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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 for 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.

Key words: Sauropoda, Eusauropoda, Jurassic, China.

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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 led to 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.

Anatomical abbreviations.—bt, basal tuber; ca, crista antotica; cp, crista prootica; cpf, craniopharyngeal foramen; ec, endocranial cavity; eo, exoccipital; f, frontal; fm, foramen magnum; fo, fenestra ovalis; fpf, frontoparietal fenestra; jf, jugular foramen (external foramen for CN IX-XI); ls, laterosphenoid; oc, occipital condyle; pa, parietal; pol, postorbital-laterosphenoid contact; pop, posterolateral wing of parietal; ppf, postparietal foramen; ptf, posttemporal foramen; so, supraoccipital; stf, supratemporal fenestra; III, foramen for oculomotor nerve (CN III); IV, foramen for trochlear nerve (CN IV); V, foramen for trigeminal nerve (CN V); VI, foramen for abducens nerve (CN VI); VII, foramen for facial nerve (CN VII); XII, foramen for hypoglossal nerve (CN XII).

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

Nebulasaurus gen. nov.

Type species.—*Nebulasaurus taito*, sp. nov.

Etymology.—*Nebulae*, misty cloud (Latin), after the alpine province of Yunnan (=southern cloudy province, Chinese); *sauros*, lizard (Greek).

Diagnosis.—As for the type and only species.

Nebulasaurus taito gen. et. 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 and 3A, B).

Horizon and locality.—The holotype was collected from the Zhanghe Formation, lower Middle Jurassic, Aalenian/Bajocian (Bureau of Geology and Mineral Resources of Yunnan Province 1990). The locality is near Xiabanjing, Jiangyi Rural Area, Yuanmou County of Yunnan Province, China (Fig. 1B).

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 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 and 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 degrees, 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 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 degrees) 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 *Limaysauris* (Calvo and Salgado 1995). Individual variations of this character exists 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 character. Nevertheless, it is significant that these openings are consistently absent in all mamenchisaurids with reasonably preserved skull roofs (Fig. 4B, C; He et al. 1988; Ouyang and Ye 2002; Xing et al. in review). 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 left 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 V₁) extends anteriorly, whereas the maxillary and mandibular branches (CN V₂₊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 V₁ (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 V₁ 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 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, 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 unpaired 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 basiptyergoid process (Knoll et al. 2012).

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/appXX-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* (Serenio et al. 2007), *Rapetosaurus* (Curry-Rogers and Forster 2004), and *Suuwassea* (Harris 2006a) 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 (1,000 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 stem 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 basiptyergoid 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 basiptyergoid process is not preserved well enough to discern orientation with confidence in *Nebulasaurus*. The orientation of the basiptyergoid process is ventrolateral in *Chebsaurus*, *Mamenchisaurus*, *Omeisaurus*, and *Turiasaurus* (He et al. 1988; Tang et al. 2001; Läng and Mahammed 2010; Ouyang and Ye 2002; 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 basiptyergoid processes arose twice independently in *Spinophorosaurus* and the *Atlasaurus*-*Jobaria* lineage (three steps) than to posit

that the posteriorly oriented basiptyergoid 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: a) careful evaluation and comparison of *Eomamenchisaurus* and *Yuanmousaurus* with each other and with other mamenchisaurids; and b) 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 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 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. 2012). 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: (1) 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); (2) their sister taxa occur in distant continents (e.g. sister taxa of *Euhelopus*, *Nemegtosaurus*, and *Opisthocoelicaudia* in Fig. 5); and (3) 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 lineages 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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References

Alifanov, V.R., and Averianov, A.O. 2003. *Ferganasaurus verzilini* gen. et sp. nov., a new neosauropod (Dinosauria, Saurischia, Sauropoda) from the Middle Jurassic of Fergana Valley, Kirghizia. *Journal of Vertebrate Paleontology* 23: 358-372.

[http://dx.doi.org/10.1671/0272-4634\(2003\)023\[0358:FVGESN\]2.0.CO;2](http://dx.doi.org/10.1671/0272-4634(2003)023[0358:FVGESN]2.0.CO;2)

Allain, R., and Anquesbi, N. 2008. Anatomy and phylogenetic relationships of *Tazoundasaurus naimi* (Dinosauria, Sauropoda) from the late Early Jurassic of Morocco. *Geodiversitas* 30: 345-424.

