A new basal eusauropod from the Middle Jurassic of Yunnan, China, and faunal compositions and transitions of Asian sauropodomorph dinosaurs

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Many sauropod ghost lineages cross the Middle Jurassic, indicating a time interval that requires increased sampling. A wide taxonomic spectrum of sauropodomorphs is known from the Middle Jurassic of China, but the braincase of a new sauropod, named here *Nebulasaurus taito* gen. et sp. nov., is distinct. *Nebulasaurus* is sister taxon to *Spinophorosaurus* from the Middle Jurassic of Africa and represents a clade of basal eusauropods previously unknown from Asia. The revised faunal list indicates dramatic transitions in sauropodomorph faunas from the Jurassic to Cretaceous of Asia; these are consistent with geographic isolation of Asia through the Late Jurassic. Non-sauropod sauropodomorphs, non-mamenchisaurid eusauropods (including basal macronarians), and mamenchisaurids successively replaced previous grades through the Jurassic, and titanosauriforms excluded all other sauropod lineages across the Jurassic–Cretaceous boundary.

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Introduction

Time-calibrated phylogenetic trees of sauropod dinosaurs indicate a large number of ghost lineages across the Middle Jurassic, including neosauropods that consist of diplodocoids and macronarians (Upchurch 1995, 1998, 1999; Wilson and Sereno 1998; Wilson 2002; Upchurch et al. 2004; Upchurch and Barrett 2005; Mannion et al. 2011; and analyses derived from their data sets). These phylogenetic analyses predict the origin and diversification of neosauropods within the interval. On the other hand, sauropods are rare compared to basal sauropodomorphs in the Early Jurassic, and the only sauropod skull from the Early Jurassic is *Tazoudasaurus* (Allain et al. 2004; Allain and Anquesbi 2008). By the Bathonian–Callovian, the sauropod fossil record is global, but localities and taxa are sparse, comprising one to four genera each for Africa, Australia-Antarctica, Europe, India-Madagascar, North America, and South America (Upchurch et al. 2004; Barrett and Upchurch 2005; Remes et al. 2009). For these reasons, the diverse sauropodomorph fauna from the Middle Jurassic of China provides an unparalleled opportunity to document sauropod anatomy and diversity in this critical time interval.

Here, a new basal eusauropod, *Nebulasaurus taito* gen. et sp. nov., is described based on a braincase from the Zhanghe Formation, the lower Middle Jurassic (Aalenian–Bajocian) of Yunnan Province, southern China (Fig. 1). This formation has previously yielded one basal sauropodomorph and two basal eusauropods and predates the well-documented sauropod fauna from the Bathonian–Callovian Shanximiao Formation, Sichuan Province, southern China. Despite its early age and

basal position within the Eusauropoda, the well-preserved braincase of *Nebulasaurus* has a number of similarities with those of highly derived neosauropods. Comparison of *Nebulasaurus* with other sauropods highlights an unusually heterogenous sauropodomorph fauna in the Middle Jurassic of China.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, New York, USA; CM, Carnegie Museum, Pittsburgh, Pennsylvania, USA; GCP-CV, Museo Paleontológico de Elche, Elche, Spain (eventually to be curated at Musée National, Niamey, Niger; Knoll et al. 2012); LDRC, Lufeng Dinosaur Research Center, Lufeng, China; ZDM, Zigong Dinosaur Museum, Zigong, China.

Systematic palaeontology

Dinosauria Owen, 1842

Sauropoda Marsh, 1878

Eusauropoda Upchurch, 1995

Genus *Nebulasaurus* nov.

Type species: *Nebulasaurus taito* sp. nov.; see below.

Included species: Type species only.

Etymology: From Latin *nebulae*, misty cloud, after the alpine province of Yunnan (= southern cloudy province, Chinese); and from Greek *sauros*, lizard.

Diagnosis.—As for the type and only species.

Nebulasaurus taito sp. nov.

Figs. 2, 3.

Etymology: In honor of the Taito Corporation of Japan, which funded the field project in and near the type locality.

Holotype: LDRC-v.d.1, a braincase (Figs. 2, 3A, B).

Type horizon: Zhanghe Formation, lower Middle Jurassic, Aalenian/Bajocian (Bureau of Geology and Mineral Resources of Yunnan Province 1990).

Type locality: The locality is in Xiabanjing, Jiangyi Rural Area, Yuanmou County of Yunnan Province, China (Fig. 1B). Information regarding precise location of the locality is protected by the local authority and available through LDRC on request.

Material.—Holotype only.

Diagnosis.—Non-neosauropod eusauropod with exoccipitals nearly excluding supraoccipital from foramen magnum (supraoccipital forming less than a tenth of margin of foramen magnum) and supraoccipital not expanded laterally between parietal and exoccipital. It is also distinguished from other non-neosauropod eusauropods by a combination of characters: crista interfenestralis incompletely partitioning fenestra ovalis and jugular foramen (present in some neosauropods such as *Apatosaurus*; distinguished from *Mamenchisaurus*, *Omeisaurus*, *Shunosaurus*, and *Spinophorosaurus*, all with a fully formed crista interfenestralis); frontoparietal fenestra at frontal-parietal suture and larger than postparietal foramen (distinguished from mamenchisaurids in which both openings are absent altogether); and craniopharyngeal foramen
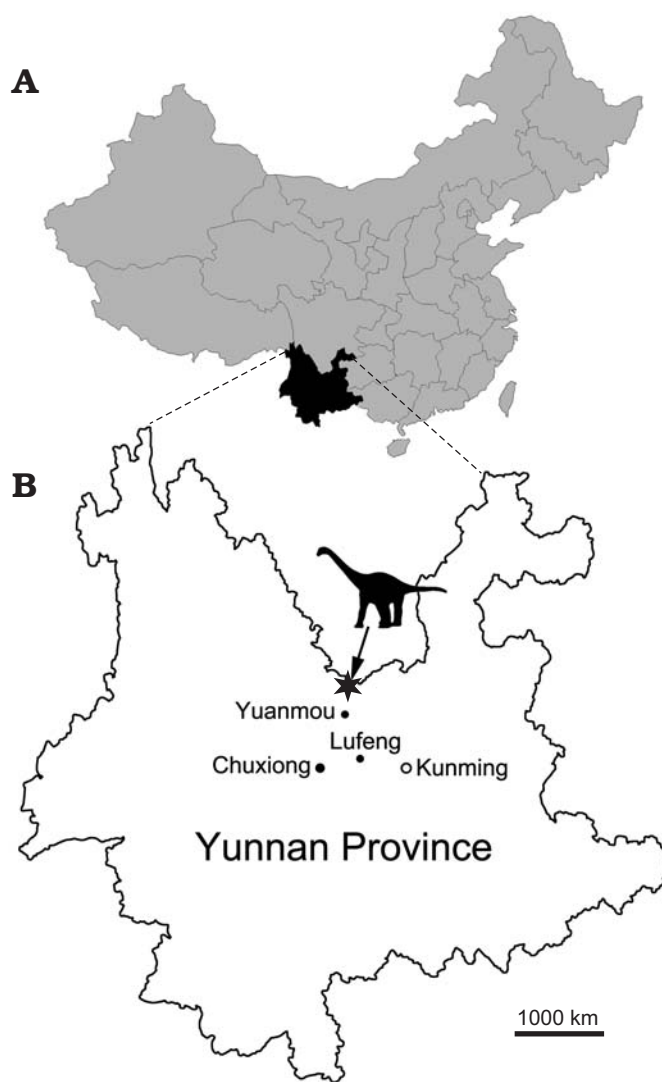

