

A giant ornithomimosaur from the Early Cretaceous of China

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Ornithomimosaur (ostrich-mimic dinosaurs) are a common element of some Cretaceous dinosaur assemblages of Asia and North America. Here, we describe a new species of ornithomimosaur, *Beishanlong grandis*, from an associated, partial postcranial skeleton from the Aptian-Albian Xinminpu Group of northern Gansu, China. *Beishanlong* is similar to another Aptian-Albian ornithomimosaur, *Harpymimus*, with which it shares a phylogenetic position as more derived than the Barremian *Shenzhousaurus* and as sister to a Late Cretaceous clade composed of *Garudimimus* and the Ornithomimidae. *Beishanlong* is one of the largest definitive ornithomimosaur yet described, though histological analysis shows that the holotype individual was still growing at its death. Together with the co-eval and sympatric therizinosaur *Suzhousaurus* and the oviraptorosaur *Gigantraptor*, *Beishanlong* provides evidence for the parallel evolution of gigantism in separate lineages of beaked and possibly herbivorous coelurosaurs within a short time span in Central Asia.

Keywords: Ornithomimosauria; body-size evolution; phylogeny; faunal assemblage; Cretaceous; Central Asia

1. INTRODUCTION

Ornithomimosaur dinosaurs are common elements of many Asian and North American Cretaceous faunas. Although phylogenetically nested among carnivorous theropods, at least advanced ornithomimosaur are believed to have had different trophic biology (Nicholls & Russell 1985; Kobayashi *et al.* 1999; Makovicky *et al.* 2004; Barrett 2005) and may have exhibited gregarious behaviours (Kobayashi & Lü 2003; Varricchio *et al.* 2008). The earliest and most basal taxa *Pelecanimimus* and *Shenzhousaurus* (Ji *et al.* 2003) are relatively small, whereas the body size within the clade culminates in *Gallimimus bullatus* (IGM 100/11), with a body length of 8 m and with estimated mass of 490 kg or more (Christiansen & Fariña 2004; but see below).

Here, we describe a new Early Cretaceous ornithomimosaur taxon from the Yujingzi Basin, Gansu Province, China, which may be the largest ornithomimosaur yet described. Shapiro *et al.* (2003) described an isolated foot possibly referable to this taxon, but they were not able to

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.0236> or via <http://rsob.royalsocietypublishing.org>.

One contribution to a Special Issue 'Recent advances in Chinese palaeontology'.

ascertain whether it represented a new taxon because of limited material. Three new specimens of this taxon have now been collected by our joint field expeditions, providing evidence for a new taxon as well as insights into the evolutionary history of ornithomimosaur and their life-history strategies.

2. SYSTEMATIC PALAEOLOGY

Theropoda Marsh 1881

Tetanurae Gauthier 1986

Coelurosauria Von Huene 1914

Ornithomimosauria Barsbold 1983

Beishanlong grandis n. gen et sp.

(a) Etymology

Beishanlong from the Mandarin *Bei Shan* for Northern Mountain, and *long* for dragon; and *grandis* from the Latin in reference to the large size of this taxon.

(b) Material

Holotype FRDC-GS GJ (06) 01–18, associated postcranial skeleton (figure 1); FRDC-GS GJ (unnumbered), hindlimb elements of large specimen; FRDC-GS JB(07)01-01, a pair of isolated pubes probably referable to this taxon. All material is housed at the Fossil

