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The Illusory Evidence for Asian Brachiosauridae: New Material of *Erketu ellisoni* and a Phylogenetic Reappraisal of Basal Titanosauriformes

DANIEL T. KSEPKA¹ AND MARK A. NORELL²

ABSTRACT

Phylogenetic relationships among the diverse Cretaceous sauropods of East Asia have long been controversial. Debate has centered on whether there is any evidence for an endemic clade of Asian species (“Euhelopodidae”) and on the placement of these taxa within the context of higher sauropod phylogeny. While most Cretaceous sauropod taxa from Asia are recognized as part of Somphospondyli, recent discoveries have suggested Brachiosauridae may have dispersed into Asia as well. We present new fossils and analyses bearing on these issues. Additional material of the holotype individual of *Erketu ellisoni* recovered on a subsequent visit to the type locality expands the character data available for this unique sauropod. Associated sauropod dorsal and caudal vertebrae were collected from the same horizon, at a location approximately 2 km from the holotype excavation. The dorsal vertebra exhibits synapomorphies suggesting a representative of Titanosauria co-occurred with *Erketu ellisoni*. These new specimens, as well as recent discoveries of contemporary Asian sauropod taxa, allow a basis for phylogenetic reappraisal of *Erketu* and related taxa. Phylogenetic results support a sister group relationship between the Asian Cretaceous sauropods *Erketu* and *Qiaowanlong*. Although *Qiaowanlong* was described as a brachiosaurid, it joins *Erketu* on the somphospondylian side of the Brachiosauridae-Somphospondyli divergence, erasing the evidence for the dispersal of Brachiosauridae into Asia.

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INTRODUCTION

Knowledge of Cretaceous Asian sauropod diversity has exploded in recent years, with over 10 new species named in the past decade. These discoveries, along with the description of new material for previously described and/or unnamed taxa, are vastly improving our understanding of the distribution and morphology of sauropods (Pang and Cheng, 2000; Dong et al., 2001; Tang et al., 2001; Averianov et al., 2002; You et al., 2003, 2004; Ksepka and Norell, 2006; Mo et al., 2006, 2008; Tomida and Tsumura, 2006; Xu et al., 2006; Wang et al., 2007; Lü et al., 2008; Wilson and Upchurch, 2009; You and Li, 2009). These finds have also sparked several novel hypotheses and renewed debates over patterns of biogeographic distribution within Sauropoda through the Cretaceous, including deliberation over the cosmopolitan or endemic nature of various clades (Russell, 1993; Upchurch, 1995, 1998; Wilson, 2002; Barrett et al., 2002). Although much progress has been made through both descriptions of new taxa and restudy of older material, discoveries have outpaced the assimilation of these new taxa into the framework of sauropod evolution and biogeography. Here we report new sauropod fossils from the early Late Cretaceous of Bor Guvé, Mongolia, and revisit the phylogenetic position of several recently described taxa.

The name Bor Guvé is applied to a laterally extensive set of deposits in Dornogov Aimag dominated by interbedded siltstones and channel sandstones that are referable to the Baynshiree Formation (Khaand, personal commun.). The holotype specimen of *Erketu ellisoni* was collected from these deposits during the 2002 American Museum of Natural History–Mongolian Academy of Sciences field expedition (Ksepka and Norell, 2006). Subsequently, the AMNH–MAS expedition revisited the type locality and nearby sites and retrieved additional remains that have recently been prepared. Three middle-posterior cervical vertebrae belonging to the holotype individual (IGM 100/1803) of *Erketu ellisoni* were retrieved, as well as dorsal and caudal vertebrae of a titanosaur from approximately 2 km to the west within the same stratigraphic interval.

Deposits at Bor Guvé were originally interpreted as late Early Cretaceous in age because beds at this locality overlie the Khar Khutul beds (= Khara Khutul or Khar Hötöl). We previously considered the Khar Khutul beds to be Early Cretaceous in age (Ksepka and Norell, 2006) based on a ~128 Ma age reported for the lower part of the Tsagaantsav Svita by Shuvalov (2000). However, the application of the chronostratigraphic Svita concept to Cretaceous terrestrial deposits in Mongolia now appears to represent an oversimplification of the complexity characterizing these deposits (Eberth et al., 2009). Recent work in the area has suggested that the fossiliferous red beds at Shine Us Khudug in the local area belong to the Upper Cretaceous Javkhalant Formation (Eberth et al., 2009). Eberth et al. (2009) showed that these beds overlie the Baynshiree laterally to the east, south, and west. It appears that the Bor Guvé locality represents an extension of the known Baynshiree beds west of Shine Us Khudug. Furthermore, the beds are extraordinarily similar in lithology to classic Baynshiree strata in the adjacent area, and recent investigation during the summer of 2009 has demonstrated the presence of two types of freshwater mollusks typical of Baynshiree strata (Khaand, personal commun.).

Provisionally we consider the sediments at the Bor Guvé locality to belong to the Baynshiree Formation. Although there has been much disagreement concerning the age and the composition of the Baynshiree Formation, Hicks et al. (1999) posit a Late Cretaceous (Cenomanian to Santonian) age for these and correlative strata on the basis of paleomagnetic and palynological evidence. Thus, fossils from Bor Guvé must now be considered early Late Cretaceous rather than late Early Cretaceous in age. Unfortunately, only this rough stratigraphic framework exists for the Bor Guvé locality and surrounding deposits. As for many central Asian continental localities, no radiometric dates have been reported that would provide a numerical age. Paleomagnetic data are likewise of limited utility because these localities fall within the ~40 Ma Cretaceous long normal polarity interval (C34). Finer temporal resolution must therefore await more comprehensive geological and biostratigraphic work.

SYSTEMATIC PALEONTOLOGY

Sauropoda Marsh, 1878

Neosauropoda Bonaparte, 1986

Macronaria Wilson and Sereno, 1998

Titanosauriformes Salgado et al., 1997

Somphospondyli Wilson and Sereno, 1998

Erketu ellisoni Ksepka and Norell, 2006

HOLOTYPE: Geological Institute of the Mongolian Academy of Sciences (IGM) 100/1803, first six articulated cervical vertebrae, right sternal plate, and articulated right tibia, fibula, astragalus, and calcaneum.

REFERRED MATERIAL: IGM 100/1803, three articulated cervical vertebrae (fig. 1). These elements pertain to the holotype individual and are therefore assigned the same specimen number and considered part of the holotype. Measurements are in table 1.

LOCALITY AND AGE: Bor Guvé, Dornogov Aimag, Mongolia. Provisionally referred to the Baynshiree Formation (early Late Cretaceous).

DESCRIPTION

The three cervical vertebrae described below were collected from the articulated neck of the holotype individual of *Erketu ellisoni* and can be identified as vertebrae 7, 8, and 9 with certainty. These specimens were left in place after the 2002 season and were recovered during the 2003 field season. Cervical vertebra 7 comprises a complete centrum with intact right postzygapophysis, lacking most of the neural arch. Cervical vertebra 8 and 9 are more complete, lacking only the right pre- and postzygapophyses, most of the diapophyses and parapophyses (left side intact in vertebra 8), and the cotyle (partially complete in vertebra 8). In describing the vertebral laminae below, we provide the complete name of each lamina the first time it is mentioned and use the abbreviations of Wilson (1999) in subsequent references.