Fig. 1. Geographical information on the locality of *Nebulasaurus*. **A**. Map of China showing Yunnan Province (shaded black). **B**. Map of Yunnan Province showing the locality indicated by a silhouette of a sauropod.

posterior to basal tubera (distinguished from *Spinophorosaurus*, the foramen of which is anterior to the basal tubera).

Description

The braincase of *Nebulasaurus* is well preserved, although it is broken along the plane from the frontals to the parasphenoid and is not attached to any lateral facial or palatal elements (Figs. 2, 3A, B). When the dorsal surface of the occipital condyle is held horizontally, the angle between the supraoccipital plane and the occipital condyle is greater than 100°, as in most sauropods other than titanosaurs (Tidwell and Carpenter 2003; Curry Rogers and Forster 2004; Paulina Carabajal and Salgado 2007; Díaz et al. 2011). The foramen magnum is transversely wider than tall. The supratemporal fenestra is transversely wider than anteroposteriorly long, as in most sauropods, but unlike basal sauropods such as *Shunosaurus* from the early Middle Jurassic of China (Chatterjee and Zheng 2002). The fenestra extends medially for more
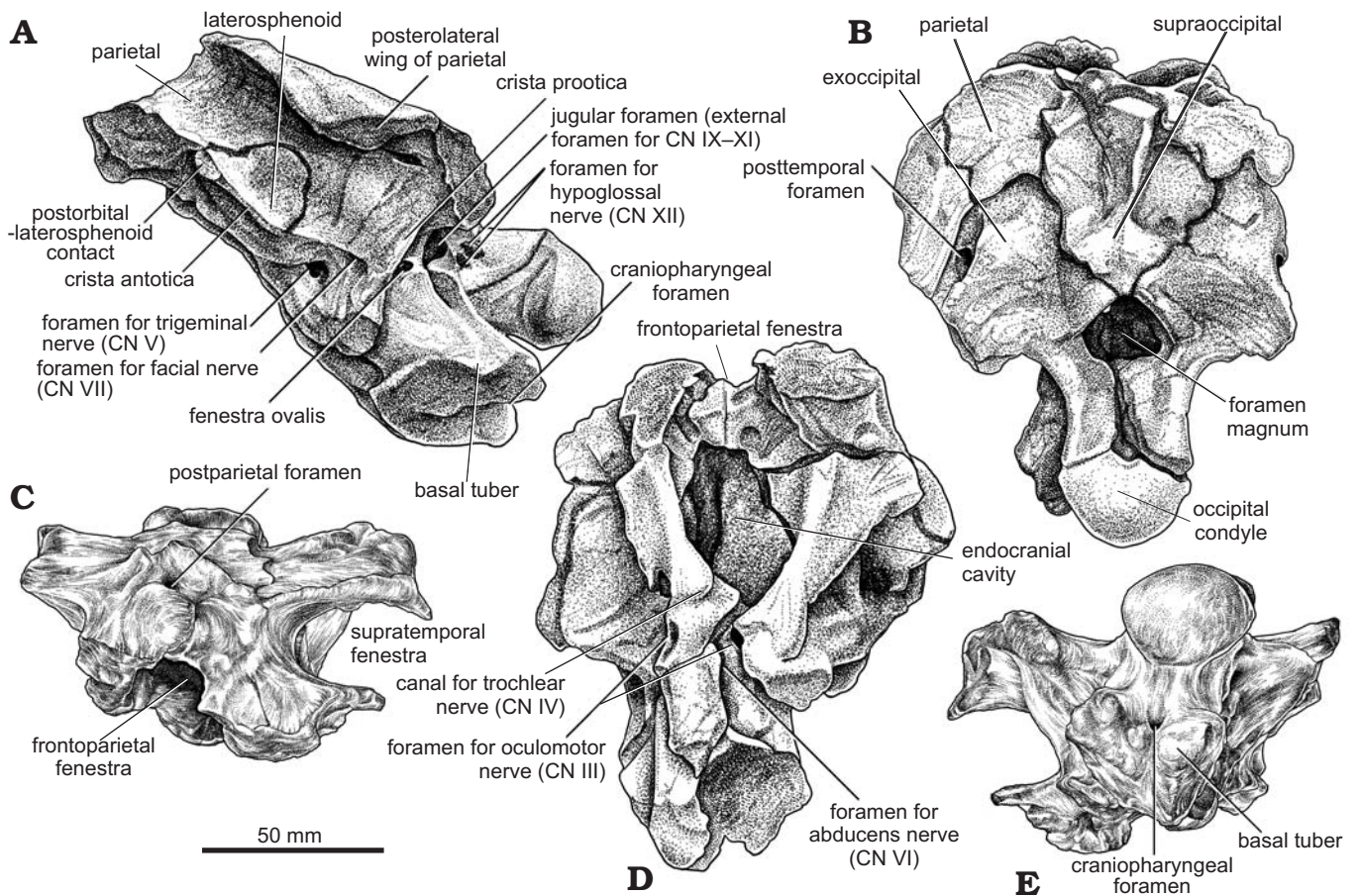
Fig. 2. Interpretive drawings of the holotype of the sauropodomorph dinosaur *Nebulasaurus taito* gen. et sp. nov., Xiabanjing, Zhanghe Formation, Middle Jurassic (LDRC-v.d.1), in left lateral (**A**), posterodorsal (approximately 45° with respect to a transverse vertical plane) (**B**), dorsal (**C**), anteroventral (approximately 45° with respect to a transverse vertical plane) (**D**), and ventral (**E**) views.

than half the distance from the lateral margin to the midline of the skull roof, as in *Atlasaurus* and *Spinophorosaurus* (Monbaron et al. 1999; Remes et al. 2009; Knoll et al. 2012).