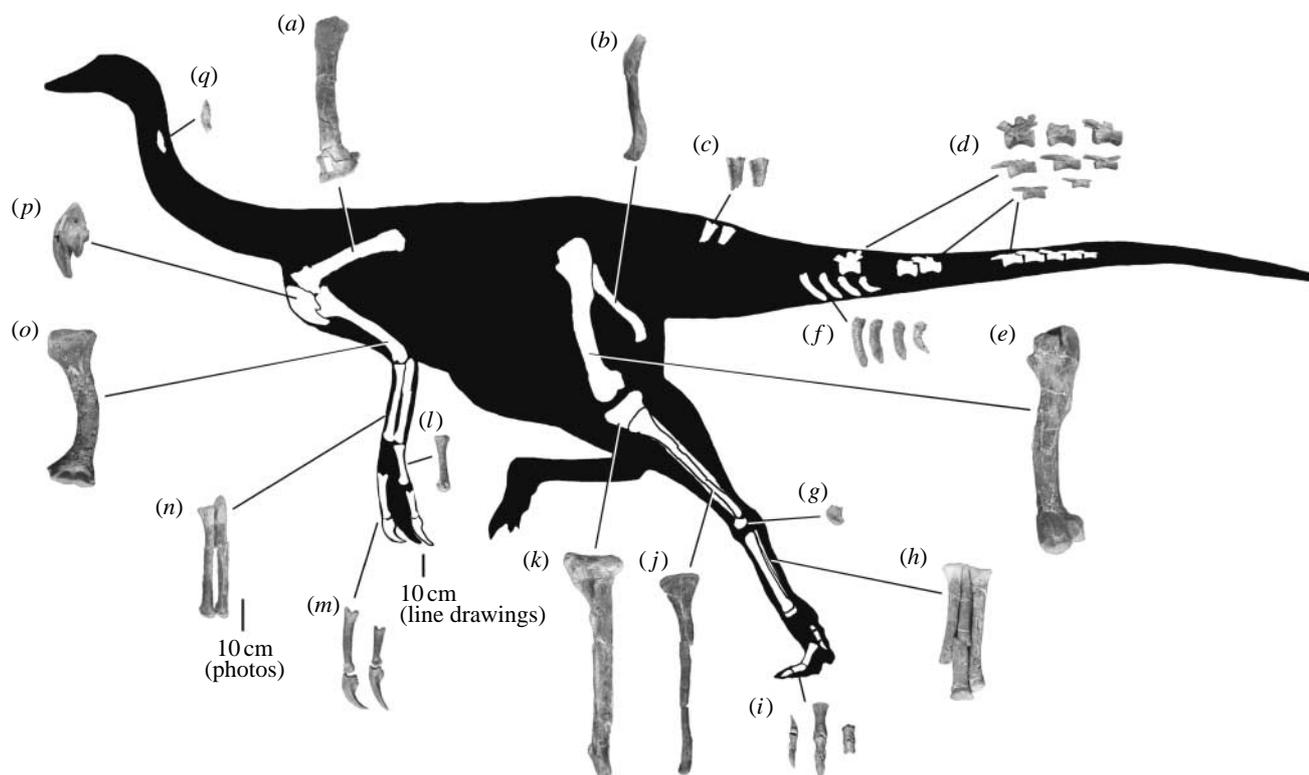


Figure 1. Overview of skeletal elements preserved with holotype (FRDC-GS GJ (06) 01–18) of *B. grandis*: (a) left scapula; (b) left ischium; (c) anterior caudal neural spines; (d) mid-caudal vertebrae; (e) left femur; (f) mid-caudal chevrons; (g) right calcaneum; (h) left metatarsus; (i) left metatarsal I and pedal phalanges from digits I, II, IV; (j) right fibula; (k) right tibia; (l) right metacarpal III; (m) right manus phalanges I-1, I-2, II-3 and III-4; (n) left radius and ulna; (o) left humerus; (p) left coracoid; (q) partial cervical neural arch. All elements are shown in lateral view. Body silhouette modified from Longrich (2008).

Research and Development Center (FRDC), Third Geology and Mineral Resources Exploration Academy, Gansu Provincial Bureau of Geo-Exploration and Mineral Development in Lanzhou, China. Other institutional abbreviations are AMNH, American Museum of Natural History, New York, USA; IGM, Mongolian Institute of Geology, Ulanbaatar, Mongolia; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada.

(c) *Locality and horizon*

White Ghost Castle field area, Yujingzi Basin, Gansu, China. The holotype derives from grey mudstones near the bottom of the Early Cretaceous (Aptian-Albian) Xinminpu Group exposed in the basin with a hadrosaurid (cf. *Equijubus*) dominated fauna. A second partial skeleton was collected from the overlying red beds, where small neoceratopsians (cf. *Auroraceratops*) are the dominant faunal element. Tang *et al.* (2001) and Li *et al.* (in press) provide further information on faunal associations of this taxon. An isolated pair of pubes probably referable to *Beishanlong* was found near the holotype at approximately the same level.

(d) *Differential diagnosis*

Large ornithomimosaur with notched anterior caudal neural spine; keeled midcaudal centra with divided neural spines and prominent ridges connecting pre- and postzygapophyses; scapula with pronounced fossa at rostral end of supraglenoid buttress; shallow coracoid with prominent lateral ridge emanating from coracoid tuber and deep notch between glenoid and postglenoid process; curved pollex ungual, but straighter unguals on digits II

and III; curved ischial shaft; third metatarsal proximally pinched but visible along extensor surface of foot; curved pedal unguals. These traits represent a combination of unique, primitive and derived traits (see Description).

