



OPEN A new mamenchisaurid from the Upper Jurassic Suining Formation of the Sichuan Basin in China and its implication on sauropod gigantism

Xuefang Wei^{1,7}✉, Yuanjun Tan², Shan Jiang^{3,4}, Jun Ding², Lei Li², Xiaobing Wang⁵, Yiyang Liu⁵, Guangbiao Wei⁶, Deliang Li⁶, Yu Liu^{3,4}, Guangzhao Peng^{3,4}, Shizhen Zhang¹ & Changling Lao⁷

The Sichuan Basin has yielded abundant sauropod dinosaurs from the Middle-Late Jurassic, and Mamenchisauridae had predominated the dinosaur faunas during the Late Jurassic in the Sichuan Basin. Here, we describe a new sauropod dinosaur, *Tongnanlong zhimingi* gen. et sp. nov. from the Upper Jurassic Suining Formation in the Sichuan Basin, southwestern China. The holotype includes three dorsal and six caudal vertebrae, scapula, coracoid, and some hindlimb bones. It is diagnosed by the complex structures of the dorsal and anterior caudal vertebrae compared to other mamenchisaurids. Phylogenetic analysis shows that it is more closely related to *Mamenchisaurus* than to *Omeisaurus*. The huge-sized scapula and coracoid also indicate that the specimen belongs to an extremely gigantic individual with a body length approaching about 25 ~ 26 m. The new specimen enriches the diversity of Mamenchisauridae and provides additional information for understanding the evolution and diversity of eusauropod dinosaurs.

Keywords Sauropoda, Mamenchisauridae, Upper Jurassic, Suining Formation, Phylogeny

Abbreviations

TNM	Tongnan Museum
ZDM	Zigong Dinosaur Museum
CQMNH	Chongqing Museum of Natural History
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences

Sauropods were gigantic, quadrupedal herbivores and the largest terrestrial dinosaurs ever existed. They appeared in the Late Triassic, achieved a global distribution by the Middle Jurassic, and finally died out at the end of the Late Cretaceous¹. More than 150 genera have been identified, including over 20 genera from the Jurassic period in China^{1–3}. The southwestern China is a key region that yields Middle-Late Jurassic sauropod dinosaurs, particularly the Sichuan Basin. The sauropod fauna from the Middle-Late Jurassic Sichuan Basin has previously been considered an endemic fauna which differs from the contemporaneous sauropod fauna from the Pangaeian terrestrial faunas. This distribution has often been interpreted by the “East Asian Isolation” hypothesis, which occurred during the Jurassic to Early Cretaceous^{1,4,5}. However, the “East Asian Isolation” hypothesis is challenged by more phylogenetic analyses and studies of neosauropod dinosaurs from China^{6,7} and mamenchisaurid dinosaurs discovered from Africa⁴ which support the idea that they were distributed globally during the Middle Jurassic.

¹Chengdu Center, China Geological Survey (Geosciences Innovation Center of Southwest China), Chengdu 610218, China. ²Tongnan District Cultural Relics Administration, Tongnan 402660, Chongqing, China. ³Research Centre of Jurassic Stratigraphy and Paleontology, Zigong Dinosaur Museum, Zigong 643010, China. ⁴Key Laboratory of Paleontology and Palaeoenvironment Coevolution (Sichuan-Chongqing Joint Construction), Zigong 643010, China. ⁵Tianyan Museum, Chongzhou 611200, China. ⁶Chongqing Institute of Paleontology, Chongqing 401120, China. ⁷Guilin University of Technology, Guilin 541006, Guangxi, China. ✉email: weixuefang1208@163.com

The sauropod fauna from the Middle Jurassic shows a different pattern compared to that from the Late Jurassic in the Sichuan Basin. Comparing to the abundant and diverse Middle Jurassic sauropods like *Shunosaurus*, *Omeisaurus*, *Datousaurus* and *Dashanpusaurus*, the Late Jurassic dinosaur fauna became simplified and was predominated by *Mamenchisaurus*^{2,8}. However, the sauropods diversity and disparity in the Late Jurassic have been gradually revised based on newly discovered sauropods fossils in recent years. Xing et al. (2015) reported a new sauropod, *Qijianglong guokr*, from the Late Jurassic Suining Formation, which is the first non-*Mamenchisaurus* sauropod dinosaur of this formation except the only reported sauropod *Mamenchisaurus anyuensis*^{9,10}.

Here we report a new sauropod dinosaur, *Tongnanlong zhimingi*, gen. et sp. nov., from the Upper Jurassic Suining Formation in the Sichuan Basin. Anatomical and phylogenetic analysis demonstrate that *Tongnanlong* is a mamenchisaurid eusauropod. This discovery increases the taxonomic diversity of mamenchisaurid and strengthens the idea that Mamenchisauridae was a non-endemic clade that radiated widely in Asia and Africa during the Middle-Late Jurassic.