Skull roof.—The frontal forms only the anterolateral corner of the supratemporal fenestra. In dorsal view, the frontal-parietal suture forms a shallow V (with an angle greater than 150°) rather than being transverse as in most other sauropods. Unlike *Shunosaurus* or non-sauropod basal sauropodomorphs (Galton 1984; Chatterjee and Zheng 2002), the parietals are wider transversely than long anteroposteriorly (Figs. 2C, 4A). The distance between the right and left laterosphenoid-postorbital contacts is about a quarter narrower transversely than the width of the skull roof between the posterolateral processes of the right and left parietals, a condition present in *Spinophorosaurus* and neosauropods such as *Camarasaurus*, *Diplodocus*, *Nemegtosaurus*, and *Suuwassea* (White 1958; Berman and McIntosh 1978; Chatterjee and Zheng 2004; Harris 2006a). In lateral view, the transverse nuchal crest gently folds over the supratemporal fenestra anteroventrally to contact the squamosal-postorbital complex. In occipital view, the parietal forms the entire dorsal margin of the post-temporal fenestra (Fig. 2B).

The frontoparietal fenestra sits at the intersection of the midline of the skull and the frontal-parietal suture, whereas the postparietal foramen at the intersection of the midline and the parietal-supraoccipital suture is much smaller an opening than the fenestra (Fig. 2C). Size and development of these two openings are taxonomically and individually variable among sauropods. In *Shunosaurus*, a single midline foramen penetrates the parietal (Fig. 4A; Chatterjee and Zheng 2002). In *Spinophorosaurus*, the postparietal fenestra is larger than the frontoparietal foramen (=pineal foramen in Knoll et al. 2012; Fig. 4D). Amongst diplodocoids, the frontoparietal and postparietal openings are comparable in size in *Amargasaurus*, *Dicraeosaurus*, and *Suuwassea* (Janensch 1935; Salgado and Calvo 1992; Harris 2006a), merged into one in *Apatosaurus* (Balanoff et al. 2010), or absent altogether in *Limaysaurus* (Calvo and Salgado 1995). Individual variations of this character exisits in *Camarasaurus* and *Diplodocus*. The single midline aperture is present in two specimens of *Diplodocus* (AMNH 694 and CM 11161) but absent in another specimen of *Diplodocus* (CM 3452) (Osborn and Mook 1921; Berman and McIntosh 1978; Witmer et al. 2008). Similarly, at least one specimen of *Camarasaurus* (CM 11338) lacks the aperture, whereas this taxon typically has a single midline opening in the parietal (Gilmore 1925; Madsen et al. 1995; Chatterjee and Zheng 2004; Witmer et al. 2008). As such, number or size of the external openings may not be always useful as a
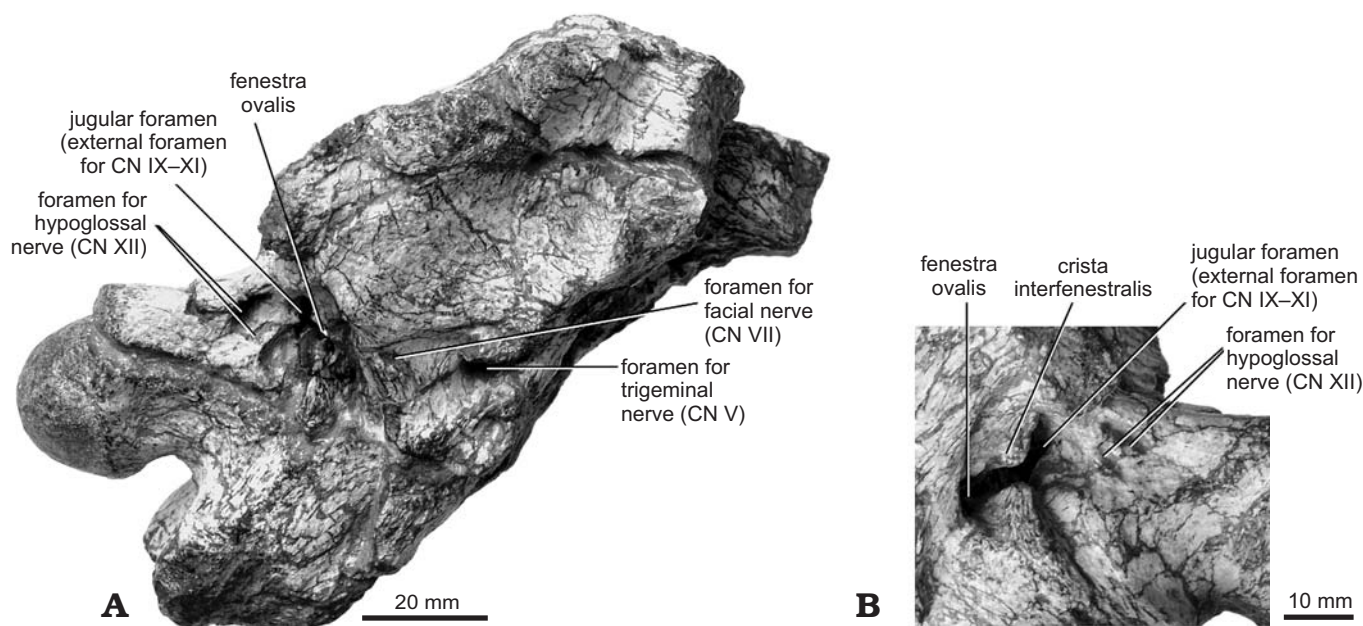
Fig. 3. Photographs of the holotype of the sauropodomorph dinosaur *Nebulasaurus taito* gen. et sp. nov., Xiabanjing, Zhanghe Formation, Middle Jurassic (LDRC-v.d.1). **A**. The braincase (holotype) in right lateral view. **B**. Details of the metotic region in left lateral view.

character. Nevertheless, it is significant that these openings are consistently absent in mamenchisaurids (Fig. 4B, C; He et al. 1988; Ouyang and Ye 2002) with the exception of a new genus and species (Xing et al. in press). As such, the braincase of *Nebulasaurus* is clearly distinguished from those of mamenchisaurids based on this character.