(e) *Description*

Beishanlong is a giant ornithomimosaur (see table 1 in the electronic supplementary material for measurements) known only from postcranial remains. Only neural arch fragments from one cervical and two dorsals are known for the presacral vertebral column. All retain an open neurocentral suture, indicating that this individual had not yet reached maturity. The isolated, broken cervical neural arch (figure 1*q*) is similar to the fourth cervical of *Sinornithomimus* (Kobayashi & Lü 2003) in having convex prezygapophyses, a short neural spine base, and a laterally overhanging diapophysis. Two broken neural spines from the rostral end of the caudal series (figure 1*c*) bear hypertrophied interspinous ligament scars, demarcated from the lateral surface of the neural spines by low ridges. The more rostral of the spines is deeply notched at its apex, a feature that appears to be unique to *Beishanlong*. Three partial ribs were recovered, of which one bears a low ridge extending from the capitulum and down the shaft as in the anteriormost dorsal ribs of other ornithomimosaur (Makovicky *et al.* 2004). Eight complete caudal vertebrae are known (figure 1*d*), two of which bear short or rudimentary transverse processes, indicating that they derive from the transition between proximal and distal caudals. These two vertebrae exhibit ventral keels, which represent an autapomorphy of *Beishanlong*, although the possible juvenile *Harpymimus* specimen

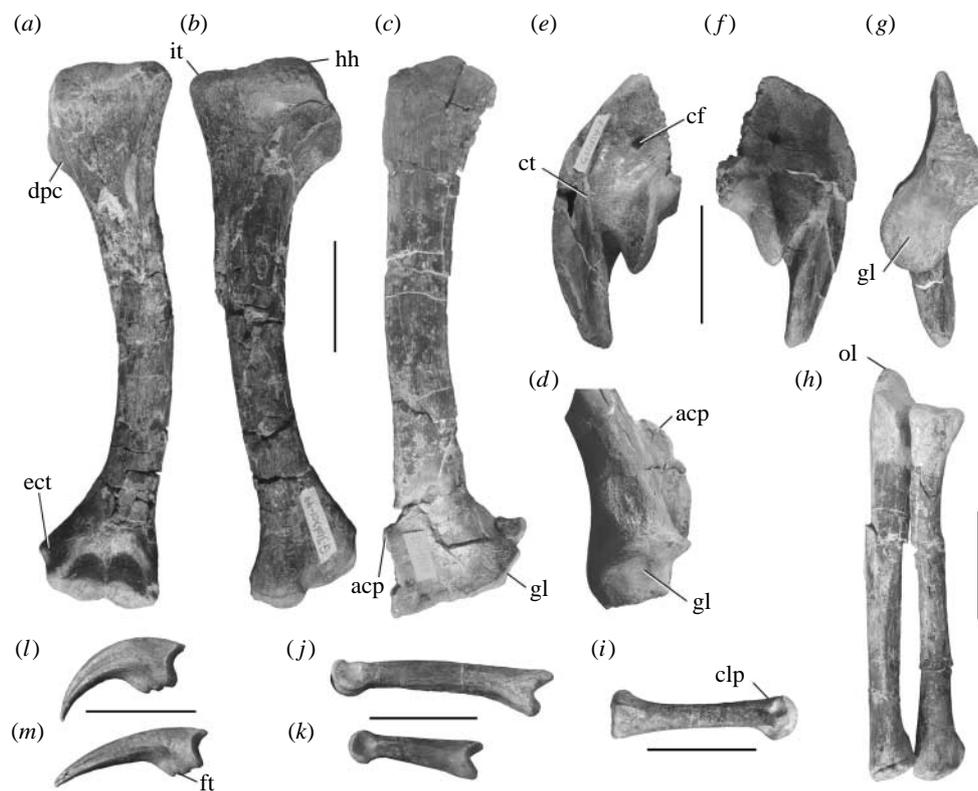


Figure 2. Pectoral girdle and forelimb elements of the holotype specimen (FRDC-GS GJ (06) 01–18) of *B. grandis*. (a,b) Left humerus in rostral and caudal views; (c) left scapula in lateral view; (d) glenoid region of left scapula in caudal view; (e–g) left coracoid in lateral, medial and dorsal views; (h) left radius and ulna in medial view; (i) right metacarpal III in lateral view; (j–m) right phalanges I-1, I-2, III-3 and III-4 in medial views. Abbreviations: acp, acromion process; cf, coracoid foramen; ct, coracoid tuber; clp, collateral ligament pit; dpc, deltopectoral crest; ect, ectepicondyle; ft, flexor tubercle; gl, glenoid; hh, humeral head; it, internal tuberosity (bicipital crest); ol, olecranon process. All scale bars equal 10 cm.

IGM 100/960910KD (Y. Kobayashi 2002, unpublished dissertation) has ventrally constricted vertebrae that approach a keeled condition save for a narrow haemal sulcus along the midline. The more rostral of the two mid-caudals bears a small midline nubbin rostral to the main lamina of the neural spine. Tall ridges connect pre- and postzygapophyses on these two caudals, defining a sulcus on either side of the neural spine. The distal caudals have slightly constricted centra as in a large ornithomimid caudal from the Late Cretaceous of Canada described by Longrich (2008), and have tapering prezygapophyses as in *Harpyimimus*, but unlike the blade-like prezygapophyses of more derived ornithomimids (Kobayashi & Barsbold 2005).