Geological background

The Sichuan Basin is an important Mesozoic continental basin located in southwestern China^{11–13}. The terrestrial strata of the basin are fully exposed and widely distributed, from the bottom to top including the Upper Triassic Xujiahe Formation, the Lower Jurassic Zhenzhuchong and Ziliujing formations, the Middle Jurassic Xintiangou and the Lower Shaximiao formations, and the Upper Jurassic Upper Shaximiao, Suining and Penglaizhen formations, and the Lower Cretaceous Jiaguan Formation. Among them, the Jurassic deposits of the Sichuan Basin is famous for yielding abundant dinosaur fossils and tracks^{8,14}. Notably, the era of Suining Formation, along with the Upper Shaximiao Formation, belongs to the late Late Jurassic is controversial. Most of the sedimentology studies assigned the Suining Formation to the Upper Jurassic^{15–17} but some chemical analyses of zircon U-Pb dating indicated that it belongs to the Lower Cretaceous^{13,18}. Dinosaur and sporopollen assemblages support the Suining Formation to the Late Jurassic^{2,8,19}. Here, in this study, we use the division scheme that suggested the Suining Formation belongs to the Late Jurassic based on the features of its dinosaur fauna⁸.

In the Sichuan Basin, almost 80% of the dinosaur and non-dinosaur vertebrate fossils were unearthed from the Middle-early Upper Jurassic strata of the Lower Shaximiao and Upper Shaximiao formations^{2,8}. Dong et al. (2015) considered that the dinosaurs from the Lower Shaximiao and Upper Shaximiao formations shows different fauna assemblages and assigned them to the *Shunosaurus* Fauna and *Mamenchisaurus* Fauna, respectively². Comparatively, the Lower Jurassic Zhenzhuchong Formation only yields several sauropod tracks but no bones, while the Ziliujing Formation includes several basal sauropod morphs and theropod tracks¹⁴. The Upper Jurassic Suining Formation has yielded rare dinosaur bones and tracks, such as *Qijianglong guokr* from the Suining Formation and *M. anyuensis* materials from the top of the Suining Formation and the bottom of the Penglaizhen Formation^{9,10,14}. It is noteworthy that the layer of *Qijianglong guokr* is lower than the specimen reported in this paper based on our field work.

In 1998, the fossil specimen reported in this paper was excavated from a building site in the Tongnan District of Chongqing area together with many well-preserved, articulated post-cranial skeletal bones (Fig. 1). Our field work shows that the fossiliferous site belongs to the lower portion of the Upper Jurassic Suining Formation, overlying by the Quaternary deposits. The Suining Formation consists of purplish red mudstone and sandstone. Abundant invertebrate fossils are known from this formation, especially ostracods and stoneworts, along with some freshwater bivalves, conchostracans. A few vertebrates are also known from this formation, such as fish *Ceratodus szechuanensis*, turtle *Plesiochelys tatsuensis*, and dinosaur *Mamenchisaurus anyuensis*^{9,20–24}.

The new specimen described in this study shows a nearly in-situ burial state and thus likely experienced a very short-distant transportation before burial. Its layered deposits are characterized by purplish red sandstone with a wavy texture, indicating a lakeshore to shallow lake environment and relatively arid climate. Here, we provide a systematic description of this new specimen and discuss its implications for sauropod palaeogeography.

Results

Systematic paleontology

Saurischia²⁵.

Sauropodomorpha²⁶.

Sauropoda²⁷.

Eusauropoda²⁸.

Mamenchisauridae²⁹.

Tongnanlong zhimingi gen. et sp. nov.

Etymology. The generic name Tongnan, Chinese Pinyin, refers to the Tongnan District, where the holotype was found; the word 'long' in Chinese Pinyin for dragon. The specific name is in honor of the world-famous dinosaur scientist Mr. Dong Zhiming for his great contributions to the dinosaur research in the Sichuan Basin.

Holotype. An incomplete individual that includes three dorsal and six caudal vertebrae, left shoulder girdle (scapula and coracoid) and hindlimb elements (partial tibia, fibula, three metatarsals, and two unguals). The specimen is housed in Tongnan Museum, with the specimen number of TNM 0254.

Type locality and horizon. The building site of Dafo Street (with GPS N30°10'44", E105°48'17"), Tongnan District; Upper Jurassic, Suining Formation.