Sphenoidal region.—Anteromedial to the crista antotica is a fenestra for the optic nerve (CN II). The dorsoventral passage for the trochlear nerve through the laterosphenoid is visible on the right side of the braincase in anterior view. The oculomotor nerve exited from a larger foramen ventral to this. Farther ventrally and slightly medially, the abducens nerve (CN VI) passed through a foramen near the laterosphenoidal-parasphenoidal suture.

In *Nebulasaurus*, the foramen for the trigeminal nerve (CN V) is posterior to the coronal plane defined by the crista antotica, as in *Camarasaurus*, *Shunosaurus*, *Spinophorosaurus*, *Suuwassea*, *Turiasaurus*, and basal sauropodomorphs in general (White 1958; Galton 1984; Benton et al. 2000; Chatterjee and Zheng 2002, 2004; Harris 2006a; Knoll et al. 2012; Royo-Torres and Upchurch 2012). In neosauropods, the foramen is generally either directly below the crista or even slightly anterior to the coronal plane defined by the crista (Berman and McIntosh 1978; Upchurch 1999; Tidwell and Carpenter 2003; Wilson 2005; Remes 2006; Paulina Carabajal and Salgado 2007; Garcia et al. 2008; Paulina Carabajal et al. 2008; Balanoff et al. 2010). In *Nebulasaurus*, the groove for the ophthalmic branch (CN V_1) extends anteriorly, whereas the maxillary and mandibular branches (CN V_{2+3}) pass ventrally. The dorsal rim of the foramen for CN V swells from the laterosphenoidal dorsal margin and hangs over the foramen. *Shunosaurus* has a separate external foramen for CN V_1 (Chatterjee and Zheng 2002), whereas only a single

external foramen exists for CN V of *Nebulasaurus*. However, numbers of external foramina for CN V may be variable below the generic level as well. Chatterjee and Zheng (2004) described a separate external foramen for CN V_1 in one specimen of *Camarasaurus* (DINO 28), but the external foramen for CN V is single in other specimens of the same genus (White 1958; Witmer et al. 2008). In the holotype braincase of *Nebulasaurus*, a flat surface above the foramen for CN V and posterior to the crista antotica indicates an epipterygoid contact. This facet is demarcated by the parietal-laterosphenoidal suture.

Otic region.—The prominent crista prootica extends from the base of the paroccipital process anteroventrally to the prootic-opisthotic suture. The crista does not cross the suture, but instead hangs over it, making itself a landmark for the boundary between the prootic and the opisthotic. The crista also separates the foramen for CN V anteriorly and the foramen for the facial nerve (CN VII) posteriorly.

The separation of the fenestra ovalis and the jugular foramen is incomplete on both sides of the braincase (Fig. 3). A pair of struts extending from the dorsal and ventral margins represents an incipient crista interfenestralis, which incompletely partitions the fenestra ovalis anteriorly and the jugular foramen posteriorly, as in *Apatosaurus* (Balanoff et al. 2010). The external foramina are largely round in shape, as in *Spinophorosaurus* (Knoll et al. 2012). In contrast, the external foramina are dorsoventrally elongate, and with complete struts separating these foramina, they form a series of slits in *Mamenchisaurus*, *Shunosaurus*, and *Turiasaurus* (Chatterjee and Zheng 2002; Ouyang and Ye 2002; Royo-Torres and Upchurch 2012).