Allain, R., Anquesbi, N., Dejax, J., Meyer, C., Monbaron, M., Montenat, C., Richir, P., Rochdy, M., Russell, D., and Taquet, P. 2004. A basal sauropod dinosaur from the Early Jurassic of Morocco. *Comptes Rendus Palevol* 3: 199-208.

<http://dx.doi.org/10.1016/j.crpv.2004.03.001>

Balanoff, A.M., Bever, G.S., and Ikejiri, T. 2010. The braincase of *Apatosaurus* (Dinosauria: Sauropoda) based on computed tomography of a new specimen with comments on variation and evolution in sauropod neuroanatomy. *American Museum Novitates* 3677: 1-29.

<http://dx.doi.org/10.1206/591.1>

Barrett, P.M., and Upchurch, P. 2005. Sauropodomorph diversity through time: possible macroevolutionary and palaeoecological implications. In: K.A. Curry-Rogers and J.A. Wilson (eds.), *Sauropod Evolution and Paleobiology*, 125-156. University of California Press, Berkeley.

Benton, M.J., Lars, J., Storrs, G.W., and Galton, P.M. 2000. Anatomy and systematics of the prosauropod *Thecodontosaurus antiquus* from the Upper Triassic of southwest England. *Journal of Vertebrate Paleontology* 20: 77-108.

[http://dx.doi.org/10.1671/0272-4634\(2000\)020\[0077:AASOTP\]2.0.CO;2](http://dx.doi.org/10.1671/0272-4634(2000)020[0077:AASOTP]2.0.CO;2)

Berman, D.S., and McIntosh, J.S. 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Bulletin of the Carnegie Museum of Natural History* 8: 1-35.

Calvo, J.O., and Kellner, A.W. 2006. Description of a sauropod dinosaur braincase (Titanosauridae) from the Late Cretaceous Riocolorado Subgroup, Patagonia. *Anais da Academia Brasileira de Ciências* 78: 175-182.

<http://dx.doi.org/10.1590/S0001-37652006000100015>

PMid:16532215

Calvo, J.O., and Salgado, L. 1995. *Rebbachisaurus tessonei* sp. nov. A new sauropoda from Albian-Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. *Gaia* 11: 13-33.

Chatterjee, S., and Zheng, Z. 2002. Cranial anatomy of *Shunosaurus*, a basal sauropod dinosaur from the Middle Jurassic of China. *Zoological Journal of the Linnean Society* 136: 145-169.

<http://dx.doi.org/10.1046/j.1096-3642.2002.00037.x>

Chatterjee, S., and Zheng, Z. 2004. Neuroanatomy and dentition of *Camarasaurus lentus*. In: V. Tidwell and K. Carpenter (eds.), *Thunder-lizards: the sauropodomorph dinosaurs*, 199-211.

Indiana University Press, Bloomington.

Curry Rogers, K., and Forster, C.A. 2004. The skull of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 24: 121-144.

<http://dx.doi.org/10.1671/A1109-10>

Díaz, V.D., Suberbiola, X.P., and Sanz, J.L. 2011. Braincase anatomy of titanosaurian sauropod *Lirainosaurus astibiae* from the Late Cretaceous of Iberian. *Acta Palaeontologica Polonica* 56: 521-533.

<http://dx.doi.org/10.4202/app.2010.0043>

Dong, Z. 1990. [On remains of the sauropods from Kelamali region, Junggar basin, Xinjiang, China.] *Vertebrate Palaeontologica* 23: 43-58. [In Chinese with English summary]

Galton, P.M. 1984. Cranial anatomy of the prosauropod dinosaur *Plateosaurus* from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. *Geologica et Palaeontologica* 18: 139-171.

Garcia, R.A., Paulina Carabajal, A., and Salgado, L. 2008. A new titanosaurian braincase from the Allen Formation (Campanian-Maastrichtian), Río Negro Province, Patagonia, Argentina. *Geobios* 41: 625-633.

<http://dx.doi.org/10.1016/j.geobios.2007.11.005>

Harris, J.D. 2006a. Cranial osteology of *Suuwassea emilieae* (Sauropoda: Diplodocoidea: Flagellicaudata) from the Upper Jurassic Morrison Formation of Montana, USA. *Journal of Vertebrate Paleontology* 26: 88-102

[http://dx.doi.org/10.1671/0272-4634\(2006\)26\[88:COOSES\]2.0.CO;2](http://dx.doi.org/10.1671/0272-4634(2006)26[88:COOSES]2.0.CO;2)

Harris, J.D. 2006b. The significance of *Suuwassea emiliae* (Dinosauria: Sauropoda) for flagellicaudatan interrelationships and evolution. *Journal of Systematic Paleontology* 4: 185-198.