Both scapulae and coracoids were recovered (figure 1a,p). The scapula is typical of ornithomimosaurs with a deep, truncated acromion process, a slender blade with a slight distal expansion, and a supraglenoid buttress that extends rostrally onto the lateral face of the scapula (figure 2c; Nicholls & Russell 1985; Makovicky *et al.* 2004). A small fossa is present beneath the rostral end of the buttress. Manipulation of the proximal end of the humerus within the articulated glenoid indicates that the proximal end would articulate with the buttress. The humerus could be raised to a near-horizontal level, but the rostrally expanded gleno-humeral articulation would limit abduction of the humerus to less than 90° from the caudal position. A shallow fossa on the caudal edge of the scapular blade slightly dorsal to the glenoid (figure 2d) is also seen in *Harpyimimus* and more derived ornithomimids (Kobayashi & Barsbold 2005). The coracoid is shallow in

lateral view, with an elongate postglenoid process that is separated from the wide, lobate glenoid by a deep notch (figure 2e–g). A long, horizontal ridge extends along most of the coracoid centring on the coracoid tuber (figure 2e), as in *Archaeornithomimus* (AMNH 5671), forming a subglenoid shelf along the dorsal aspect of the postglenoid process. The humerus is robust with a curved shaft and a quadrangular proximal end in rostral view (figure 2a,b) as in *Harpyimimus* (Kobayashi & Barsbold 2005). A large ectepicondyle and distal condyles that wrap onto the rostral aspect of the element are traits typical of many basal coelurosaurs. Both the radius and ulna (figure 2h) are nearly straight, and are tightly adhered at the proximal and distal ends (Nicholls & Russell 1985). The olecranon is tall and mound-like as in other ornithomimosaurs.

Right metacarpal III has a flat, trapezoidal proximal articulation with two low ridges extending a short distance down the lateral side, and a non-ginglymoid distal articulation with deep ligament pits as in *Harpyimimus*. Four recovered phalanges (figure 2j–m) compare to phalanges I-1, I-2, III-3 and III-4 of other basal ornithomimosaurs. Both non-terminal phalanges have deeply notched rather than arched proximal articulations. Digit I ends with a curved ungual, while that of digit III is much straighter as in *Struthiomimus* (RTMP 90.26.01) and other derived ornithomimids. Both unguals bear a distally situated flexor tubercle circumscribed by a groove, as described for large isolated elements from the Dinosaur Park Formation (Longrich 2008).

The shaft of the left ischium (figure 3k) is the only pelvic element preserved in the holotype material. It has a