Occiput.—The overall shape of the supraoccipital resembles a butterfly in occipital view. The supraoccipital has no
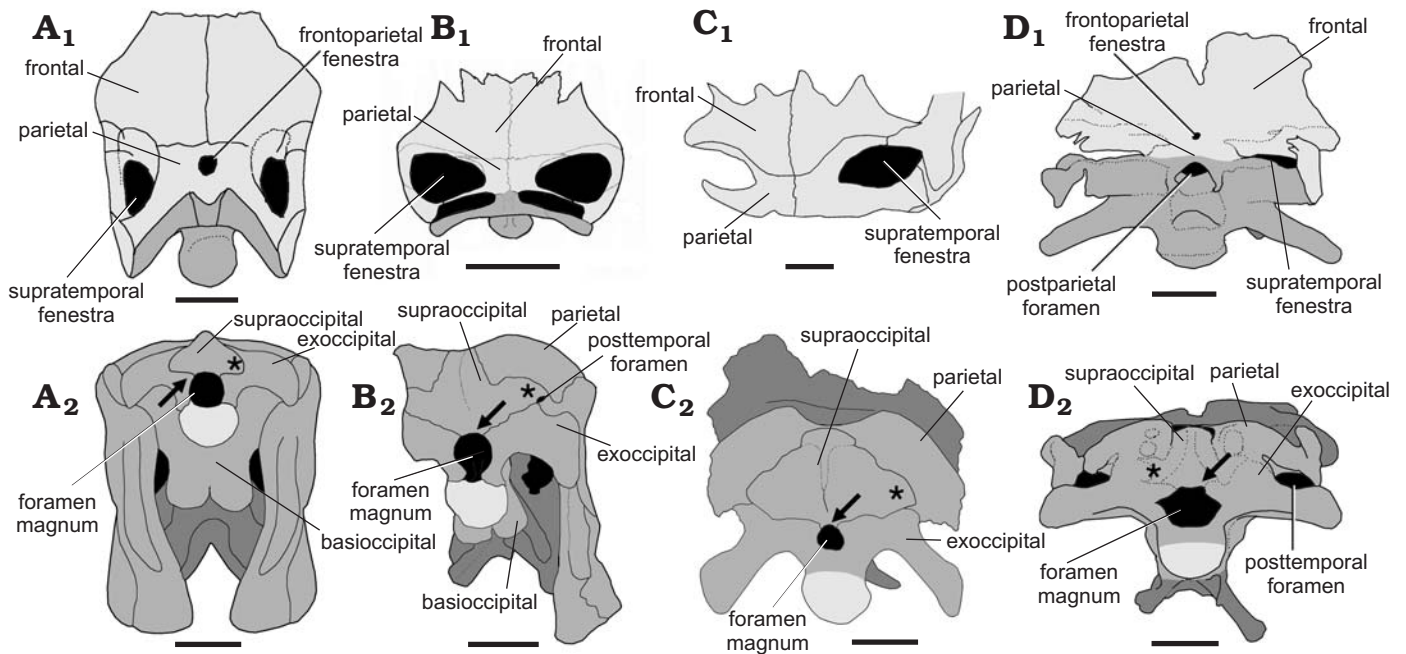
Fig. 4. Comparison of non-neosauropod eusauropod braincases illustrates general conditions against unique features of the braincase of *Nebulasaurus taito* gen. et sp. nov. (e.g., frontoparietal fenestra larger than postparietal foramen, supraoccipital not expanding laterally, and supraoccipital contributing little to foramen magnum). **A**. *Shunosaurus lii* Dong, Zhou and Zhang, 1983; China, Xiashaximiao Formation, Middle Jurassic (ZDM 65430), in dorsal (A$_1$) and posterior (A$_2$) views (modified after Chatterjee and Zheng 2002; supraoccipital was redrawn based on Zhang 1988). **B**. *Mamenchisaurus youngi* Pi, Ouyang and Ye, 1996; China, Shangshaximiao Formation, Middle Jurassic (ZDM 83), in dorsal (B$_1$) and posterior (B$_2$) views (modified after Ouyan and Ye 2002). **C**. *Omeisaurus tianfuensis* He, Li, Cai and Gao, 1984; China, Xiashaximiao Formation, Middle Jurassic; ZDM 5702, in dorsal view (C$_1$); ZDM 5703 in posterior view (C$_2$) (modified after He et al. 1988). **D**. *Spinophorosaurus nigerensis* Remes, Ortega, Fierro, Joger, Kosma, Ferrer, PALDES, SNHM, Ide, and Maga, 2009; Niger, Irhazer Group, Middle Jurassic (GCP-CV-4229), in dorsal (D$_1$) and posterior (D$_2$) views (modified after Knoll et al. 2012). Arrows indicate wide participation of supraoccipital in the margin of foramen magnum. Asterisks indicate lateral expansion of supraoccipital along exoccipital-parietal contact. Scale bars 5 cm.

marked lateral expansion between the parietal and exoccipital or near their contact. This condition is unique among sauropods (Figs. 2B, 4). The ventral part of the supraoccipital is constricted medially by the exoccipitals. Its contribution to the foramen magnum is less than 10% of the margin of the foramen. This is substantially less than in most sauropods in which the supraoccipital forms at least 25% or more of the margin (Fig. 4). An important exception to this is *Suuwassea* (Harris 2006a), the supraoccipital of which contributes little to the foramen magnum, as in *Nebulasaurus*. As in *Suuwassea* (Harris 2006a) and *Tornieria* (Remes 2006), the supraoccipital ridge is transversely narrow and does not form a knob near the skull roof. In diplodocids such as *Apatosaurus* and *Diplodocus* (Berman and McIntosh 1978; Balanoff et al. 2010), the ridge expands dorsally and forms a pronounced knob at the posterior margin of the skull roof. The preserved part of the exoccipital shows that the paroccipital process extended laterally such that the complete paroccipital process would have only obscured the neck for the occipital condyle in lateral view, but not the condyle itself.

The basioccipital forms the entire articular surface of the occipital condyle and the floor of the median condylar incisure. At the base of the occipital condyle, paired ridges extend from the neck down to the basal tubera, forming the triangular craniopharyngeal fossa below the condyle. An un-paired foramen at the dorsal margin of this fossa represents the craniopharyngeal foramen (Fig. 2E; Balanoff et al. 2010), a remnant of the embryonic hypophyseal fenestrae that separate trabecular cartilages (Bellairs and Kamal 1981). The position of the foramen posterior to the basal tubera is also seen in *Rapetosaurus* (Curry Rogers and Forster 2004; the foramen is visible in their figure 24), *Suuwassea* (Harris 2006a), and a titanosaur braincase (Calvo and Kellner 2006). In other taxa, the craniopharyngeal foramen opens more anteriorly in position. The foramen sits at the midline of the basicranium, slightly anterior to the basal tubera in *Apatosaurus* (Balanoff et al. 2010), *Nemegtosaurus* (Wilson 2002), and a titanosaur braincase (Tidwell and Carpenter 2003). In *Spinophorosaurus*, the craniopharyngeal foramen is between the posteriorly deflected basipterygoid process (Knoll et al. 2012).

Stratigraphic and geographic range.—Type locality only.

Phylogenetic analysis

A data set used for a comprehensive analysis of sauropod interrelationships from Harris (2006b) with 331 characters was supplemented with 9 newly identified braincase characters (see SOM, Supplementary Online Material available

at http://app.pan.pl/SOM/app60-Xing_etal_SOM.pdf, SOM 1: full character list, SOM 2: data matrix). Characters 38 and 76 were modified (rationale in SOM 1). The data matrix consists of 38 operational taxonomic units with Theropoda as an outgroup. Most of the taxa were adopted from the original source. Prosauropoda was split into *Plateosaurus* (Galton 1984) and *Thecodontosaurus* (Benton et al. 2000) because well-preserved braincases are known for these taxa. *Mamenchisaurus* was re-coded as *Mamenchisaurus youngi* (Ouyang and Ye 2002). Codings for *Euhelopus* (Wilson and Upchurch 2009), *Nemegtosaurus* (Wilson 2005), *Nigersaurus* (Sereno et al. 2007), *Rapetosaurus* (Curry-Rogers and Forster 2004), and *Suuwassea* (Harris 2006a; Whitlock and Harris 2010) were revised, and five new taxa were introduced: *Atlasaurus* (Monbaron et al. 1999; Upchurch et al. 2004), *Lirainosaurus* (Sanz et al. 1999; Díaz et al. 2011), *Nebulasaurus, Spinophorosaurus* (Remes et al. 2009; Knoll et al. 2012), *Turiasaurus* (Royo-Torres et al. 2006; Royo-Torres and Upchurch 2012), and *Yuanmousaurus* (Lü et al. 2006). All multistate characters were treated as unordered. The maximum parsimony analysis was conducted by PAUP b.4.01 (Swofford 2002) with multiple TBR+TBR search strategy (1000 replications).