<http://dx.doi.org/10.1017/S1477201906001805>

He, X.-L., Li, C., and Cai, K.-J. 1988. [The Middle Jurassic Dinosaur Fauna from Dashampu, Zigong, Sichuan: Sauropod Dinosaurs. Vol. 4, *Omeisaurus tianfuensis*]. Sichuan Publishing House of Science and Technology, Chengdu. 143 pp. (In Chinese with English summary)

Janensch, W. 1935. Die Schädel der Sauropoden *Brachiosaurus*, *Barosaurus* und *Dicraeosaurus* aus den Tendaguru-Schichten Deutsch-Ostafrikas. *Palaeontographica*, Supplement 7: 147–298.

Knoll, F., Witmer, L.M., Ortega, F., Ridgely, R.C., and Schwarz-Wings, D. 2012. The braincase of the basal sauropod dinosaur *Spinophorosaurus* and 3D reconstructions of the cranial endocast and inner ear. *PLoS ONE* 7(1): e30060.

<http://dx.doi.org/10.1371/journal.pone.0030060>

PMid:22272273 PMCID:3260197

Ksepka, D.T., and Norell, M.A. 2010. The illusory evidence for Asian *Brachiosauridae*: new material of *Erketu ellisoni* and a phylogenetic reappraisal of basal titanosauriformes. *American Museum Novitates* 3700: 1-17.

<http://dx.doi.org/10.1206/3700.2>

Läng, E., and Mahammed, F. 2010. New anatomical data and phylogenetic relationship of *Chebsaurus algeriensis* (Dinosauria, Sauropoda) from the Middle Jurassic of Algeria. *Historical Biology* 22: 142-164.

<http://dx.doi.org/10.1080/08912960903515570>

Lü, J., Li, T., Ji, Q., Wang, G., Zhang, J., and Dong, Z. 2006. New eusauropod dinosaur from Yuanmou of Yunnan Province. *Acta Geologica Sinica* 80: 1-10.

<http://dx.doi.org/10.1111/j.1755-6724.2006.tb00788.x>

Lü, J., Li, T., Zhong, S., Azuma, Y., Fujita, M., Dong, Z., and Ji, Q. 2007. New yunnanosaurid dinosaur (Dinosauria, Prosauropoda) from the Middle Jurassic Zhanghe Formation of Yuanmou, Yunnan Province of China. *Memoir of Fukui Prefectural Dinosaur Museum* 6: 1-15.

Lü, J., Li, T., Zhong, S., Ji, Q., and Li, S. 2008. A new mamenchisaurid dinosaur from the Middle Jurassic of Yuanmou, Yunnan Province, China. *Acta Geologica Sinica* 82: 17-26.

Mannion, P.D., Upchurch, P., Carrano, M.T., and Barrett, P.M. 2011. Testing the effect of the rock record on diversity: a multidisciplinary approach to elucidating the generic richness of sauropodomorph dinosaurs through time. *Biological Reviews* 86: 157-181.

<http://dx.doi.org/10.1111/j.1469-185X.2010.00139.x>

PMid:20412186

Monbaron, M., Russell, D.A., and Taquet, P. 1999. *Atlasaurus imerakei* n.g., n.sp., a brachiosaurid-like sauropod from the Middle Jurassic of Morocco. *Comptes rendus de l'Académie des Sciences de la Terre et des Planètes* 329: 519-526.

Nair, J.P., and Salisbury, S.W. 2012. New anatomical information on *Rhoetosaurus brownie* Longman, 1926, a gravisaurian sauropodomorph dinosaur from the Middle Jurassic of Queensland, Australia. *Journal of Vertebrate Paleontology* 32: 369-394.

<http://dx.doi.org/10.1080/02724634.2012.622324>

Osborn, H.F., and Mook, C.C. 1921. *Camarasaurus*, *Amphicoelias*, and other sauropods of Cope. *Memoir of American Museum of Natural History* 3: 249-386.