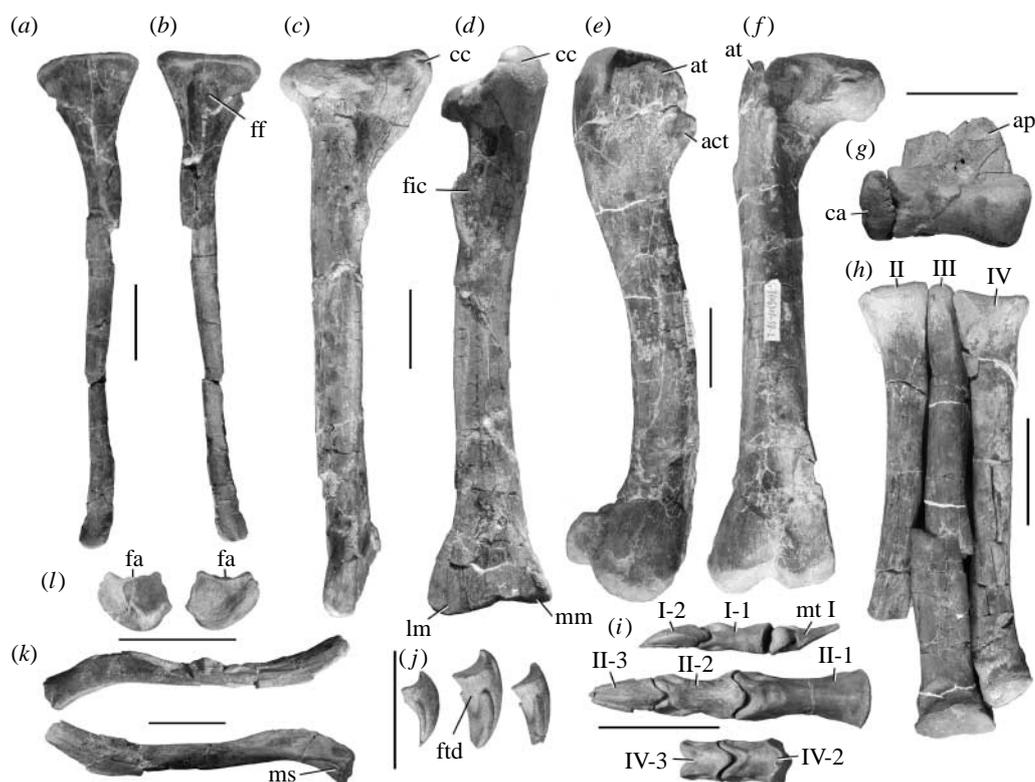


Figure 3. Pelvic girdle and hindlimb elements of the holotype specimen (FRDC-GS GJ (06) 01–18) of *B. grandis*: (a,b) left fibula in lateral and medial views; (c,d) right tibia in medial and rostral views; (e,f) right femur in lateral and rostral views; (g) right proximal tarsals in rostral view; (h) right metatarsals in dorsal (extensor) view; (i) metatarsal I and phalanges of digits I, II and IV of right foot; (j) pedal unguals of digits I, II and IV in oblique ventromedial view; (k) left ischial shaft in medial and lateral views; (l) right calcaneum in medial and lateral views. Abbreviations: act, accessory trochanter; ap, ascending process of astragalus; at, anterior (lesser) trochanter; ca, calcaneum; cc, cnemial crest; fa, articulation for fibula; ff, fossa on medial face of fibula; fic, fibular crest; ftd, flexor tubercle depression; lm, lateral malleolus; mm, medial malleolus; ms, muscle scar; mt, metatarsal. Combinations of Roman and Arabic numerals designate pedal phalanges. All scale bars equal 10 cm.

rosto-ventrally recurved, sigmoid shaft as in ornithomimids, but unlike *Shenzhousaurus* (Ji *et al.* 2003). As in other ornithomimosaur and tyrannosauroids, a large muscular scar is present along the caudal edge of the shaft near the proximal end (Holtz 1994). An isolated pair of pubes recovered in the Yujingzi Basin in 2007 is generally similar to those of other basal ornithomimosaur, but the lack of pubes in the holotype precludes definitive referral. The femur (figure 3e,f) is robust, with a convex rostral profile between the head and greater trochanter in proximal view. The anterior (lesser) trochanter is alariform, as is typical of ornithomimosaur, and bears a large accessory trochanter as in *Garudimimus* (Kobayashi 2005). It is separated from the greater trochanter by a deep cleft. The fourth trochanter is pronounced and a distinct ridge extends proximally along the shaft from the medial condyle as in other ornithomimosaur.

The dorsal surface of the tibial cnemial crest (figure 3c,d) rises slightly above the proximal articulation. Its lateral surface bears a low vertical ridge. The fibular condyle is deeply incised both rostrally and caudally. The robust tibial shaft bears a tall fibular crest that does not reach the proximal end. The distal end is gently expanded, with a slight notch between lateral and medial malleoli. The fibular shaft (figure 3a,b) constricts rapidly below the proximal end and lacks a distinct iliofibularis tubercle. Its medial face is excavated by a deep fossa as in other ornithomimosaur and in tyrannosauroids (Holtz 1994). The astragalus and calcaneum (figure 3g) are unfused to

each other and to the tibia, providing further evidence that the individual is not full grown. The tall, broad ascending process of the astragalus is broken near its base. The calcaneum (figure 3l) forms just under half of the lateral condylar surface. Its dorsal surface is concave for reception of the distal end of the fibula, while its rostral surface forms part of the convex articular condyle. Its caudal edge is straight and it bears a raised medial ridge that fits into a slot in the astragalus as in other ornithomimosaur (Shapiro *et al.* 2003).

The foot is subarctometatarsal with metatarsal III attenuating proximally in rostral view (figure 3h), although it is exposed along the whole extensor surface of the metatarsus as in *Harpyimimus* (Kobayashi & Barsbold 2005) and *Garudimimus* (Kobayashi 2005). It lacks the medial expansion of the diaphysis reported for *Garudimimus* and more derived ornithomimids. In proximal view, metatarsal III makes the smallest contribution to the ankle articulation, forming a rostrally tapered wedge between the other metatarsals. The distal half of its shaft is subtriangular in cross section, again indicating an intermediate step in the evolution of the arctometatarsal foot within Ornithomimosauria. As in *Garudimimus*, but unlike more derived ornithomimids, digit I is present in *Beishanlong* (figure 3i). The digits terminate in short, broad unguals, which are gently curved, unlike the elongated and straight pedal unguals of more derived ornithomimids. All recovered pedal unguals are triangular in cross section and bear shallow ventral depressions