In the strict consensus of 108 most parsimonious trees (tree length = 996; consistency index = 0.430; retention index = 0.644; rescaled consistency index = 0.277), *Nebulasaurus* is recovered as sister to *Spinophorosaurus* outside the Neosauropoda, but well within the Eusauropoda (Fig. 5). The sister-group relationship between *Nebulasaurus* and *Spinophorosaurus* is supported by four unambiguous character changes (characters 28, 33, 333, 342, 344): frontal-parietal suture anterior to supratemporal fenestra (28); postparietal foramen present (33); foramen magnum wider transversely than tall vertically (333); incipient crista interfenestralis (342); and craniopharyngeal foramen forming a notch between basal tubera (344). Placement of *Nebulasaurus* as sister to any of non-neosauropod branches requires more than five extra character changes.

The consensus tree differs from other recent phylogenetic trees of sauropods (Harris 2006b; Royo-Torres et al. 2006; Remes et al. 2009; Läng and Mahammed 2010; Nair and Salisbury 2012; Royo-Torres and Upchurch 2012) in two important ways. First, mamenchisaurids form a clade in a relatively basal part of the eusauropod branch toward the Neosauropoda. Three unambiguous symplesimorphies that pull this clade toward that position are: thoracic spinous process longer anteroposteriorly than wide transversely (character 154); preacetabular wing of ilium parallel with body axis (262); tibia wider lateromedially than anteroposteriorly (296).

Second, *Spinophorosaurus* from the Middle Jurassic of Niger is recovered as a derived eusauropod. This taxon is generally recovered outside the Eusauropoda (Remes et al. 2009; Nair and Salisbury 2012). Here, the lineage is recovered well within the Eusauropoda. The position of the *Spinophorosaurus* lineage is consistent with observations by Knoll et al. (2012) who pointed out the overall similarity of the braincase of *Spinophorosaurus* to that of the putative basal

neosauropod *Atlasaurus*. Furthermore, the posteriorly oriented basipterygoid process occurs in *Spinophorosaurus, Atlasaurus*, and another basal neosauropod *Jobaria* (Monbaron et al. 1999; Knoll et al. 2012). Knoll et al. (2012) suggested the phylogenetic significance of this character. Unfortunately, the basipterygoid process is not preserved well enough to discern orientation with confidence in *Nebulasaurus*. The orientation of the basipterygoid process is ventrolateral in *Chebsaurus, Mamenchisaurus, Omeisaurus*, and *Turiasaurus* (He et al. 1988; Tang et al. 2001; Ouyang and Ye 2002; Läng and Mahammed 2010; Royo-Torres and Upchurch 2012). Precise phylogenetic positions of these non-neosauropod sauropods and putative basal neosauropods such as *Atlasaurus, Bellusaurus*, and *Jobaria* are far from stable, and reconstruction of ancestral states is not reliable at current resolution. In the tree presented here, however, it is more parsimonious to infer that the posteriorly oriented basipterygoid processes arose twice independently in *Spinophorosaurus* and the *Atlasaurus–Jobaria* lineage (three steps) than to posit that the posteriorly oriented basipterygoid process is a symplesiomorphy for the two lineages (four steps).

Discussion

Taxonomic remarks.—Three other sauropodomorph taxa occur in the Zhanghe Formation, the type horizon for *Nebulasaurus*. None of the known specimens of these taxa has a braincase, although *Nebulasaurus* is solely diagnosed by characters in the braincase. Amongst the three sauropodomorphs, *Yunnanosaurus youngi* clearly represents a basal sauropodomorph (Lü et al. 2007) and therefore is not considered further. Compelling evidence places the two other Zhanghe sauropodomorphs—*Eomamenchisaurus yuanmouensis* (Lü et al. 2008) and *Yuanmousaurus jiangyiensis* (Lü et al. 2006)—well within the Mamenchisauridae and away from *Nebulasaurus* (Sekiya 2011; Fig. 5). Both of these taxa are represented by incomplete postcranial skeletons. *Eomamenchisaurus* is identified as a mamenchisaurid based on fusion between the 9th and 10th dorsal vertebrae, a condition unique to that clade (Lü et al 2008), and thus is not likely to represent the grade of *Spinophorosaurus* to which *Nebulasaurus* belongs. On the other hand, *Yuanmousaurus* cannot be clearly distinguished from *Eomamenchisaurus* and *Mamenchisaurus* spp. Indeed, Sekiya's (2011) phylogenetic analysis found this taxon amongst species of *Mamenchisaurus*.

Dealing with diagnostic characters of *Yuanmousaurus* listed by Lü et al. (2006) one at a time, the spinodiapophyseal fossa is present not only in *Omeisaurus* and *Yuanmousaurus*, but also in a wide variety of sauropods including *Mamenchisaurus* (Ouyang and Ye 2002; Wilson et al. 2011). Neither is it unique to *Yuanmousaurus* that the neural arch of the dorsal vertebra has three fossae: prezygapophyseal centrodiapophyseal fossa; centrodiapophyseal fossa; postzygapophyseal centrodiapophyseal fossa (Wilson et al. 2011). The narrow deltopectoral crest is hardly an informative character when it

is not quantified or compared to other taxa, and the humerus-femur length ratio of 0.72 falls in the range of a typical mamenchisaurid. For example, the holotype of *Mamenchisaurus youngi* (ZDM 0083) has the humerus-femur ratio of 0.71 (Ouyang and Ye 2002). In the data matrix for a maximum parsimony analysis, *Yuanmousaurus* scores identically with *Mamenchisaurus youngi* for all but two characters: dorsal vertebral centra are amphicoelous (characters 132, 150).