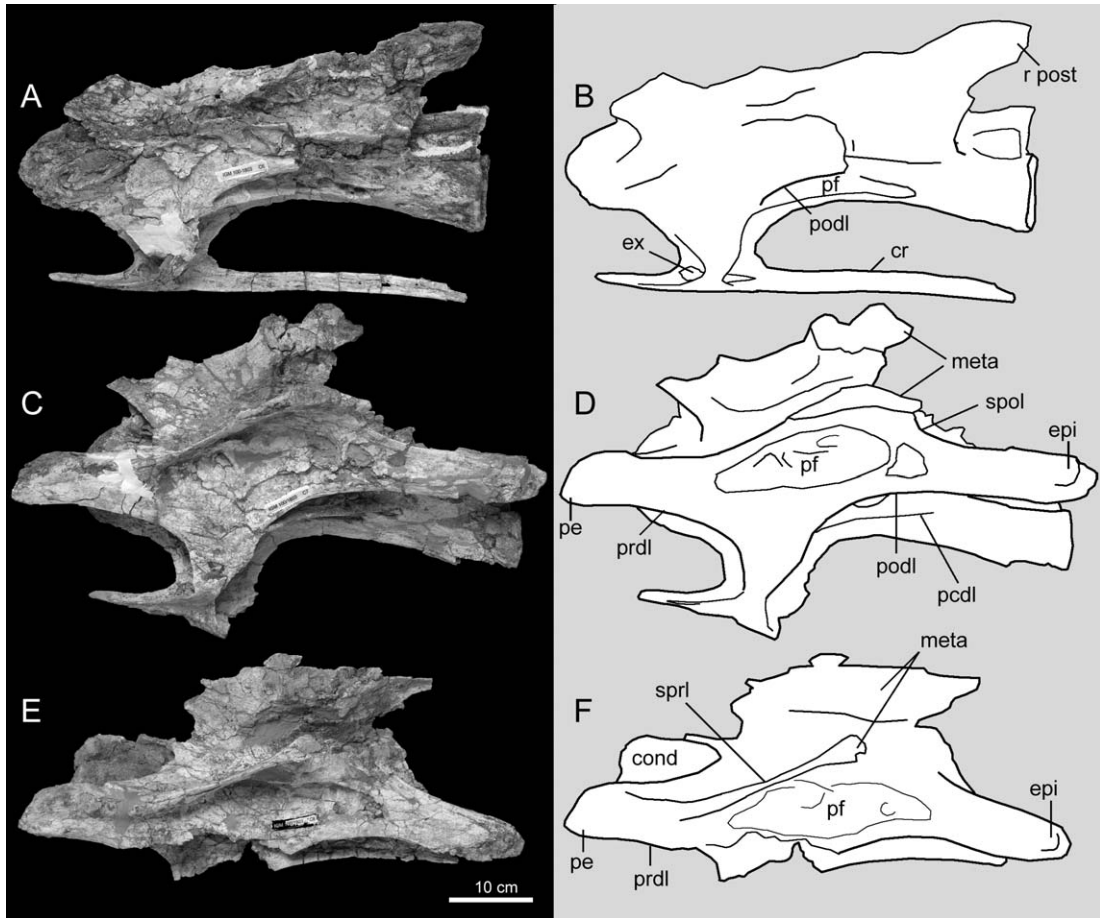


FIGURE 1. Photographs and line drawings of new cervical vertebrae of *Erketu ellisoni* (IGM 100/1803) in lateral view: cervical vertebra 7 (A, B), cervical vertebra 8 (C, D), cervical vertebra 9 (E, F). Note that deformation causes more of the dorsal surface of each element to be partially visible. Abbreviations: **cond**: condyle; **cr**: cervical rib; **epi**: epiphysis; **ex**: excavation on cervical rib; **meta**: metapophyses; **pe**: pre-epiphysis; **pf**: pneumatic fossa; **pcdl**: posterior centrodiapophyseal lamina; **podl**: postzygodiapophyseal lamina; **prdl**: prezygodiapophyseal lamina; **r post**: right postzygapophysis; **spol**: spinopostzygapophyseal lamina; **sprl**: spinopostzygapophyseal lamina.

Abrasion of the condyle has removed most of the surface layer of bone in all three vertebrae, exposing a camellate internal structure with multiple small chambers separated by thin laminae of bone. This matches the internal structure of cervical vertebra 4 as previously revealed by CT imagery (Ksepka and Norell, 2006: fig. 7). The cotyle is deeply concave and is wider than high in the only complete example from the new material, vertebra 7. However, the asymmetry of the cotyle and compression of the neural arch and centrum indicate that the shape of the cotyle has been modified by postmortem deformation. In the undeformed cervical vertebrae 3 and 4, the cotyle is higher than wide. The centra of all newly collected vertebrae are excavated by large lateral pneumatic fossae, leaving only a thin midline septum of bone near the midpoint

of each centrum. This fossa is subdivided by a posteroventrally directed lamina that shows only very weak development in vertebrae 3–5 but is strongly projected in vertebrae 6–9.

A short, stout centroprezygapophyseal lamina (CPRL) supports the prezygapophysis ventrally. The prezygodiapophyseal lamina (PRDL) is strongly developed and projects well anterior to the articular facet

of the prezygapophysis. This extension forms a flange termed the pre-epipophysis by Wilson and Upchurch (2009). In *Erketu*, the CPRL fades to a weak ridge as it runs onto the ventromedial surface of the pre-epipophysis, thus the pre-epipophysis in *Erketu* is formed primarily by an extension of the PRDL. Pre-epipophyses are also developed in *Euhelopus*, but it is primarily the CPRL that forms these structures in that taxon (Wilson and Upchurch, 2009). A strong postzygodiapophyseal lamina (PODL) connects the postzygapophysis and diapophysis. Well-developed epipophyses (torus dorsalis of Wedel and Sanders, 2002; Ksepka and Norell, 2006) lie above the postzygapophyses, but an epipophyseal-prezygapophyseal lamina (EPRL) is absent. Presence of the EPRL throughout the cervical series is considered an autapomorphy of *Euhelopus* and is also present in a few non-titanosauriforms (Wilson and Upchurch, 2009).

All neural spines are deeply bifurcated. In vertebra 8, the lateral face of each metapophysis bears several fossae divided from one another by short, smooth-edged laminae. These fossae are very shallow, serving to reduce the already thin metapophysis to a paper-thin sheet of bone within their bounds. In vertebra 7, the metapophyses are broken near their bases, but they are largely intact in vertebrae 8 and 9. The dorsal apices of the metapophyses are swollen, forming rugose expansions in vertebra 8. Breakage in vertebra 9 reveals that these expansions are nearly hollow and subdivided into large internal chambers (exceeding the size of the exposed camellae of the centrum). Although expansion of the metapophyses is relatively modest in this vertebra, a trend of progressive expansion posterior in the cervical column is evident. The dorsal surface of the neural arch is smooth between the metapophyses, with no evidence of the median tubercle that is present in *Euhelopus* and some other sauropods including *Camarasaurus* and *Diplodocoidea* (Wilson, 2002; Tsuihiji, 2004; Wilson and Upchurch, 2009). As noted in the original description, however, the point at which this tubercle arises varies in sauropods and its presence in the unpreserved posteriormost cervicals cannot be ruled out.

Extreme elongation of the cervical vertebrae is one of the notable autapomorphies of *Erketu ellisoni*. The cervical vertebrae reach their greatest length at either the sixth or seventh element (the sixth is incomplete) and begin gradually decreasing in length moving posteriorly along the cervical column. It is uncertain how many total cervical vertebrae were present, but in most sauropods the cervical vertebrae continue to progressively lengthen up to a more posterior point in the vertebral column. Among exemplars with nearly complete necks, the longest cervical element is vertebra 8 in *Phuwiangosaurus sirindhornae* (Suteethorn et al., 2009), vertebra

TABLE 1. Measurements of new vertebrae of *Erketu ellisoni* (IGM 100/1803) described in this paper. All values in millimeters. Cotyle dimensions are not presented as deformation makes these values misleading.

	Centrum length (condyle to rim of cotyle)	Length from prezygapophysis to postzygapophysis
Cervical 7	542	
Cervical 8	523	595
Cervical 9		569

10 in *Malawisaurus* (Gomani, 2005), vertebra 10 or 12 in *Rapetosaurus* (Curry Rogers, 2009), vertebrae 10 and 11 in *Giraffatitan* (Janensch, 1950), and vertebra 11 in *Euhelopus* (Wilson and Upchurch, 2009).

Cervical ribs are completely fused to the vertebrae and extend at least to the posterior end of the centrum, though no complete element is intact. Cervical ribs associated with vertebra 4 extend beyond the succeeding vertebrae (Ksepka and Norell, 2006). The dorsal surface of each rib is excavated anterior and posterior to the site of fusion with the parapophysis, and these two excavations are separated by a short lamina.

BOR GUVÉ TITANOSAUR

Titanosauriformes Salgado et al., 1997
Titanosauria Bonaparte and Coria, 1993

Titanosauria indet.

MATERIAL: IGM 100/3005, posterior dorsal vertebra (fig. 2) and 15 caudal vertebrae (fig. 3). Measurements are in table 2.

LOCALITY AND AGE: Bor Guvé, Dornogov Aimag, Mongolia. Provisionally referred to the Baynshiree Formation (early Late Cretaceous). This specimen was collected approximately 2 km due west of the *Erketu ellisoni* holotype site. GPS coordinates are available to qualified researchers from M. Norell.

DESCRIPTION

A single, nearly complete dorsal vertebra was collected in association with the caudal vertebrae series. Additional vertebrae still lie at the locality and were not collected. Because of the distance separating the new dorsal and caudal vertebrae from the *Erketu ellisoni* holotype locality and lack of overlap between the two sets of specimens, there is no a priori justification for referring either set of specimens to *Erketu ellisoni* or for firmly excluding them from that species. However, because the dorsal vertebra can be referred to Titanosauria based on the absence of a hyposphene-hypantrum system (Powell, 1986; Wilson, 2002; see below) and *Erketu ellisoni* is currently recovered as occupying a phylogenetic position just outside Titanosauria (Ksepka and Norell, 2006; see below), this specimen is most parsimoniously interpreted as belonging to a separate taxon.