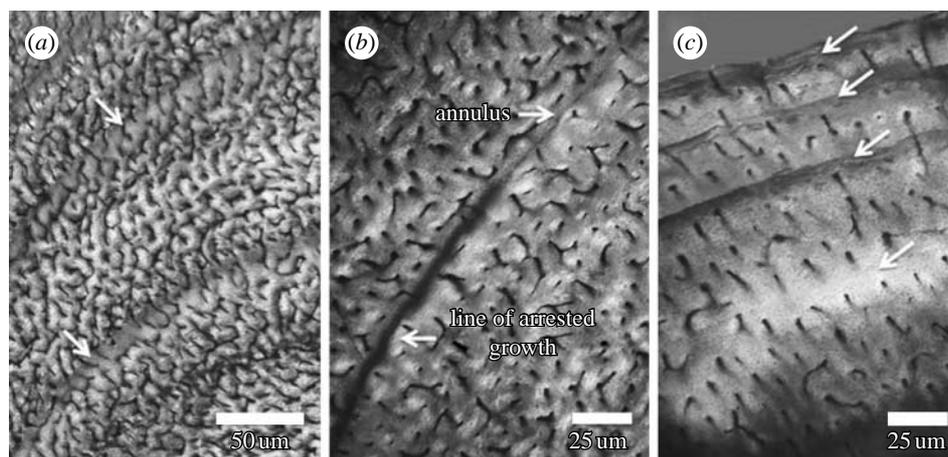


Figure 4. Details of histological section of the distal part of the fibular diaphysis of the holotype (FRDC-GS GJ (06) 01–18) of *B. grandis*: (a) lines of arrested growth (LAGs) near the centre of fibular section; (b) detail of transition between LAG and annulus in one of the growth rings (Erickson 2005); and (c) details of the last four LAGs approaching the outer cortex of the fibula, demonstrating that FRDC-GS GJ (06) 01–18 was still growing, albeit more slowly, at the time of death.

surrounding the highly reduced flexor tubercle (figure 3j) (Shapiro *et al.* 2003; Longrich 2008). The ridges defining the ventral depression terminate short of the proximal articulation as rugose spurs.

Despite its large size, unclosed cervical neurocentral sutures and lack of fusion between the proximal tarsals in the holotype skeleton of *Beishanlong* suggest that it was actively growing at the time of death. In order to assess the age and growth stage of this individual, a transverse histological thin section was generated from a half section of the right fibular diaphysis that was sampled 27 cm from the proximal end. The section was viewed using polarized and reflected light microscopy. The histological matrix was described (figure 4) and a total count of presumed annual growth lines made. Thirteen to fourteen growth lines span from the innermost cortex to the periosteal surface. The innermost and outermost growth rings are true lines of arrested growth (LAG; figure 4a,c). Those at mid-cortex are primarily annuli. However, a few also show LAG structuring for a small portion of their length before turning into annuli (figure 4b). Spacing between concentric LAGs diminishes moderately towards the periphery and the vascularization shifts from a reticular pattern to a longitudinal one. Collectively, this points to the holotype (FRDC-GS GJ (06) 01–18) of *Beishanlong* as being a young adult that died during the transition to the stationary stage of development (Erickson 2005), thus approaching somatic maturity.

3. DISCUSSION

Phylogenetic analysis (see the electronic supplementary material) posits *Beishanlong* as a basal ornithomimosaur, more derived than *Pelecanimimus* and *Shenzhousaurus* (figure 5), but basal to the edentulous clade composed of *Garudimimus* and the Ornithomimidae. Incomplete overlap between preserved body parts across specimens prevents full resolution of relationships between *Beishanlong*, *Harpymimus* and more derived ornithomimosaur, but both of the Early Cretaceous taxa exhibit characters more derived than *Shenzhousaurus*. The ischium of *Beishanlong* is rostro-ventrally recurved as in ornithomimids, and *Harpymimus* possesses a ventrally curving

dentary with a distinct ‘chin’ as observed in *Garudimimus* and ornithomimids, as well as an ilium with an expanded postacetabular blade terminating in a vertical border. By contrast, *Shenzhousaurus* has a rounded postacetabular blade, and both it and *Pelecanimimus* possess a shallow, tapering dentary with a straight lower edge.