Despite the lack of overlapping materials, the present description provides unambiguous evidence against a mamenchisaurid affinity of the holotype LDRC-v.d.1 based on several characters, including the presence of the frontoparietal and postparietal openings. An alternative is to describe the braincase LDRC-v.d.1 as an unnamed eusauropod. However, this alternative provides no solution to the current taxonomy of sauropods from the Zhanghe Formation, because there is no evidence that suggests LDRC-v.d.1 is a mamenchisaurid, and because the uncertainty lies in diagnosis of the coeval mamenchisaurids *Eomamenchisaurus* and *Yuanmousaurus*. Future discovery of a well-preserved non-mamenchisaurid, non-neosauropod eusauropod specimen without a braincase from the Zhanghe Formation could create confusion with *Nebulasaurus*. However, no such specimen has been recovered yet. The solutions are: (i) careful evaluation and comparison of *Eomamenchisaurus* and *Yuanmousaurus* with each other and with other mamenchisaurids; and (ii) future discovery of a more complete material for any of the existing taxa from the Zhanghe Formation.

Biogeographical and biostratigraphic insights.—*Nebulasaurus* represents a basal grade of eusauropods previously unknown in Asia and expands the breadth of a remarkably diverse sauropodomorph fauna in the Middle Jurassic of Asia (Table 1). At this interval, the last of the Asian non-sauropod sauropodomorphs, various lineages of basal eusauropods, mamenchisaurids, and possibly basal macronarian neosauropods occurred in Asia. Many of these lineages likely coexisted. The basal sauropodomorph *Yunnanosaurus*, the *Spinophorosaurus*-grade eusauropod *Nebulasaurus*, and the mamenchisaurids *Eomamenchisaurus* and *Yuanmousaurus* all occur in the Zhanghe Formation. This highly heterogeneous sauropodomorph fauna in the Middle Jurassic of Asia preceded the mamenchisaurid dominance that followed in East Asia during the Late Jurassic.

Despite high diversity during the Middle Jurassic of Asia, mamenchisaurids dominated the sauropodomorph fauna in that continent throughout the Late Jurassic. There is no definitive record of other sauropodomorph lineages
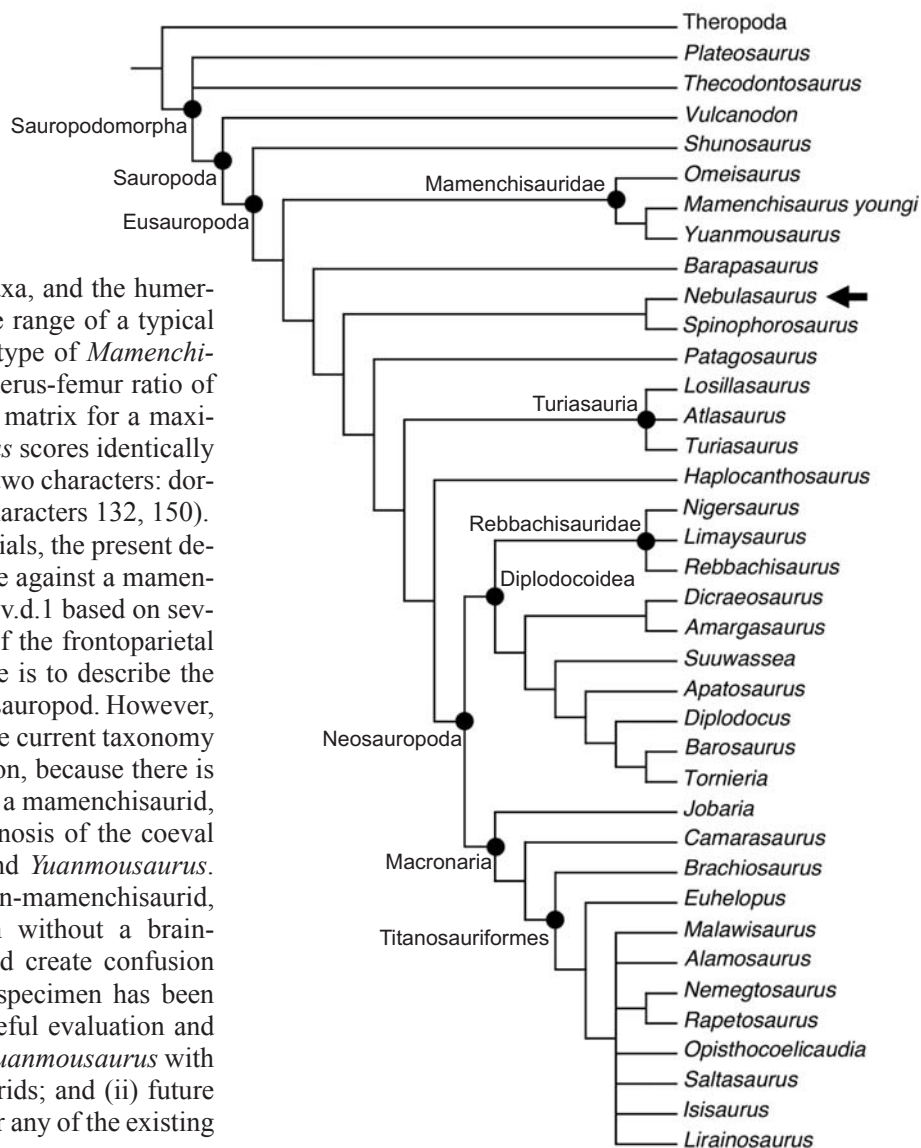

Fig. 5. Strict consensus of 108 most parsimonious trees of 38 taxa with 344 characters (tree length = 996; consistency index = 0.430; retention index = 0.644; rescaled consistency index = 0.277). An arrow points to *Nebulasaurus*. See main text for details of the analysis.