Ouyang, H. 1989. [A new sauropod dinosaur from Dashanpu, Zigong County, Sichuan Province (*Abrosaurus dongpoensis* gen. et sp. nov.)]. *Newsletter of Zigong Dinosaur Museum* 2: 10-14. (In Chinese)

Ouyang, H., and Ye, Y. 2002. The first mamenchisaurian skeleton with complete skull *Mamenchisaurus youngi*. Sichuan Science and Technology Press, Chengdu. 111 pp.

Paulina Carabajal, A. 2012. Neuroanatomy of titanosaurid dinosaurs from the Upper Cretaceous

of Patagonia, with comments on endocranial variability within Sauropoda. *Anatomical Record*.

Published online ahead of print. DOI: 10.1002/ar.22572

<http://dx.doi.org/10.1002/ar.22572>

Paulina Carabajal, A., and Salgado, L. 2007. Un basicráneo de titanosaurio (Dinosauria, Sauropoda) del Cretácico Superior del norte de Patagonia: descripción y aportes al conocimiento del oído interno de los dinosaurios. *Ameghiniana* 44:109-120.

Paulina Carabajal, A., Coria, R.A., and Chiappe, L.M. 2008. An incomplete Upper Cretaceous titanosaur (Sauropoda) braincase: new insights on the dinosaurian inner ear and endocranium. *Cretaceous Research* 29: 643-648.

<http://dx.doi.org/10.1016/j.cretres.2008.01.011>

Remes, K. 2006. Revision of the Tendaguru sauropod dinosaur *Tornieria Africana* (Fraas) and its relevance for sauropod paleobiogeography. *Journal of Vertebrate Paleontology* 26: 651-669.

[http://dx.doi.org/10.1671/0272-4634\(2006\)26\[651:ROTTSD\]2.0.CO;2](http://dx.doi.org/10.1671/0272-4634(2006)26[651:ROTTSD]2.0.CO;2)

Remes, K, Ortega, F., Fierro, I., Joger, U., Kosma, R., Marin Ferrer, J.M., Project Paldes, Project SNHM, Ide, O.A., and Maga, A. 2009. A new basal sauropod dinosaur from the Middle Jurassic of Niger and the early evolution of Sauropoda. *PLoS One* 4:e6924.

<http://dx.doi.org/10.1371/journal.pone.0006924>

PMid:19756139 PMCID:2737122

Royo-Torres, R., and Upchurch, P. 2012. The cranial anatomy of the sauropod *Turiasaurus riodevensis* and implications for its phylogenetic relationships. *Journal of Systematic Palaeontology* 10: 553-583.

<http://dx.doi.org/10.1080/14772019.2011.598577>

Russell, D.A. 1993. The role of Central Asia in dinosaur biogeography. *Canadian Journal of Earth Sciences* 30: 2002-2012.

<http://dx.doi.org/10.1139/e93-176>

Salgado, L., and Calvo, J.O. 1992. Cranial osteology of *Amargasaurus cazau* Salgado and Bonaparte (Sauropoda, Dicraosauridae) from the Neocomian of Patagonia. *Ameghiniana* 29:337-346.

Suteethorn, S., Le Loeuff, J., Buffetaut, E., Suteethorn, V., and Wongko, K. In press. First evidence of a mamenchisaurid dinosaur from the Late Jurassic/Early Cretaceous Phu Kradung Formation of Thailand. *Acta Palaeontologica Polonica*.

Tidwell, V., and Carpenter, K. 2003 Braincase of an Early Cretaceous titanosauriform sauropod from Texas. *Journal of Vertebrate Paleontology* 23: 176-180.

[http://dx.doi.org/10.1671/0272-4634\(2003\)23\[176:BOAECT\]2.0.CO;2](http://dx.doi.org/10.1671/0272-4634(2003)23[176:BOAECT]2.0.CO;2)

Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society London, Series B* 349: 365-390.

<http://dx.doi.org/10.1098/rstb.1995.0125>

Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* 124: 43-103.

<http://dx.doi.org/10.1111/j.1096-3642.1998.tb00569.x>

Upchurch, P. 1999. The phylogenetic relationships of the Nemegtosauridae (Saurischia, Sauropoda). *Journal of Vertebrate Paleontology* 19: 106-125.

<http://dx.doi.org/10.1080/02724634.1999.10011127>

Upchurch, P., and Barrett, P.M. 2005. Phylogenetic and taxic perspectives on sauropod diversity. In: K.A. Curry-Rogers and J.A. Wilson (eds.), *Sauropod Evolution and Paleobiology*, 104-124. University of California Press, Berkeley.