Beishanlong and *Harpymimus* are very similar throughout the preserved skeletal parts common to both, although many of these traits are plesiomorphic. Both retain ginglymous distal articulations on metacarpal I (inferred from phalanx I-1 in *Beishanlong*), a deep ligament pit on metacarpal III and a strongly curved pollex claw, but straighter claws on other digits. Both taxa possess a subarctometatarsal foot with the diaphysis of metatarsal III pinched dorsally and exhibits a wedge-like exposure on the ankle, although this condition persists in *Garudimimus* (Kobayashi 2005) and the feet of *Pelecanimimus* and *Shenzhousaurus* are unknown. Of considerable interest in this regard is the keeled condition of two of the caudal vertebrae of *Beishanlong* and the near-keeled condition of caudal vertebrae in a juvenile ornithomimosaur specimen possibly referable to *Harpymimus* (Y. Kobayashi 2002, unpublished data). In the latter specimen (IGM 100/960910KD), the preserved caudals bear relatively taller neural spines and transverse processes compared with the mid-caudals of *Beishanlong*, so it is possible that the lack of haemal groove may be related to their position in the caudal series rather than representing a taxonomic difference. Although mid-caudal vertebrae of *Garudimimus* are unknown, those of other ornithomimosaur do not exhibit a ventral midline keel or keel-like anatomy, so this trait could represent a possible synapomorphy uniting *Beishanlong* and *Harpymimus* as sister taxa. Both species are considered to be of Aptian-Albian age (Hicks *et al.* 1999; Tang *et al.* 2001).

Nevertheless, *Beishanlong* differs from *Harpymimus* in several traits, such as the notched anterior caudal neural spine (figure 1c), more prominent humeral ectepicondyle (figure 2a) and more prominent disparity in ungual curvature between the pollex and other digits. Probably the most significant distinguishing trait, however, appears to be the difference in body size between the two taxa, with *Beishanlong* having an estimated body mass almost three

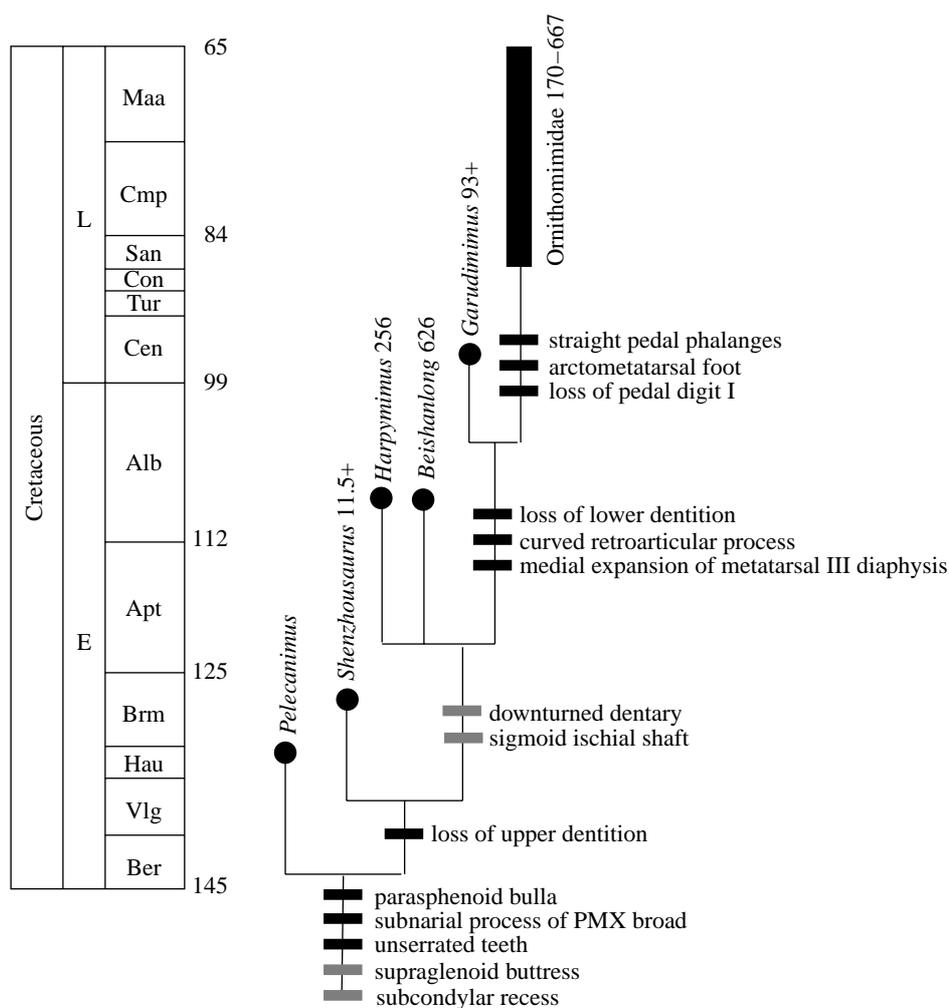


Figure 5. Phylogeny of Ornithomimosauria excerpted from the strict consensus of the results of a larger analysis of 293 characters in 72 theropod taxa conducted with the program TNT (Goloboff *et al.* 2008; see the electronic supplementary material 2–5). Optimizations of select characters are indicated with black bars representing unambiguous synapomorphies, whereas those indicated in grey are ambiguous due to either missing data or unresolved relationships at adjacent nodes. Estimated body masses in kilograms (see text) are indicated next to terminals. Estimates suffixed with a ‘+’ are for taxa known from clearly subadult individuals and estimated masses are probably well below those for somatically mature individuals.

times greater than that of *Harpymimus*. This disparity may be greater, however; Kobayashi & Barsbold (2005) noted that the neurocentral fusion pattern indicates that the holotype specimen of *Harpymimus* appears to be somatically mature, whereas the holotype of *Beishanlong* is from an actively growing subadult.