The dorsal vertebra is identified as a posterior element based on the combination of the dorsal position of the parapophyses on the neural arch, the small size of the parapophyses, and the nearly vertical orientation of the neural spine. The centrum is slightly wider than high, strongly opisthocoelous, and bears a large, deep teardrop-shaped pneumatic fossa which branches internally within the centrum. Ventrally, the centrum is smoothly rounded with no trace of a keel or of concavities like those present in *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977).

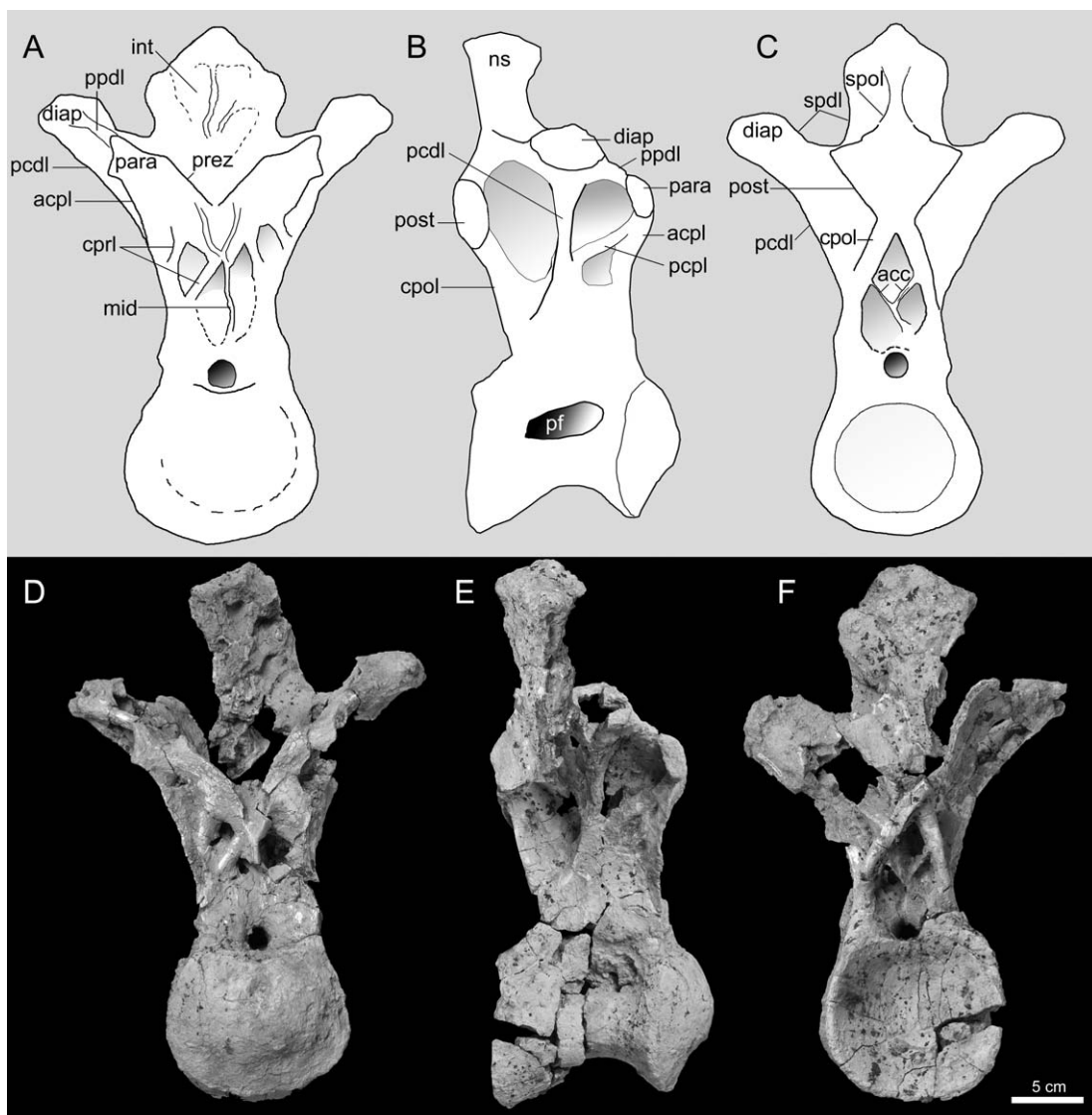


FIGURE 2. Photographs and line drawing reconstructions of the dorsal vertebra of the Bor Guvé titanosaur (IGM 100/3005) in anterior (A, D), lateral (B, E), and posterior (C, F) views. The neural spine was photographed separately and digitally reattached in E and F so as to avoid damage to the fragile specimen. Abbreviations: **acc**: accessory lamina (see text); **acpl**: anterior centroparapophyseal lamina; **cpol**: centropostzygapophyseal lamina; **cprl**: centroprezygapophyseal lamina; **diap**: diapophysis, **int**: internal structure of broken neural spine; **spol**: spinopostzygapophyseal lamina; **ns**: neural spine; **para**: parapophysis; **pcdl**: posterior centrodiapophyseal lamina; **pcpl**: posterior centroparapophyseal lamina; **post**: postzygapophysis; **ppdl**: parapodiapophyseal lamina; **prez**: prezygapophysis; **spdl**: spinodiapophyseal lamina.

The parapophyseal facet is small and ovoid, with its long axis oriented dorsoventrally. The articular facet faces directly laterally. A thin, sharp anterior centroparapophyseal lamina (ACPL) projects from the ventral base of the facet to the anterodorsal corner of the condyle margin. The posterior centroparapophyseal (PCPL) is much more stout and short. It merges with the posterior centrodiapophyseal lamina (PCDL) before reaching the centrum. A well-developed transverse process supports the diapophysis and is oriented dorsolaterally so as to place the diapophysis dorsal to the level of the prezygapophysis. The diapophysis is positioned dorsal and posterior to the parapophysis, and is significantly larger. The long axis of the articular facet of the diapophysis is oriented anteroposteriorly.

A short, stout, dorsomedially oriented centroprezygapophyseal lamina (CPRL) supports the prezygapophysis. This lamina is dorsally bifurcated forming a hollow under the ventral margin of the prezygapophysis. The CPRL merges with the ACPL ventrally. A pair of additional laminae in the prezygapophyseal region is visible in anterior view. These short, sharp accessory laminae extend ventromedially from the medial margins of the articular facets, merging on the midline to continue to form a midline septum extending vertically downward to the roof formed by the neural arch above the neural canal. The prezygapophyseal articular facets are large and flat. These facets are positioned just ventral to the level of the parapophysis. The portion of the neural arch directly between the prezygapophyses is broken, making it impossible to confirm the presence or absence of a hypantrum. Nonetheless, given the lack of a hyposphene, the hypantrum was likely absent as well.

The postzygapophyseal articular facets are also large and flat. No hyposphene is present ventral to the facets. Two very stout, pillarlike centropostzygapophyseal laminae (CPOL) buttress the articular facets and diverge as they extend toward the centrum where they meet their counterpart PCDLs. This morphology is very similar to that seen in *Argentinosaurus huinculensis* (Bonaparte, 1999; Apesteguía, 2005). Two thin, asymmetrical accessory laminae occur within the space bounded by the CPOLs and the centrum. The larger of these two laminae runs from the left CPOL to the dorsal margin of the centrum, while the smaller runs from the right CPOL to the larger accessory lamina.

Several fossae occur on the lateral face of the neural arch. A deep fossa is bounded by the PCDL and CPOL. A second deep fossa is bounded by the PPDL, PCDL, and PPDL. Ventral to this, a shallow fossa is bounded by the ACPL, PCDL, and PCPL.

The neural spine is single, mediolaterally wide and modestly expanded dorsally. It is oriented nearly vertically. In general, titanosaur neural spines are posteriorly oriented in the anteriormost dorsal vertebrae and become more vertically oriented toward the posterior part of the dorsal series (e.g., Gomani, 2005; Curry Rogers, 2009). A well-developed spinopostzygapophyseal lamina (SPOL) is present, but because a tightly adhering layer of matrix cannot be removed without compromising the integrity of the fragile bone beneath, further details of the neural spine lamination are not observable. The broken anterior wall reveals that the neural spine is divided into two along the midline by a thick septum, and that the internal volume is made up of multiple hollow chambers subdivided by irregular thinner laminae.

