunas of the Iren Dabasu Formation and the Wangshi Group (considered by him a formation) of Shandong. He depicted both rock units as Campanian on a stratigraphic chart (Morris, 1936: pl. 1), while emphasizing the provisional nature of this placement. Gilmore (1933), the first worker to describe the fossil vertebrates of the Erlian Formation in any detail, made a strong case for a Late Cretaceous age based on perceived similarities between the Erlian dinosaur assemblage and those from "the Belly River and Edmonton formations in Canada and their equivalents in the United States" (Gilmore, 1933: p. 25). The units mentioned are now termed the Belly River and Edmonton groups, and known to be Campanian and Campanian—Maastrichtian, respectively (Zubalich et al., 2021).

Gilmore's (1933) conclusion that the Erlian Formation could be assigned to the Upper Cretaceous has been accepted by almost all subsequent authors, although Russell (1972: p. 378) considered the formation to be among the few "early and middle Cretaceous" units from which ornithomimids had been recovered. The position of the Erlian Formation within the Upper Cretaceous, however, has been a matter of ongoing debate. The Erlian ornithopods *Bactrosaurus johnsoni* and *Gilmoreosaurus mongoliensis*, regarded by Gilmore (1933) as hadrosaurids, were reassessed by Rozhdestvenskiy (1966) as "considerably more primitive" than the "well-studied hadrosaurs of North America" (Rozhdestvenskiy, 1966: p. 565—566), and are now considered early-diverging (i.e. non-hadrosaurid) hadrosauroids (Prieto-Márquez and Norell, 2010; Tsogtbaatar et al., 2019). Many researchers either explicitly argued, or strongly implied, that the plesiomorphic nature of these taxa showed the Erlian Formation to be Cenomanian or Turonian (Rozhdestvenskiy, 1966; Rozhdestvensky, 1977; Brett-Surman, 1979, 1980; Weishampel and Horner, 1986; Godefroit et al., 1998).

Other authors have considered the vertebrate fauna of the Erlian Formation more broadly, and drawn comparisons with potentially equivalent assemblages from the Upper Cretaceous of central Asia.

Although a detailed review of such comparisons is beyond the scope of this paper, Jerzykiewicz and Russell (1991) noted a few faunal similarities between the Erlian Formation and the Bayn Shire Formation of Mongolia. They tentatively suggested that "Bayn-shirenian" time might extend from the early Turonian to the early Campanian, but did not explicitly consider the age of the Erlian Formation or assign this formation to their "Baynshirenian" time interval. Currie and Eberth (1993) made more extensive comparisons between the Erlian and Bayn Shire vertebrate assemblages, and also noted the presence in both formations of the unionid bivalve *Pseudohyria*. They placed particular emphasis on the presence of the turtle genus *Lindholmemys* in both the Erlian Formation and the upper part of the Bayn Shire Formation. However, Currie and Eberth also considered the Erlian Formation to contain specimens referable to the theropods *Saurornithoides*, *Avimimus* and *Velociraptor*, "genera…characteristic of Djadokhta (Campanian) and younger sediments in Mongolia" (Currie and Eberth, 1993: p. 140). They regarded the Erlian Formation as equivalent in age to the "uppermost levels of the Bayn Shire". While other biostratigraphic evidence including the occurrence of *Lindholmemys* suggested the upper Bayn Shire Formation to be Coniacian-Santonian, the putative presence of *Saurornithoides*, *Avimimus* and *Velociraptor* led Currie and Eberth (1993: p. 140) to propose that the Erlian Formation, and by implication the uppermost Bayn Shire Formation, might "ultimately prove to be as young as Campanian". They concluded more firmly that the Erlian Formation was post-Cenomanian. More recently, Tsogtbaatar et al. (2019) strengthened the case for faunal similarity between the Bayn Shire and Erlian formations by assigning hadrosauroid material from various Bayn Shire localities to *Gobihadros mongoliensis*, a new species comparable in evolutionary grade to *Bactrosaurus johnsoni* and *Gilmoreosaurus mongoliensis*.