Mass predictions for the holotype of *Beishanlong* yield an estimate of 626 kg using the equation relating body mass to femoral length devised by Christiansen & Fariña (2004). This exceeds estimated body masses for almost all other published ornithomimosaur specimens (figure 5) and is comparable to the largest known specimens of *Gallimimus*. Given its proportionately more robust forelimb elements, *Beishanlong* appears stockier than Late Cretaceous ornithomimids and may in fact have been somewhat heavier for a given femoral size. Mass estimates for ornithomimosaur taken from Christiansen & Fariña (2004), or calculated from femoral lengths (*Gallimimus*, *Garudimimus*, *Beishanlong*) or distal tibial width (*Harpymimus*) using equations presented in the same publication and superimposed on ornithomimosaur phylogeny (figure 5), suggest that this lineage did not follow a directional trend of body-size evolution such as has recently been shown for some paravian lineages

(Turner *et al.* 2007). Body mass for *Gallimimus* was calculated from a published femoral length of 673 mm (Christiansen & Fariña 2004) instead of using their model-derived mass estimate of 490 kg, which falls outside the 95 per cent confidence interval for their equation. *Beishanlong* is the second largest theropod in Xinminpu fauna (after the therizinosaur *Suzhousaurus*; Li *et al.* 2008), whereas the largest known predatory taxon, *Xiongguanlong* (Li *et al.* in press), is distinctly smaller. The discovery of exceptionally large-bodied, beaked coelurosaurs such as *Beishanlong*, *Suzhousaurus* (Li *et al.* 2007, 2008) and *Gigantraptor* (Xu *et al.* 2007) in late Early to early Late Cretaceous strata of northern China represents an intriguing evolutionary and ecological pattern. E. L. Zanno (2008, unpublished data) has suggested that the evolution of non-predatory trophic habits, as evinced by tooth and jaw anatomy, led to an increase in coelurosaurian diversity and also dramatic body-size increase in non-avian clades exhibiting characters associated with herbivory (Clark *et al.* 1994; Ji *et al.* 1998; Kobayashi *et al.* 1999). It is remarkable that such body-size shifts in three different coelurosaurian lineages are so tightly clustered geographically and stratigraphically.

The holotype of *Beishanlong* co-occurs with therizinosauroids, hadrosauroids, turtles and tyrannosauroids in the lower mesic facies of Xinminpu Group (grey facies of Tang *et al.* 2001), and a strong and remarkably invariant degree of faunal association between these particular clades persists in mesic environments throughout the Cretaceous of Central Asia, such as those represented by the Iren Dabasu Formation (Currie & Eberth 1993), the Khuren Dukh Formation (Hicks *et al.* 1999), the Bayn Shiree Formation (Jerzykiewicz & Russell 1991; Khand *et al.* 2000) and the Nemegt Formation (Jerzykiewicz & Russell 1991). Nevertheless, as noted by Makovicky & Norell (1998) and Ksepka & Norell (2004), ornithomimosaur fossils are infrequently found in strata representing more xeric environments, such as the widespread red-bed formations of the Gobi Basin that are dominated by neoceratopsian and maniraptoran dinosaurs. With regard to this observation, it is worth noting that one of our three specimens of *Beishanlong* was recovered from red-bed facies that overlie grey mesic beds within the Yujingzi Basin, which yield a fauna of basal neoceratopsians and maniraptoran dinosaurs.

We thank the members of the Fossil Research and Development Center, Gansu Bureau of Geology and Mineral Resources Exploration, Mick Ellison and Gabe Bever (AMNH), Brandon Kilbourne (FMNH), Dan Ksepka (NCSU), Pei Rui (PKU) and Zhou Cheng-Fu (Shenyang Normal Univ.) for their assistance in the field. Marlene Donnelly (FMNH) created figures 1–3. Fieldwork was supported by The Grainger Foundation (to P.J.M.), and funds from the AMNH (MAN) and Peking University (to K.-Q.G.). We acknowledge research support from the National Science Foundation NSF EAR 0228607 to P.J.M. and M.A.N., NSF EAR 0207744 to G.M.E. and M.A.N., NSF EAR 0418648 to P.J.M. and G.M.E., and NSFC 40532008 to K.-Q.G. Reviews by Dr Y. Kobayashi and an anonymous reviewer helped improve the manuscript.

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