Fifteen caudal vertebrae were collected in association with the dorsal vertebra described above and appear to represent the incomplete tail of a single individual. One additional caudal

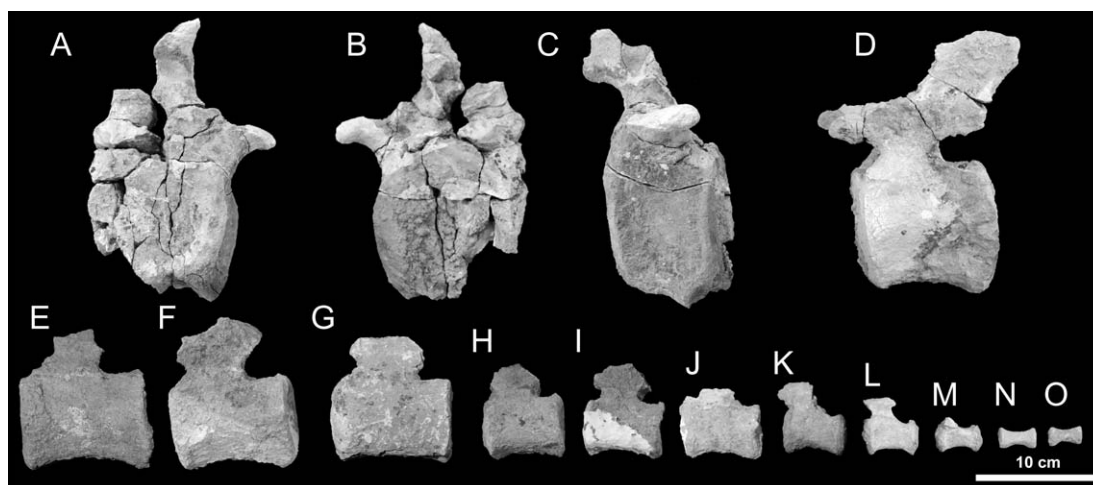


FIGURE 3. Caudal vertebrae of the Bor Guvé titanosaur (IGM 100/3005). Middle caudal in (A) anterior, (B) posterior, and (C) left lateral view. Posterior caudal vertebrae (D–L) in left lateral view and distal caudal vertebrae (M–O) in left lateral view.

vertebral centrum was surface-collected nearby. This element belongs to an immature animal based on the open sutural surface for the missing neural arch. The remaining vertebrae appear to be fully fused, and indeed in some the neural arch is broken off at the base rather than separating cleanly from the centrum at a suture. A layer of tough matrix adheres tightly to the bone surface, however, so whether the sutures were completely obliterated cannot be discerned. Based on the ontogenetic stages implied by the juvenile vertebra, it seems plausible two individuals may be represented, though no discrete morphological differences are present in the centrum to suggest the presence of multiple species. Because the locality is on a flat open plane, elements from different stratigraphic levels often are concentrated on the surface. Given the context, we treat the dorsal vertebra and 15 caudal vertebrae excavated in place as a single specimen but exclude the caudal vertebra collected as float.

A large caudal bearing short, knoblike transverse processes is identified as a middle caudal vertebra (fig. 3A–C). The centrum is taller than long, with a flat anterior face and a subtly concave posterior face. No pneumatic fossae are present, and broken regions reveal an internal bone texture without evidence of pneumatization. Ventrally, the centrum bears hemapophyseal ridges. The neural arch is positioned near the anterior margin of the centrum, a feature considered synapomorphic for Titanosauriformes (Upchurch et al., 2004). The left prezygapophysis is intact and is very weakly projected, barely surpassing the anterior margin of the centrum. The neural spine is lost.

Several posterior caudals are identified based on the lack of transverse processes and presence of a well-developed neural spine. In the most complete element (fig. 3D), the centrum has a flat anterior face and a subtly concave posterior face, is slightly constricted at midlength, and lacks pneumatic features. Facets for the chevrons are present at both the anterior and posterior margins of the centrum, and those at the posterior margin are much larger. The neural arch is

TABLE 2. Measurements of titanosaurian dorsal and caudal vertebrae from Bur Guvé (IGM 100/3005). All values in millimeters.

	Centrum length (condyle to rim of cotyle)	Centrum height (posterior face)	Centrum width (posterior face)	Height including neural spine
Posterior dorsal	207	175	179	
Middle caudal	95.6	~140	~130	
Posterior caudal	99.5	92.4	92.4	191.3
Posterior caudal	98.5	91.9	84.6	
Posterior caudal	97.4	70.7	74.1	
Posterior caudal	94.0	68.5	73.7	
Posterior caudal	92.9	61.8	65.4	
Posterior caudal	82.8	54.7	59.6	
Posterior caudal	67.7	46.4	45.3	
Posterior caudal	66.6	42.7	41.7	
Posterior caudal	66.3	46.5	45.0	
Posterior caudal	51.2	33.9	34.0	
Posterior caudal	44.1	29.7	26.7	
Posterior caudal	41.2	21.8	22.0	
Distal caudal	31.7	17.1	17.1	
Distal caudal	29.5	15.1	15.0	

positioned anteriorly on the centrum and the neural spine is posterodorsally inclined. The prezygapophyses are oriented parallel to the long axis of the vertebra and extend further beyond the anterior margin of the centrum than in the middle caudal. The postzygapophyses are greatly reduced, with just a slight extension of the articular facets from the posterior margin of the neural spine. Eight additional posterior caudals (fig. 3E–L) spanning a size range from 66–99 mm were collected, but all are missing most of the neural arch. These elements are similar to the complete posterior caudal in having a platycoelous centrum with the neural arch positioned anteriorly.

The three smallest posterior caudal vertebrae (fig. 3K–L) show some transitional morphologies. All three centra show stronger wasting at midpoint than the preceding caudals. Each centrum preserves the base of an anteriorly positioned neural arch, but the neural spine appears to be weakly developed. The centrum of the first of these vertebrae has a gently convex rather than concave posterior articular face. The second and third have a more strongly convex posterior articular face.

Two diminutive distal caudals are represented (fig. 3N–O). These are reduced to spool-shaped centra with circular anterior and posterior faces and strong wasting toward the midpoint. The articular faces are flat, and bear foveae near their midpoints similar to those described in *Suuwassea* (Harris, 2006a).

PHYLOGENETIC ANALYSIS

CHARACTER AND TAXON SAMPLING: Our previous phylogenetic analysis did not completely resolve the position of *Erketu*, but found six equally most parsimonious trees in which *Erketu* was placed either as sister taxon to *Euhelopus* or the sister taxon to all included representatives

of Titanosauria (Ksepka and Norell, 2006). Since this time, a meticulous redescription of *Euhelopus* (Wilson and Upchurch, 2009), discovery of new sauropod taxa (see Introduction), and the collection of the additional material of *Erketu* described here have made available new character data with the potential to resolve this uncertainty.

In order to reevaluate the phylogenetic position of *Erketu* and also to explore the interrelationships of new, potentially closely related sauropod taxa, we utilized the phylogenetic matrix of Wilson (2002). We modified the original matrix to reflect the revised scorings for *Euhelopus* recommended by Wilson and Upchurch (2009) and also added nine characters from the literature relevant to Titanosauriformes (appendix 1). Fifteen taxa were newly added to the matrix (appendix 2) and “*Brachiosaurus*” was divided into two terminals, *Brachiosaurus* and *Girafatitan*, following the coding recommendations of Taylor (2009). The titanosaur specimen described above (IGM 100/3005) was also included as a separate terminal. The complete matrix includes 45 taxa and 243 characters.

Aside from new scorings based on the material reported in this paper, we rescored one character for *Erketu*, changing character 81 (neural arch lamination) from state 1 (poor) to state 0 (good). For several other taxa, coding additions and/or modifications were made based on newly published descriptions (appendix 3).

ANALYSIS: Searches were run using PAUP 4.0b10 (Swofford, 2003). Ordering of characters follows the original suggestions of Wilson (2002). Search strategy consisted of a heuristic search with 10,000 random taxon-addition sequences with TBR branch swapping. Multistate scorings were treated as polymorphism. Branches with minimum length 0 were collapsed. Bremer support was calculated in PAUP 4.0b10 using a script generated in MacClade 4.08 (Maddison and Maddison, 1992).

RESULTS: Sixty most parsimonious trees (MPTs) of 513 steps were recovered. The strict consensus cladogram is shown in figure 4. *Erketu* and *Qiaowanlong* are recovered as a novel clade within Somphospondyli. Monophyly of the clade uniting *Qiaowanlong* and *Erketu* is supported by one unambiguous synapomorphy: bifurcated anterior cervical neural spines (85: 1). Also of note, the new data help resolve the polytomy including *Erketu*, *Euhelopus*, and Titanosauria that previously obscured the relationships of these taxa. The *Erketu* + *Qiaowanlong* diad is recovered as more closely related to Titanosauria than to *Euhelopus*. This relationship is supported by two unambiguous synapomorphies: distal breadth of tibia more than twice midshaft breadth (205: 1) and medial edge of astragalus reduced, so the bone does not reach the medial margin of tibia (243:1). Two additional character states potentially support this relationship: crescent-shaped sternal plates (158: 1) and ischium shorter than pubis (192: 0). Unfortunately, the first cannot be scored for *Euhelopus* or *Qiaowanlong*, while the second cannot be scored for *Euhelopus* or *Erketu* because the relevant elements are not intact, leaving their optimizations ambiguous.