Averianov (2002) and Averianov and Sues (2012) agreed that the Erlian Formation was likely to be roughly similar in age to the upper Bayn Shire Formation, but put more emphasis on the faunal similarities between the Erlian Formation and the Bissekty Formation of Uzbekistan. Averianov (2002) listed a number of dinosaur and turtle genera as occurring in all three units, along with the crocodyliform *Shamosuchus*. Averianov and Sues (2012) were more conservative, and pointed out that some of the purported Bissekty dinosaur occurrences, in particular, were based on fragmentary specimens that could not be reliably identified at the generic level. They considered *Shamosuchus* to be common throughout the Upper Cretaceous of central Asia, and the turtle *Lindholmemys* to occur in the lower Bayn Shire Formation as well as in the upper Bayn Shire Formation and the Bissekty and Erlian formations, reducing the biostratigraphic value of these taxa. However, Averianov and Sues (2012: p. 476) accepted a general resemblance "in composition and evolutionary level" between the Bissekty and Erlian vertebrate faunas, noting in particular the presence of the turtle genus *Khunnuchelys* and the inferred phylogenetic proximity

of *Bactrosaurus johnsoni* to the Bissekty hadrosauroid *Levnesovia transoxiana* (see Sues and Averianov, 2009). Averianov and Sues (2012: p. 477) likewise argued that the therizinosauroids and ankylosaurids from the Bissekty and upper Bayn Shire formations were of "similar evolutionary levels", citing resemblances between the therizinosauroid *Erlikosaurus andrewsi* and the ankylosaurid *Talarurus plicatospineus* from the upper Bayn Shire Formation and, respectively, an unnamed therizinosauroid and *Bissektipelta archibaldi* from the Bissekty Formation.

Following Averianov and Sues (2012), we acknowledge the Erlian Formation's faunal ties to the upper Bayn Shire Formation, and consider the resemblances between the vertebrate faunas of the Erlian and Bissekty formations to be even more compelling, at least based on currently available evidence (Table 2). *Gilmoreosaurus mongoliensis* can be placed alongside *Bactrosaurus johnsoni* as an Erlian Formation hadrosauroid similar in evolutionary grade to *Levnesovia transoxiana* from the Bissekty Formation (Tsogtbaatar et al., 2019). Among theropods, an indeterminate ornithomimid is known from the Bissekty Formation (Sues and Averianov, 2016a), and may be of similar evolutionary grade to *Archaeornithomimus asiaticus* (Fig. 3). The oviraptorosaur genus *Caenagnathasia* is present in both the Bissekty Formation (Currie et al., 1994; Sues and Averianov, 2015) and the Erlian Formation (Yao et al., 2015). Sues and Averianov (2016b) described fragmentary therizinosauroid material from the Bissekty Formation that they considered to represent at least two separate taxa, but treated as a single operational taxonomic unit for purposes of phylogenetic analysis. They recovered the "Bissekty therizinosauroids" just outside a poorly resolved Therizinosauridae that included the Erlian Formation taxa *Neimongosaurus youngi* and *Erliansaurus bellamanus*, whereas Zanno (2010) posited the two Erlian species just outside a more taxonomically restricted Therizinosauridae. Taken together, these results provide tentative support for regarding *Neimongosaurus youngi* and *Erliansaurus bellamanus* as representing approximately the same evolutionary grade as the Bissekty therizinosauroids.

The Bissekty Formation can be dated fairly precisely, being constrained to the middle−late Turonian by the known temporal ranges of inoceramid clams found in the underlying Dzheirantui Formation and overlying Aitym Formation (Feldmann et al., 2007). By contrast, the Bayn Shire Formation resembles the Erlian Formation in being of uncertain age. Hicks et al. (1999) collected paleomagnetic data from the Bayn Shire strata at the Bayn Shire and Burkhant localities, and found that they had been deposited during a time of normal magnetic polarity, identifiable as the Cretaceous Long Normal interval that extended from about 121 to 83.5 Ma. The end of the Cretaceous Long Normal approximately coincided with the age of the Santonian-Campanian boundary, but Hicks et al. (1999) acknowledged that the sections they had sampled might be too incomplete to capture the very uppermost strata of the Bayn Shire Formation, which could possibly be

Table 2
Similar faunal elements from the Erlian and Bissekty formations.