from the Late Jurassic of Asia except for a non-neosauropod eusauropod *Hudiesaurus*. In particular, neosauropods were absent. Among putative Asian diplodocoid neosauropods, *Nemegtosaurus* from the Late Cretaceous of Mongolia is a titanosaur macronarian (Upchurch 1999; Wilson 2005). The diplodocoid affinity of a caudal vertebra from the Early Cretaceous of China is now called into question (Upchurch and Mannion 2009; Whitlock et al. 2011). These studies suggest that diplodocoid neosauropods never existed in Asia. As for macronarian neosauropods, *Daanosaurus* was previously posited as a brachiosaurid, but this taxon was primarily compared to the Middle Jurassic putative basal macronarian *Bellusaurus* because of their overall similarity in body size (Ye et al. 2005). The authors did not find in *Daanosaurus* any characters diagnostic of brachiosaurids, and its systematic

Table 1. Chronological distribution of sauropods from the Early Jurassic to Early Cretaceous of East Asia. The table only lists valid taxa from China with two exceptions (*): *Ferganasaurus* from the Balabansai Formation of Kyrgyzstan (Alifanov and Averianov 2003); *Mamenchisaurus* sp. from the Phu Kradon Formation of Thailand that is uncertain of chronological age between Late Jurassic and Early Cretaceous (Suteethorn et al. 2012). The taxonomic status is uncertain (**): *Eomamenchisaurus*, *Yuanmousaurus*, and *Daanosaurus* (possibly not represents a macronarian neosauropod; Ye et al. 2005). Rationale for these assessments in Discussion. Genera under the same group are arranged alphabetically within that category. Sources cited in text, except for Lü et al. (2013). Note added in proof: this table has been revised with new information in Xing et al. (in press).

Early Jurassic	Late Jurassic
Sauropodomorpha	Sauropodomorpha
Chuxiongosaurus lufengensis	Eusauropoda
Jingshanosaurus xinwaensis	*Hudiesaurus sinojapanorum*
Lufengosaurus huenei	Mamenchisauridae
Xixiposaurus suni	*Mamenchisaurus anyuensis*
Yimenosaurus youngi	*Mamenchisaurus constructus*
Yunnanosaurus huangi	*Mamenchisaurus hochuanensis*
Yunnanosaurus robustus	*Mamenchisaurus jingyanensis*
Sauropoda	*Mamenchisaurus youngi*
Chinshakiangosaurus chunghoensis	*Mamenchisaurus* sp.*
Gongxianosaurus shibeiensis	Eusauropoda incertae sedis
Mamenchisauridae	*Daanosaurus zhangi***
Tonganosaurus hei	
Middle Jurassic	Early Cretaceous
Sauropodomorpha	Sauropodomorpha
Yunnanosaurus youngi	Neosauropoda
Eusauropoda	Macronaria
Chuanjiesaurus anaensis	Titanosauriformes
Datousaurus bashanensis	*Chiayusaurus lacustris*
Nebulasaurus taito (this study)	*Daxiatitan binglingi*
Shunosaurus lii	*Dongbeititan dongi*
Mamenchisauridae	*Erketu ellisoni*
*Eomamenchisaurus yuanmouensis***	*Euhelopus zdanskyi*
Mamenchisaurus sinocanadorum	*Fukuititan nipponensis*
Mamenchisaurus fuxiensis	*Fusuisaurus zhaoi*
Omeisaurus jiaoi	*Gobititan shenzhouensis*
Omeisaurus junghsiensis	*Huanghetitan liujiaxiaensis*
Omeisaurus tianfuensis	*Jiangshanosaurus lixianensis*
?*Yuanmousaurus jiangyiensis***	*Jiutaisaurus xidiensis*
Neosauropoda	*Liubangosaurus hei*
*Ferganasaurus verzilini**	*Mongolosaurus haplodon*
Macronaria	*Phuwiangosaurus sirindhornae*
Abrosaurus dongpoi	*Pukyongosaurus millenniumi*
Bellusaurus sui	*Qiaowanlong kangxii*
Eusauropoda incertae sedis	*Tangvayosaurus hoffeti*
Klamelisaurus gobiensis	*Yunmenglong ruyangensis*

position is uncertain. Therefore, the data currently available suggest that neosauropods and non-mamenchisaurid basal eusauropod lineages went extinct by the Middle–Late Jurassic boundary, and *Hudiesaurus* and mamenchisaurids formed an endemic megaherbivorous fauna in Asia.

Mamenchisaurids were replaced by titanosauriforms across the Jurassic–Cretaceous boundary. By this point, non-neosauropod eusauropods likely went extinct in Asia, with the possible exception of a mamenchisaurid from the Late Jurassic–Early Cretaceous of Thailand (Suteethorn et al. 2013). The appearance of titanosauriforms in the Cretaceous of Asia results from multiple invasion events, and no macronarian ghost lineages are identified in Asia through the Late Jurassic. This is because: (i) the Cretaceous sauropods from Asia previously classified as branchiosaurids or diplodocoids are now resolved as titanosauriforms that fall into a variety of independent lineages (Wilson 2005; Wilson and Upchurch 2009; Ksepka and Norell 2010; Whitlock et al. 2011); (ii) their sister taxa occur in distant continents (e.g., sister taxa of *Euhelopus*, *Nemegtosaurus*, and *Opisthocoelicaudia* in Fig. 5); and (iii) the possible basal macronarians from the Middle Jurassic of China (*Abrosaurus* and *Bellusaurus*) represent the basal grade of macronarians outside Titanosauriformes (Ouyang 1989; Dong 1990; Upchurch et al. 2004).

Transitions in the Asian sauropodomorph fauna from the Early to Middle Jurassic and from the Middle to Late Jurassic

are more gradual than the drastic transition at the Jurassic–Cretaceous boundary. This pattern is consistent with the hypothetical geographic isolation of Asia in late Middle to Late Jurassic times and its reconnection with the rest of Laurasia in Early Cretaceous times (Russell 1993), and also appears to follow the global trend of extinction of non-neosauropods, basal macronarians, and diplodocids (Mannion et al. 2011). With the Asian record alone, the Early–Middle Jurassic transition may be interpreted as a case of gradual, competitive sorting of linages with intercontinental exchange of the faunal members, because eusauropod lineages in the Middle Jurassic of Asia each have sister taxa or closely related lineages that occur outside Asia (e.g., *Nebulasaurus* and *Spinophorosaurus*).

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