These results also support exclusion of *Erketu* from Titanosauria, a finding that previously could not be demonstrated given the absence of *Andesaurus* in the original matrix. Titanosauria was originally coined as a taxon uniting the now abandoned families Titanosauridae and Andesauridae (Bonaparte and Coria, 1993). Wilson and Upchurch (2003) formally defined Titanosauria as the common ancestor of *Andesaurus delgadoi* and *Saltasaurus loricatus*, and all

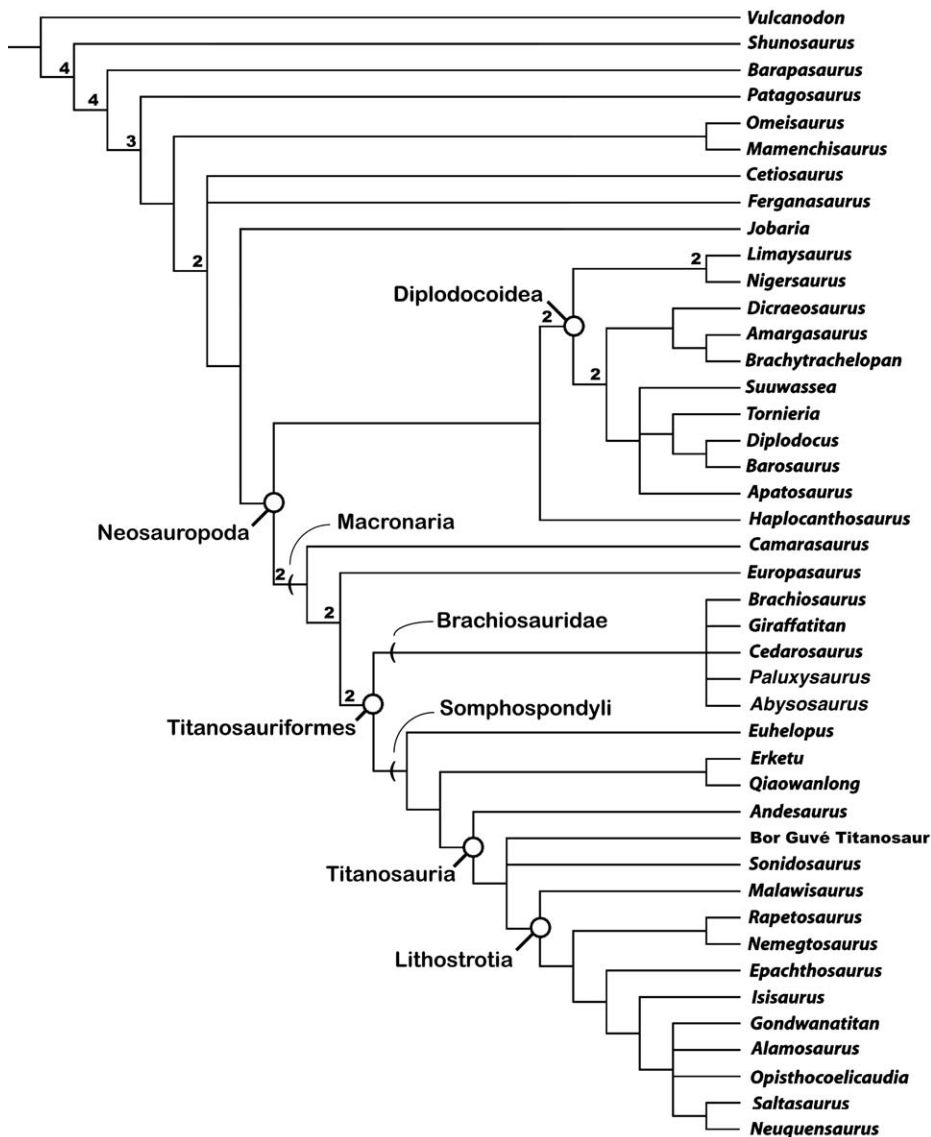


FIGURE 4. Strict consensus of 60 MPTs (TL = 513) from phylogenetic analysis (45 taxa, 243 characters) using the matrix presented in appendix 4. Bremer support (decay index) values >1 are indicated above the branches they pertain to.

descendants of that common ancestor. Unfortunately, *Andesaurus* remains relatively poorly known (e.g., >90% characters are coded “?” in the present analysis). This taxon has frequently been excluded from phylogenetic analyses of Sauropoda, resulting in difficulty establishing the precise phylogenetic positions of taxa near the base of Titanosauria. In the present study, we were able to fully resolve the position of *Andesaurus* and thus determine membership of other sampled taxa within Titanosauria. A single unambiguous synapomorphy supports monophyly of Titanosauria to the exclusion of the clade *Erketu* + *Qiaowanlong*: lack of emargination of the

ischial blade (193: 1). It must be noted that this character can be scored in *Qiaowanlong*, but not *Erketu*. Alternative topologies nesting *Erketu*, *Qiaowanlong*, or *Euhelopus* within Titanosauria are one, two, and three steps longer than the most parsimonious trees, respectively. The relatively small increases in tree length required by these alternative hypotheses may be due to a low number of character changes occurring on the branch(es) separating these taxa from Titanosauria, but could also stem from missing data due to the incompleteness of the *Andesaurus* holotype.

IGM 100/3005 is placed within Titanosauria in our results, occupying a position one node more highly nested than *Andesaurus*. This placement is supported by one unambiguous synapomorphy, absence of hyposphene-hypantrum articulations in the dorsal vertebrae (106: 1). Because *Erketu* is placed outside of Titanosauria, this result suggests that a second, unidentified sauropod taxon also ranges through the Bor Guvé deposits. Whether the Late Cretaceous titanosaur *Sonidosaurus saihangaobiensis* from Inner Mongolia and IGM 100/3005 form a clade remains unresolved, as trees resolving these two terminals as sister taxa and those placing either taxon one node basal to the other are equally parsimonious. Because IGM 100/3005 lacks the apomorphies of the dorsal vertebrae in *Sonidosaurus saihangaobiensis* listed by Xu et al. (2006), referral to that species can at least be ruled out. *Sonidosaurus* and IGM 100/3005 do share one possible synapomorphy, the presence of a PCDL. However, the presence of this lamina may be primitive for Titanosauria and also shows some homoplasy, being absent in some highly nested titanosaurs but present in *Opisthocoelicaudia*, *Saltasaurus*, and *Neuquensaurus*. The caudal vertebrae provide relatively few informative character codings. Although these elements are considered part of the same individual as the dorsal vertebra, we note that excluding codings from the caudal vertebrae results in the same phylogenetic placement for IGM 100/3005.

DISCUSSION

EVIDENCE FOR A NEW ASIAN SOMPHOSPONDYLIAN CLADE: Relationships among East Asian sauropods have been one of the central issues in sauropod phylogenetics for more than a decade. Upchurch (1995, 1998) recovered a clade of Asian sauropods (Euhelopodidae) including *Euhelopus*, *Shunosaurus*, *Omeisaurus*, and *Mamenchisaurus*. This clade, however, was not supported in analyses by Wilson and Sereno (1998) and Wilson (2002) who instead found *Euhelopus* to be more closely related to Titanosauria. The clade uniting *Euhelopus* and Titanosauria was named Somphospondyli (Wilson and Sereno, 1998). Recently, Wilson and Upchurch (2009) reexamined the original material of *Euhelopus zdanskyi* resulting in a number of proposed modifications to previous phylogenetic matrices (Wilson, 2002; Upchurch et al., 2004). Reanalysis using the revised codings resulted in *Euhelopus* retaining its position within Somphospondyli using the matrix of Wilson (2002). These revisions resulted in *Euhelopus* shifting from a position outside of Neosauropoda to one within Somphospondyli when the matrix of Upchurch et al. (2004) was reanalyzed with a posteriori deletion of two labile taxa.