	Erlian Formation	Bissekty Formation
Ornithomimidae	*Archaeornithimimus asiaticus* (Gilmore, 1933; Smith and Galton, 1990) LH-02-01 (this paper)	Bissekty ornithomimid (Sues and Averianov, 2016a)
Oviraptorosauria	*Caenagnathasia* sp. (Yao et al., 2015)	*Caenagnathasia martinsoni* (Currie, 1994; Sues and Averianov, 2015)
Therizinosauria	*Neimongosaurus youngi* (Zhang et al., 2001) *Erliansaurus bellamanus* (Xu et al., 2002)	Bissekty therizinosauroids (Sues and Averianov, 2016b)
Hadrosauroidea	*Gilmoreosaurus mongoliensis* (Gilmore, 1933; Prieto-Márquez and Norell, 2010) *Bactrosaurus johnsoni* (Gilmore, 1933; Godefroit et al., 1998; Prieto-Márquez, 2011)	*Levnesovia transoxiana* (Sues and Averianov, 2009)
Trionychidae	*Khunnuchelys erinhotensis* (Brinkman et al., 1993)	*Khunnuchelys kizylkumensis* (Brinkman et al., 1993)

reversed in polarity and Campanian in age. Similarly, Kurumada et al. (2020) obtained U−Pb dates from two caliche samples from the Bayn Shire Formation at Khongil Tsav, and found that the stratigraphically higher caliche was no younger than 85.6 Ma (early Santonian), but this caliche does not appear to have been from the uppermost part of the formation. The lower caliche was no older than 101.9 Ma (latest Albian). In combination, the paleomagnetic and caliche dating results weigh against the suggestion that the upper Bayn Shire Formation might extend into the Campanian (Currie and Eberth, 1993), but otherwise offer little chronostratigraphic precision.

With respect to the age of the Erlian Formation, the vertebrate faunal resemblances to the well-dated Bissekty Formation favor a middle−late Turonian date, whereas those to the upper Bayn Shire Formation merely strengthen the case that the Erlian Formation is most likely pre-Campanian. This assessment is contradicted only by the reported occurrence in the Erlian Formation of *Avimimus*, *Saurornithoides* and *Velociraptor* (Currie and Eberth, 1993), but the putative Erlian *Saurornithoides* and *Velociraptor* specimens have never been described or illustrated. The only well-known Erlian avimimid material is taxonomically indeterminate below the level of Avimimidae, but appears to differ from both *Avimimus portentosus* and *Avimimus nemegtensis* from the Nemegt Formation (Averianov, 2002; Funston et al., 2019). The presence of some sort of avimimid in the Erlian Formation (Currie and Eberth, 1993; Longrich and Currie, 2009; Averianov and Sues, 2012; Funston et al., 2019), differing from both Nemegt species, is at best a loose faunal tie to the Nemegt Formation. The purported *Saurornithoides* and *Velociraptor* specimens from the Erlian Formation are even more biostratigraphically tenuous. Whether they really represent the genera in question is uncertain, particularly considering the extent to which knowledge of theropod diversity has expanded since Currie and Eberth (1993) published their assessment of the material. Accordingly, the overall vertebrate signal from the Erlian Formation indicates that this unit is of middle−late Turonian age.

Non-vertebrate biostratigraphy, however, suggests that the Erlian Formation is younger. Chen (1983) reviewed the stratigraphy of China's continental Cretaceous sequences based on evidence from fossil invertebrates and charophytes, and inferred a Maastrichtian age for the Erlian Formation. Similarly, Ma (1994) reported the occurrence in the Erlian Formation of a characteristically Campanian and Maastrichtian bivalve fauna. Intriguingly, the key constituents of this fauna included the genus *Pseudohyria*, various species of which were noted by Currie and Eberth (1993) to be present in the Bayn Shire Formation. Van Itterbeeck et al. (2005) noted strong similarities between the charophyte and ostracod assemblages of the Erlian Formation and those of the Nemegt Formation of Mongolia, a correlation favoring a Campanian−Maastrichtian, and most probably a late Campanian to early Maastrichtian, age for the Erlian Formation. Similarly, Van Itterbeeck et al. (2007) assessed a palynomorph sample from the Erlian Formation as indicating a Maastrichtian date. Bonnetti et al. (2014) also examined Erlian palynomorphs, and emphasized the occurrence in both their own sample and that of Van Itterbeeck et al. (2007) of *Ulmoideipites*, which appears in the record at the top of the Campanian and therefore is inconsistent with a pre-Maastrichtian age for the Erlian Formation.