Upchurch, P., and Mannion, P.D. 2009. The first diplodocid from Asia and its implications for the evolutionary history of sauropod dinosaurs. *Palaeontology* 52:1195-1207

<http://dx.doi.org/10.1111/j.1475-4983.2009.00909.x>

Upchurch, P., Barrett, P.M., and Dodson, P. 2004. Sauropoda. In: D. B. Weishampel, H. Osmólska, and P. Dodson (eds.), *The Dinosauria* (2nd edition), 259-322. University of California

Press, Berkeley.

<http://dx.doi.org/10.1525/california/9780520242098.003.0015>

White, T.E. 1958. The braincase of *Camarasaurus lentus* (Marsh). *Journal of Paleontology* 32: 477-494.

Whitlock, J.A., and Harris, J.D. 2010. The dentary of *Suuwassea emiliae* (Sauropoda: Diplodocoidea). *Journal of Vertebrate Paleontology* 30:1637-1641.

<http://dx.doi.org/10.1080/02724634.2010.501452>

Whitlock, J.A., D'Emic, M.D., and Wilson, J.A. 2011. Cretaceous diplodocids in Asia? Re-evaluating the phylogenetic affinities of a fragmentary specimen. *Palaeontology* 54:351-364.

<http://dx.doi.org/10.1111/j.1475-4983.2010.01029.x>

Wilson, J.A. 2002. Sauropod dinosaur phylogeny: critique and cladistics analysis. *Zoological Journal of the Linnean Society* 136:217-276.

<http://dx.doi.org/10.1046/j.1096-3642.2002.00029.x>

Wilson, J.A. 2005. Redescription of the Mongolian sauropod *Nemegtosaurus mongoliensis* Nowinski (Dinosauria: Saurischia) and comments on Late Cretaceous sauropod diversity.

Journal of Systematic Palaeontology 3:283-318.

<http://dx.doi.org/10.1017/S1477201905001628>

Wilson, J.A., and Sereno, P.C. 1998. Early evolution and higher-level taxonomy of sauropod dinosaurs. *Memoir of the Society of Vertebrate Paleontology* 5: 1-68.

<http://dx.doi.org/10.2307/3889325>

Wilson, J.A., and Upchurch, P. 2009. Redescription and reassessment of the phylogenetic affinities of *Euhelopus zdanskyi* (Dinosauria: Sauropoda) from the Early Cretaceous of China. *Journal of Systematic Palaeontology* 7: 199-239.

<http://dx.doi.org/10.1017/S1477201908002691>

Witmer, L.M., Ridgely, R.C., Dufeu, D.L., and Semones, M.C. 2008. Using CT to peer into the past: 3D visualization of the brain and ear regions of birds, crocodiles, and nonavian dinosaurs. In: H. Endo and R. Frey (eds.), *Anatomical Imaging: towards a new morphology*, 67-87. Springer.

Ye, Y., Gao, Y.-H., and Jiang, S. 2005. A new genus of sauropod from Zigong, Sichuan. *Vertebrata Palasiatica* 43: 175-181.

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 Kirghystan (Alifanov and Averianov 2003); *Mamenchisaurus* sp. (§) from the Phu Kraton Formation of Thailand that is uncertain of chronological age between Late Jurassic and Early Cretaceous times (Suteethorn et al. 2012). The taxonomic status of *Eomamenchisaurus* (*) and *Yuanmousaurus* (*) is uncertain. Similarly, there is a question whether or not *Daanosaurus* (§) represents a macronarian neosauropod (Ye et al. 2005). Rationale for these assessments in Discussion. Genera under a same group are arranged alphabetically within that category. Sources cited in text, except for Lü et al. (2013).