Although consensus on the phylogenetic position of *Euhelopus* seems to have been reached, whether this taxon belongs to an endemic Asian sauropod clade remains to be resolved. Wilson and Upchurch (2009) noted several interesting characters shared by *Erketu* and *Euhelopus*. One

such similarity is the presence of strongly projecting pre-epipophyses of the cervical vertebrae. However, these flangelike projections are formed by the PRDL in *Erketu* but by the CPRL in *Euhelopus*, suggesting they may be nonhomologous structures. Pre-epipophyses were not referenced in the original description of *Qiaowanlong*, but seem to be present in the undescribed cervical vertebra 6 based on published images (fig. 2a of You and Li, 2009). Unfortunately, it is not clear which laminae contribute to formation of the pre-epipophyses in *Qiaowanlong*. Primary homology of the pre-epipophyses across these and other sauropod taxa such as *Jobaria* (in which the pre-epipophyses appear to be formed by the PRDL—Serenó et al., 1999: fig. 3) needs to be established before this character can be properly scored for phylogenetic analyses.

While an *Erketu* + *Euhelopus* clade is not recovered here, an *Erketu* + *Qiaowanlong* clade is only weakly supported. For the present, the only unambiguous character state supporting this clade is bifurcation of the cervical neural spines. However, weak support may stem primarily from the limited skeletal overlap between the two taxa, which is aggravated by the limited detail available from the initial account of *Qiaowanlong*. A more substantial description of the laminae and internal structure of the vertebrae in *Qiaowanlong* would allow additional phylogenetically informative features to be evaluated. For the present, we acknowledge that the support for these two taxa forming a clade will remain limited until more of the skeletons of both taxa become known.

QIAOWANLONG AND THE SUPPORT FOR ASIAN BRACHIOSAURIDAE: *Qiaowanlong kangxii* is based on a specimen collected by the Gansu Department of Land Resources, Peking University, Field Museum, and American Museum of Natural History joint field party in 2007. This taxon was originally described as a member of Brachiosauridae, though a phylogenetic analysis was not presented in support of this hypothesis (You and Li, 2009).

Brachiosaurids are well known from North America, Europe, and Africa but previously only tenuous evidence has been put forth supporting the dispersal of this clade into Asia. Before biogeographic inferences are drawn, confirmation of this putative range extension is required. Our results indicate that *Qiaowanlong* is not a brachiosaurid, but belongs to a small endemic Asian clade near the base of Somphospondyli. In light of this result, a reexamination of the potential character support for the alternate hypothesis of brachiosaurid affinities is warranted.

Several morphologies shared with *Brachiosaurus* and/or *Sauroposeidon* were presented as evidence for the brachiosaurid affinities of *Qiaowanlong* by You and Li (2009). One of these features is the presence of “fossa 4”—a pneumatic fossa positioned on the lateral face of the neural spine, bounded by the spinoprezygapophyseal and postzygodiapophyseal laminae. This fossa is present in at least cervical vertebrae 5, 6, and 9 of *Qiaowanlong* (You and Li, 2009: fig. 2). Other elements are either not figured or do not preserve the relevant part of the neural arch. This area is also occupied by a pneumatic fossa in both *Erketu* (starting in cervical 5) and *Euhelopus* (starting in cervical 3). In the latter taxon, the fossa is divided by the epipophyseal-prezygapophyseal lamina. The resulting two fossae are labeled 1h and 2h by Wilson and Upchurch (2009). Based on its relationship to the laminae, “fossa 4” in *Qiaowanlong* and *Erketu* appears to be homologous to fossae 1h and 2h in *Euhelopus*. The observed distribution of this

fossa in a wide array of taxa from both Brachiosauridae and Somphospondyli indicates its presence is likely primitive for Titanosauriformes.

Absence of an anterior centrodiapophyseal lamina was considered a possible feature uniting the brachiosaurid *Sauroposeidon* and *Qiaowanlong*. However, because only anterior and middle cervicals are known for both taxa, it is not possible to ascertain whether the absence of this lamina characterizes the entire cervical series. Indeed, this lamina is poorly developed or absent over most of the cervical series in *Euhelopus*, becoming well developed at cervical 17 (Wilson and Upchurch, 2009). Importantly, this lamina is present in *Giraffatitan brancai* (= *Brachiosaurus brancai*), so its absence can hardly be regarded as an unambiguous synapomorphy of Brachiosauridae. Posterior cervicals in *Sauroposeidon* and *Qiaowanlong* must be identified before the distribution of this lamina is fully understood, but the status of its absence as a brachiosaurid synapomorphy is doubtful.

A third character cited as supporting brachiosaurid affinities for *Qiaowanlong* is a midcervical transition point showing a pronounced shift in neural spine height (You and Li, 2009). The degree of height shift qualifying as “pronounced” has to our knowledge not been previously quantified, but in our estimation the shift in *Qiaowanlong* is closer to that in outgroups than in Brachiosauridae, accounting for a 25% increase in neural spine height (You and Li, 2009). Compared to *Sauroposeidon* and *Giraffatitan*, the shift in height at the transition point is modest.

Several additional character states have been proposed as synapomorphies of Brachiosauridae in previous studies and therefore merit consideration. Wedel et al. (2000a) proposed four synapomorphies uniting *Sauroposeidon* and *Brachiosaurus*. Of these, *Qiaowanlong* lacks the first (cervical centrum length $> 4 \times$ diameter). *Qiaowanlong* cannot be scored for the second (cervical ribs exceed length of two cervical vertebrae). Hyperelongate cervical ribs have moreover been recently documented in the titanosaur *Rapetosaurus* (Curry Rogers, 2009). A third feature (camellate vertebral structure) remains uncertain for *Qiaowanlong* from the published description, which provides no details of the internal morphology. Pneumatic details should be easily observable due to breaks in the figured vertebrae, and it is hoped they will be further explored in future investigations of this taxon. Regardless, camellate internal structure of the vertebrae appears not to be a unique brachiosaurid synapomorphy given that camellate structure has been documented in *Euhelopus*, *Erketu*, and multiple members of Titanosauria (Wiman, 1929; Powell, 1986; Wedel et al., 2000b; Ksepka and Norell, 2006). The fourth feature, a pronounced shift in neural spine height at the midcervical transition point is, as discussed above, doubtfully present.

Upchurch et al. (2004) listed two character states not reviewed above as unambiguous synapomorphies of Brachiosauridae: enlarged deltopectoral crest of the humerus and humerus/femur length ratio close to 1.0. Neither of these can be scored in *Qiaowanlong* due to the absence of limb bones in the holotype.

Taylor (2009: 798) listed seven features diagnostic of brachiosaurids, but of these only two pertain to an element preserved in the *Qiaowanlong* holotype: ilium with strongly developed anterior wing and ilium with compressed public peduncle. The first of these is present in *Qiaowanlong*, but also homoplastically present in some titanosaurs (e.g., *Rapetosaurus*). The

second cannot be scored as present in *Qiaowanlong* due to the expanded distal end of the public peduncle.

Aside from the character states discussed above, the present analysis identifies some possible additional synapomorphies for Brachiosauridae. However, because the five taxa recovered as part of this clade are collapsed into a polytomy it is not possible to ascertain whether these are synapomorphies of Brachiosauridae or of a more exclusive clade within Brachiosauridae. These character states include: presence of an anterior process of the lacrimal (11: 0), forked posteroventral process of the dentary (235: 1) (Chure et al., 2010), first caudal with prominent ventral bulge on transverse process (239: 1) (Chure et al., 2010), rectangular manual phalanx I-1 (182: 0), and transversely expanded distal condyle of the fibula (209: 1). Though potentially useful in testing the affinities of future sauropod specimens, none of these characters can be scored for *Qiaowanlong* from available material.

There appear to be no unambiguous synapomorphies of Brachiosauridae present in *Qiaowanlong* and in light of broader taxon sampling two putative apomorphies of *Qiaowanlong* can instead be recognized as synapomorphies of larger clades. As mentioned above, bifurcated neural spines are considered a synapomorphy of *Erketu* + *Qiaowanlong*. Reduction of the ischium is most parsimoniously interpreted as a synapomorphy of Somphospondyli. In *Brachiosaurus* and other non-somphospondyliian sauropods the pubis and ischium are subequal in length.

CONCLUSIONS: Evidence for Asian brachiosaurs has proven illusory. A single tooth from South Korea assigned to Brachiosauridae was reported as a putative record from Asia (Lim et al., 2001). However, this tooth lacks the characteristic chisellike wear facets of *Giraffatitan*, and is more reasonably considered an indeterminate taxon of Titanosauriformes (Barrett et al., 2002). Brachiosaurid teeth have also been reported from Lebanon, but because present-day Lebanon was part of the Afro-Arabian plate and faunal province during the Early Cretaceous, this is more accurately interpreted as a Gondwanan occurrence (Buffetaut et al., 2006). Expulsion of *Qiaowanlong*, the most substantial specimen forwarded as a member of Brachiosauridae, leaves no reliable evidence for this sauropod clade in Asia.