The conflict between vertebrate and non-vertebrate lines of biostratigraphic evidence regarding the age of the Erlian Formation is stark, and remains unresolved. However, it is notable that the palynomorph assemblage from the Erlian Formation is diverse and includes taxa of high biostratigraphic value (Van Itterbeeck et al., 2007; Bonetti et al., 2014). In particular, Van Itterbeeck et al. (2005) identified in the Erlian Formation two ostracod species

and three charophyte species that occur in the Nemegt Formation but not in older Mongolian formations, and no species of either group that occur in older Mongolian formations but not in the Nemegt Formation. Of the vertebrate-based correlations between the Erlian and Bissekty formations, by contrast, the most precise involve the genera *Lindholmemys*, *Khunnuchelys* and *Caenagnathasia*, rather than particular species within those genera, and the balance involve vaguely defined evolutionary grades. Vertebrate faunal links between the Erlian Formation and the upper Bayn Shire Formation, based on present evidence, are even less definite. The vagueness and ambiguity of the correlations involving vertebrates contrasts with the relative precision and consistency of those involving invertebrates, charophytes and palynomorphs. Accordingly, the latter should be provisionally accepted as more persuasive and the Erlian Formation provisionally regarded, based on currently available data, as Campanian-Maastrichtian, a conclusion ironically consistent with Gilmore's (1933) original vertebrate-based comparison to the Belly River and Edmonton Groups of western Canada. Averianov and Sues (2012: p. 476) considered the biostratigraphic correlations between the Erlian Formation and the Nemegt Formation to reflect "fluvial depositional settings and mesic climatic conditions", rather than similarity in age, but the Bayn Shire Formation is also a fluvial deposit (Currie and Eberth, 1993) and lacks the distinctive charophyte and ostracod species that link the Erlian Formation to the Nemegt Formation (Van Itterbeeck et al., 2005). We see no compelling reason to assume that the invertebrate, charophyte and palynomorph evidence predominantly reflects an environmental signal rather than a temporal one. However, we acknowledge that acceptance of a Campanian-Maastrichtian age for the Erlian Formation requires the assumption that a vertebrate assemblage with some relictual elements persisted into that part of the Cretaceous in the Iren Nor region, for reasons that are presently unclear. The vertebrate faunal evidence will continue to pose a legitimate challenge to the view that the Erlian Formation is Campanian-Maastrichtian until a convincing explanation emerges for why a partially relictual assemblage existed in the Iren Nor region, but not at Mongolian and Chinese sites of purportedly similar age located less than 1000 km to the west.

5. Conclusions

Specimen LH-02-01, fully described in this paper, demonstrates the presence of a second ornithomimosaurian taxon from the Upper Cretaceous Erlian Formation of Nei Mongol, China, regardless of whether LH-02-01 represents a new distinct taxon or is referable to *Archaeornithomimus asiaticus*. The phylogenetic analysis presented in this paper suggests an early-diverging position within Ornithomimosauria for LH-02-01. A comprehensive review of vertebrate-based biostratigraphic correlations between the Erlian Formation and comparable dinosaur-bearing rock units from Asia suggests a strong resemblance to the Bissekty Formation from the Turonian of Uzbekistan, but non-vertebrate correlations suggest a much younger age for the Erlian Formation. The conflict between these two lines of evidence is likely to be fully resolved only on the basis of careful future investigation, but at present the non-vertebrate biostratigraphic data are more precise and persuasive, indicating that the Erlian Formation is most likely Campanian−Maastrichtian.

Acknowledgements

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Appendix A. Supplementary data

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