1 TABLE 1.

Early Jurassic	Middle Jurassic
Sauropodomorpha	Sauropodomorpha
<i>Chuxiongosaurus lufengensis</i>	<i>Yunnanosaurus youngi</i>
<i>Jingshanosaurus xinwaensis</i>	Eusauropoda
<i>Lufengosaurus huenei</i>	<i>Chuanjiesaurus anaensis</i>
<i>Xixiposaurus suni</i>	<i>Datousaurus bashanensis</i>
<i>Yimenosaurus youngi</i>	<i>Nebulasaurus taito</i> (this study)
<i>Yunnanosaurus huangi</i>	<i>Shunosaurus lii</i>
<i>Yunnanosaurus robustus</i>	Mamenchisauridae
Sauropoda	<i>Eomamenchisaurus yuanmouensis</i> *
<i>Chinshakiangosaurus chungoensis</i>	<i>Mamenchisaurus sinocanadorum</i>
<i>Gongxianosaurus shibeiensis</i>	<i>Mamenchisaurus fuxiensis</i>
Mamenchisauridae	<i>Omeisaurus jiaoi</i>
<i>Tonganosaurus hei</i>	<i>Omeisaurus junghsiensis</i>
	<i>Omeisaurus tianfuensis</i>
	? <i>Yuanmousaurus jiangyiensis</i> *
	Neosauropoda
	<i>Ferganasaurus verzilini</i> **
	Macronaria
	<i>Abrosaurus dongpoi</i>
	<i>Bellusaurus sui</i>
	Eusauropoda <i>incertae sedis</i>
	<i>Klamelisaurus gobiensis</i>

2

3

4 TABLE 1. (cont.)

Late Jurassic	Early Cretaceous
Sauropodomorpha	Sauropodomorpha
Eusauropoda	Neosauropoda
<i>Hudiesaurus sinojapanorum</i>	Macronaria
Mamenchisauridae	Titanosauriformes
<i>Mamenchisaurus anyuensis</i>	<i>Chiayusaurus lacustris</i>
<i>Mamenchisaurus constructus</i>	<i>Daxiatitan binglingi</i>
<i>Mamenchisaurus hochuanensis</i>	<i>Dongbeititan dongi</i>
<i>Mamenchisaurus jingyanensis</i>	<i>Erketu ellisoni</i>
<i>Mamenchisaurus youngi</i>	<i>Euhelopus zdanskyi</i>
<i>Mamenchisaurus</i> sp.§	<i>Fukuititan nipponensis</i>
Eusauropoda incertae sedis	<i>Fusuisaurus zhaoi</i>
<i>Daanosaurus zhangii</i> ¶	<i>Gobititan shenzhouensis</i>
	<i>Huanghetitan liujiaxiaensis</i>
	<i>Jiangshanosaurus lixianensis</i>
	<i>Jiutaisaurus xidiensis</i>
	<i>Liubangosaurus hei</i>
	<i>Mongolosaurus haplodon</i>
	<i>Phuwiangosaurus sirindhornae</i>
	<i>Pukyongosaurus millenniumi</i>
	<i>Qiaowanlong kangxii</i>
	<i>Tangvayosaurus hoffeti</i>
	<i>Yunmenglong ruyangensis</i>

6 FIGURE CAPTIONS

7

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

11

12 Fig. 2. Interpretive drawings of the holotype of *Nebulasaurus* in: **A**, left lateral view; **B**, posterodorsal
13 view, approximately 45° with respect to a transverse vertical plane; **C**, dorsal view; **D**, anteroventral
14 view, approximately 45° with respect to a transverse vertical plane; and **E**, ventral view.

15

16 Fig. 3. Photographs of the holotype of *Nebulasaurus*. **A**, the braincase (holotype) in right lateral view.
17 **B**, details of the metotic region in left lateral view.

18

19 Fig. 4. Comparison of non-neosauropod eusauropod braincases illustrates general conditions against
20 unique features of the braincase of *Nebulasaurus* (e.g., frontoparietal fenestra larger than postparietal
21 foramen, supraoccipital not expanding laterally, and supraoccipital contributing little to foramen
22 magnum). **A**, *Shunosaurus lii* (ZDM 65430) in dorsal (A₁) and posterior (A₂) views (modified after
23 Chatterjee and Zheng 2002; supraoccipital was redrawn based on Zhang 1988). **B**, *Mamenchisaurus*
24 *youngi* (ZDM 83) in dorsal (B₁) and posterior (B₂) views (modified after Ouyang and Ye 2002). **C**,
25 *Omeisaurus tianfuensis* in dorsal (C₁: ZDM 5702) and posterior (C₂: ZDM 5703) views (modified after
26 He et al. 1988). **D**, *Spinophorosaurus nigerensis* (GCP-CV-4229) in dorsal (D₁) and posterior (D₂)
27 views (modified after Knoll et al. 2012). Arrow head indicates wide participation of supraoccipital in
28 the margin of foramen magnum. Asterisk (*) indicates lateral expansion of supraoccipital along
29 exoccipital-parietal contact. Scale bars all equal 5 cm.

30

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

34

A



B