This raises the question of whether Brachiosauridae dispersed into Asia or were limited to North America, Europe, and Africa. During the Aptian-Albian, large-scale faunal interchange between Europe and Asia is believed to have occurred, possibly in conjunction with a major regression of the Turgai Sea (Upchurch et al., 2002). One key question is whether brachiosaurs ever had an opportunity to utilize this emergent dispersal route. Precise timing of the extinction of Brachiosauridae remains uncertain as stratigraphic precision is wanting for most species. Given the currently understood geographic and temporal distribution of Brachiosauridae (summarized by Upchurch et al., 2004), it is possible the clade had vanished at least from Europe, if not globally, by the time a dispersal route into East Asia had opened. As more Asian sauropod remains are discovered and described with no convincing evidence of Brachiosauridae emerging, the case that this pattern is real rather than a sampling artifact becomes increasingly compelling.

Ultimate resolution of this question hangs on further evaluation of a large number of recently discovered titanosauriforms. Titanosauriformes has in many ways become a “holding pen” for new sauropod taxa in the absence of phylogenetic analyses. Asian localities of Aptian-

Albian age have yielded a diversity of Titanosauriformes (Wilson and Upchurch, 2009: table 7). Many of these taxa, however, await full description and incorporation into phylogenetic analyses in some cases years after preliminary descriptions (e.g., *Dongbeititan*). While these taxa may fall on either the Brachiosauridae or Somphospondyli side of Titanosauriformes, it is worth noting that none have been formally proposed as members of Brachiosauridae and all those incorporated into analyses have been recovered as members of Somphospondyli (Upchurch et al., 2004; You et al., 2006; Wilson and Upchurch, 2009; this study).

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APPENDIX 1

NEW CHARACTERS ADDED TO THE MATRIX OF WILSON (2002)

235. Dentary, posteroventral process: single (0); forked (1). After Chure et al. (2010).
236. Cervical vertebrae, prezygapophyses: extend beyond anterior margin of centrum (0); do not extend beyond anterior margin of centrum (1). After Powell (1986).
237. Cervical vertebrae, parapophyses, dorsal excavation: absent (0); present (1). After Upchurch et al. (2004).
238. Middle and posterior cervical vertebrae, ventral keel: absent (0); present (1). After Upchurch et al. (2004).
239. First caudal vertebra, transverse process; blade-shaped (0); with prominent ventral bulge (1). After Chure et al. (2010).
240. Anterior caudal vertebrae: prezygodiapophyseal lamina: absent (0); present (1). After Chure et al. (2010).
241. Ilium, highest point on dorsal margin: occurs posterior to base of pubic process (0); occurs anterior to base of pubic process (1). After Upchurch et al. (2004).
242. Ischium, distal shaft width: narrow, less than 15% of shaft length (0); wide, more than 15% of shaft length (1). After Upchurch et al. (2004).
243. Astragalus: caps most or all of the distal end of the tibia (0); reduced so that medial edge of tibia is uncapped (1). After Upchurch and Wilson (2009).

APPENDIX 2

TAXA ADDED TO THE MATRIX OF WILSON (2002) AND SOURCE OF CODINGS

<i>Abydosaurus</i>	Chure et al. (2010)
<i>Andesaurus</i>	Calvo et al. (1991), Upchurch et al. (2004)
<i>Brachiosaurus</i>	Taylor (2009)
<i>Brachytrachelopan</i>	Rauhut et al. (2005)
<i>Cedarosaurus</i>	Tidwell et al. (1999), Upchurch et al. (2004)
<i>Cetiosaurus</i>	Upchurch et al. (2004)
<i>Epachthosaurus</i>	Martinez et al. (2004)
<i>Europasaurus</i>	Sander et al. (2006)
<i>Ferganosaurus</i>	Alifanov and Averianov (2003)
<i>Giraffatitan</i>	Taylor (2009)
<i>Gondwanatitan</i>	Kellner and Azevado (1999), Upchurch et al. (2004)
<i>Paluxysaurus</i>	Rose, 2007
<i>Qiaowanlong</i>	You and Li (2009)
<i>Sonidosaurus</i>	Xu et al. (2006)
<i>Suuwassea</i>	Harris and Dodson (2004)
<i>Tornieria</i>	Remes (2006)

APPENDIX 3

MODIFICATIONS TO THE EXISTING SCORINGS IN THE MATRICES OF
WILSON (2002) AND KSEPKA AND NORELL (2006)

1. Codings were added for *Erketu* based on study of the new material reported in this contribution: 87 (1), 88 (0) and 89 (1). Additionally, the coding for character 81 was changed from (0) to (1).
2. Codings for *Euhelopus* were altered to reflect the suggestions of Wilson and Upchurch (2009: table 5).
3. Additional codings for *Nigersaurus* were added based on Sereno and Wilson (2005) and Sereno et al. (2007).
4. Codings for *Mamenchisaurus* and *Omeisaurus* were updated following Harris (2006b).
5. Character 30 (anterior extension of laterotemporal fenestra) was modified to include a three states: (0) restricted to posterior to orbit; (1) reaching midpoint of orbit; and (2) reaching or surpassing rostral margin of orbit.
6. Character 86 (elongation index of midcervical vertebrae) was divided into two states: state (0) $EI < 4.0$ and state (1) $EI > 4.0$ in order to allow scoring for taxa falling into the gap between the previously defined cutoffs (2.5–3.0 and >4.0).
7. Character 191 (pubioischial contact length) was divided into the states (0) pubioischial contact $<40\%$ pubis length and state (1) pubioischial contact $>40\%$ total pubis length in order to allow scoring for taxa falling into the gap between the previously defined cutoffs (approximately $\frac{1}{3}$ and approximately $\frac{1}{2}$).
8. A third state was added to character 128 (anterior caudal transverse process shape): the character states are now: (0) all triangular and tapering; (1) winglike on first caudal only; (2) winglike over several anterior caudals.
9. A third state was added to character 197 (morphology of lesser trochanter of femur) resulting the following three states: well developed (0); weakly developed (1); and absent (2), following Upchurch et al. (2004).
10. *Nemegtosaurus* was coded state 1 for character 27 (minimum diameter of supratemporal fenestra subequal to foramen magnum), and state 0 for character 68 (tooth wear facets interlocking and V-shaped) following Wilson (2005).
11. *Neuquensaurus* and *Saltasaurus* were coded state 1 for character 116 (shape of first caudal centrum procoelous) based on Powell (1986).
12. *Rapetosaurus*, *Neuquensaurus*, and *Saltasaurus* were coded state 1 for character 121 (SPRL present in anterior caudal vertebrae) based on Curry Rogers (2009) and Salgado et al. (2005).
13. *Opisthocoelicaudia* was coded state 1 for character 115 (caudal transverse processes disappear by caudal 15), following Borsuk-Bialynicka (1977).
14. *Rapetosaurus* was coded state 1 for character 18 (frontal contribution to supratemporal fenestra absent), state 1 for character 27 (minimum diameter of supratemporal fenestra subequal to foramen magnum), state 4 for character 80 (13 cervical vertebrae present), and state 0 for character 178 (metacarpal I longest), following the more detailed description in Curry Rogers and Forster (2004) and Curry Rogers (2009).

APPENDIX 4

PHYLOGENETIC MATRIX

Characters 1–234 correspond to the matrix of Wilson (2002); characters 235–243 are described in appendix 2.

Theropoda

000000000000000000000000000000000000?0000000000000?00000000000000000?00000000000010?0000
00?000000000000000000?0000000000000000000000000?00000?000001000000000001100?0000000
000000000000000000000?000000000000000000?0000000000000?001?0000

Prosauropoda

?000000000000000000000000000000000000?00000000000000000000000000000?00000000000110?0000
?0?1000000000000000000?00000000000000000000000000000?00000?000000000000000001000?00000000
001000000000000000000?000000000000000000000000000000000000000?001?0000

Abydosaurus

11?100?101010?10??100?001011?0111001?0????0?0???1000?00010????212?201?210101?0??110?0??????
????????????????????0????????????????????0?????????1?10?????0?10?????????11?111?????????
??01??11???

Alamosaurus

??11??1100001?0??101011010110
1110?????01231100101101110001010???????0?111111011?1?11?11101100111??111112?????1?0??0111
?????0????????????????????????????????????0?0?????1?

Amargasaurus

?????????1?00101111?1101111????????????00111011?011?????????????????1?????001401?01010105111??1
?1?0000?12?1?1????0?????????????????0?????0?0????1?0?1????0101011010?001????????????1100???????12
00?00?????????????????????????????????0?0????1??

Andesaurus

??11?????????????0??????1?010?
?????0????0?????0????0?0?0?????????1???1???1?1????????????
??1?

Apatosaurus

00111112011111?010111?101011211100020?1?000010000011????????2212021211??01160110101111
5101111111100000021?11001100?0111101121100000111110011001011001100000101011010100111110
00011111100110100012001001101110111101111111?11111110?010?0000

Barapasaurus

??1?0????00?01??0100??101011011101
00001100?0?0?00?0000000?00001?00?0110000000?0101011110100????????????0110001010101
2001000101111?1?10??010?000001?1?11?0?001?00?

Barosaurus

??01??011?1111115101?11111100
000021????0?110111111011211110011?11?01?00?011?0?????00?0?????10?001?1?0?000001111001101000
12001001??1110?1110??11111????????0?010?0000

Brachiosaurus

??1?????????????101?11?11110010
 121?01???000?0011001?0?????????1?????????1?????000?101????????2????????????11101??????1210000????
 ???111??

Brachytrachelopan

??00?01???0111?31101?11111?00
 0?1???1??10??1?????????????????1?0??
 ???1?????

Camarasaurus

1111001111110001010110010101120011011011110000000010011001111111110111210000103011010
 10113101011011110010021101001000000011011100000000?100?1010101101010000010101111010011
 111110011111100011101112?01001101110111100111101111111111110001000000

Cedrosaurus

??11?????????????????1?????????????1??
 ??????????010????01???00?00??????0?1???1?0???0???0?1?111?1002????1?????????????????????1?????????????
 ??????????????????????1?1???????????

Cetiosaurus

??1?????01?4010000100??101?11000??1
 0000?????0?0001????01?0000?0000?100?0?00??110001000001?10?1110??1?110?????1100?10??1012
 ?00?00??11????????????????????????????????????010?00?

Dicraeosaurus

00?11????0?00?0111111011112?????1?0??10001110101011110???????221202121??00113011010101131
 11110011100000121?1?0?1100001011011200000011?11001?00??110001000?0101011110??1??????????
 11100110100012?0100110111011110??111111?11????11?0?01?00?

Diplodocus

0011112011111101011101010112111000201110000100001011110101101?2212021211100116011011
 11115101111111000000211100110111111101121111001111100110010110001000001010111101001
 ??????????11100110100012?01011101110111100111111111111?11110?010?000

Epachthosaurus

??11?????????????????10?01??10??0110
 ?3????0?1?1001?1??0110?0??1000?????1??1?????????11101??1?00?101??1111?12??1?11?????????1??110??
 ???10??1?1111????11?1??0????0?????????

Erketu

??110?011111101??????????????????
 ?????????????????????????????????????10?????????1?????????1??111?
 ?10111?00?????????????????????010?????1

Euhelopus

01110?11??1????10???????0??????11??011???????????????1001??????111011121?1011?70111011011210101
 111011001?03?01?????????????????????????????1011?????110010000?110101?????????????????????111?011?01
 112011001101?10111?00?11101?11?1???11?0?0?0?110

Europasaurus

1111?01111?1001101?01?10010111011100101???100000?11001?001111?1?1110?11110?101??01100000?
?101011011110010011??001?000000?11001?00000000??110?0010?01101000000101011110100???11????
??111101?11101112?01001??111011110?11?1??1?1?1?11??010?????

Ferganasaurus

??01????????????????0????????0??2
1?0?0000?000??1100110?01?00?0????????????1????????01010111?0011??110000?11?1100010101?02?0100
1??11111?1?0????????????????????????????00

Giraffatitan

1111001111?1000101011000010112111001011110000?0110011011111112111001121000?10401?0011
00?3101?11?11110010021?0?0?100000001100110000000??1011??10?01101010000?10101111011021111
1111101111010111011121100011011111110011110111?1111?111?010101110?

Gondwanatitan

??11????????0?????11??????11?
3??????1?110?????110001?10??1?1??1??1????????1110????????????????????1?111????1?1?????????1?
????????????????????????????????1?1??

Haplocanthosaurus

??0????????????????????????01?4011000100?210101101111
00000211010?10000000110011000000??1100??10??100001000????????????????????1110001010111
2?0100????????????????????????????0??100000?

IGM 100/3105

??10?011110?1?0?1
?????0????????????????000000??
??

Isisaurus

??11??110000100??101011010100
?1103120?????10?001101110001010??1??10?11?0101010????1101111101????????????????111110110111?
??0????11?

Jobaria

11110011111100010101100001011201110?10?11?000?000?001000?????11101110000001?4011000100
?3101011111110000021101001000000110011000000??10001?00101101010000010101111010010111
00001111100010101112?010011011101111001111011111????????0?0?0000?

Limaysaurus

????????01?0011100110?1???1{12}0?110?0?0???10010??11011????????????1??212??101??011000100??11
10??111000001????001000?000110111002000011?1????10??11020?000101000111101001????00?????1
1?010?01112?0?00????1?1?1?0??10001111????????0??????0?

Malawisaurus

11????1??1????????????????????10????????????0????1100?????1?10?11210?011??1100011?0??10?01?01?
110111031?????1??10000111011000100000?01?0?11?01????00011101011000100??1?111?????????????
11?2?1?????11110?????1?1?????1?1?????1?00001???

Mamenchisaurus

1110?0111010000?0?010000010?1101110?10?111?00????0?0?1100001101111011110000110{67}0101010
1103101011011101000021?0??011010000000011000?000???10001100?0110??00?0010101111010011101
?0001???11000??01012?01001101?1101110?11?101?1?1111?1?0???1?00?

Nemegtosaurus

0??1?011?101000101010101110201111211111?11001100010110111?01?111002121000?????????????
??
??

Neuquensaurus

??11??010?00100??101?1111?1?01
11031?0?1?2111001011?111000101110??????1???11101?111111101101111????????????1111101?0111
2?11111111?10111111?1110????1??????1?10????11

Nigersaurus

0011011100???0011?0010??1????201110?2????00011001?01110?100???2110212010101?4011001110?3
???1?01???1???1?????????0?????????????????11?1100??????1020?00??1?0?????????????????????0??
??1??0???????

Omeisaurus

111000110110000?01011000010111?11?0?1??11100?0?0?00110000?1???111011111?0001070111010?0?
3101?11011100000021101?010010000000011000?000???100?11000011000?0000010101101001010000
0011101100010101012?000?01011??0101001111111111111111000?100000

Opisthocoelicaudia

??11?????????01041010111101101
11031?0?01221200001101110001000100??110?1111110111111111011011111?1111112??1111?0100
111121111?11111101111111110111111011110??????111

Paluxysaurus

?1???11??01112?00011?011?01?00??1010111?1??
001?021???0???0000011011100000000??1011??10??11010100000101011101?02??1?11??11?0?01?101
11211100010111????????????????????????????????0???????

Patagosaurus

1?100?11????????0????????????????????????????1????????????0????????1?10111??0001??011?00100??10101101?
?0100002??0?????00?????1??0?000??1?00?00??110?0?000?010111110100????????????110001010101
2?0100001?????????101011????????????0?011?00?

Qiaowanlong

??1?011010101????????????????
????????????????????????????????0??111010?000????????????
????????????????????????????0?0?11?

Rapetosaurus

0011?111?10?000?010101010111020?1121111???1100100?110100111????11110212100011?71100011?0?
510101101011011103?0???1??10?1?1?01100?00?100??101???11??111010100111011011001101??111011?
??11101010011112?11011??110?????11?0??1?11?????1?001??1?

Saltasaurus

????????????00??101?00101?????????????01000101???1????????????????????11??011000110??101011110
1101110312011??1?10?011111000101110?1?????11?011101?1111111101101111?????????2??1111011
011112?11111111110?????????????????????1?100?11?

Shunosaurus

01100011011000000001??000001110110001001100000000?000110000?101?111011120?00000411?10010
0?210000100000000?010?000010000000000110000000?0?0?00111010100000000010101101010010100
00011010110001010?012?0100?10111001010011110111011111111100?010000?

Sonidosaurus

??11????????????????01?11????11?
?????????2?????????110?00????????????1??1101??101?????????????
??1?

Suuwassea

?0?????1?????00??111010?1???100????????00?00?10?11?????????2?????12?1?0011?011000?110??01????
?????????????00?????????????????000???10?????11000100???10100????????????????????????????????
????1???11?????0?11110?1?1?1011????010?????

Tornieria

????????????01????01?1010?????????????0??00?00?1????????????????????????????????1???1????????????????
??????0???1111??01121011000????????????110001???00101011110??1????????????1100???00012?0101
1??101011110????????????????????????????0?

Vulcanodon

?????????????0????????????????????????????????0????????????????????????????0????????????????????????1
?????0?0?00?????100001?????????00??10??????1010?11101001????0????001?00010101011001?000
?00001000010?1001001000011000????????00

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