Diagnosis. A huge-bodied mamenchisaurid dinosaur with the following unique combination of characters: dorsal centra opisthocelous, camerate pneumatic structures of dorsal centra, well-developed spinopostzygapophysial lamina of dorsal vertebrae, anterior caudal centra procoelous, neural spine of anterior caudal vertebrae oriented posterodorsally, small lamina within the pleurocoels on dorsal centra, neural spine of the dorsal vertebrae and postozygapophyses forming laminae and fossae, fossa developed between the

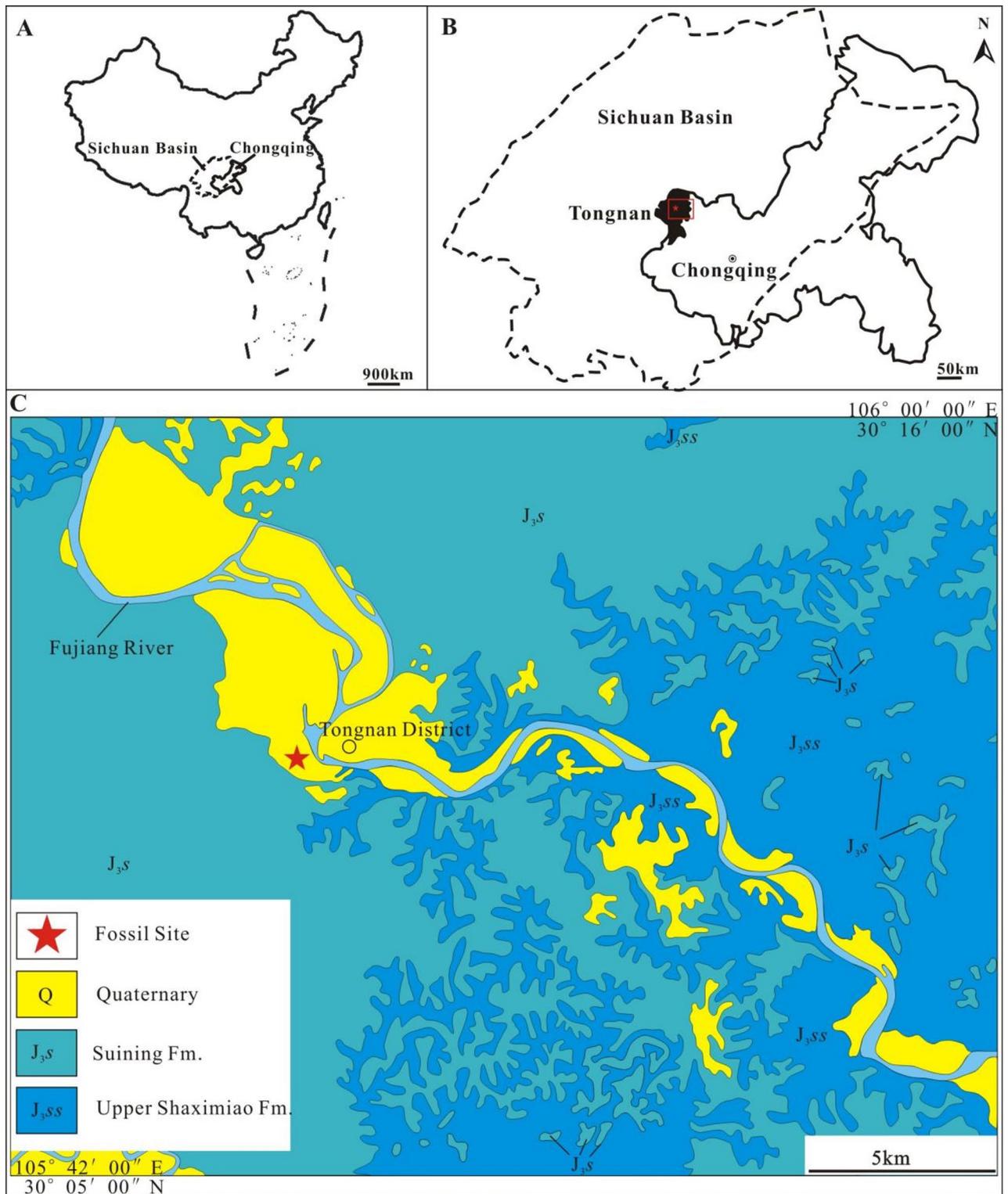


Fig. 1. Maps of the fossil locality in Tongnan District, Sichuan Basin, China. The star represents the fossil site. (A) Sketch map of China showing the geographical locations of Sichuan Basin. The base map of China is modified after the Standard Map Service of the National Administration of Surveying, Mapping and Geoinformation of China (<http://bzdt.ch.mnr.gov.cn/>) (No. GS (2016)1585); (B) Locality of Tongnan District (marked by a irregular black area); (C) Fossil site and its geological background (marked by a red rectangle in B) modified from the 1:200 000 standard map of Suining (Map No.: H-48-(16) published in 1981).

postzygapophysis and hyposphene on anterior caudal vertebra, S-shaped suture of scapula and coracoid, obtuse angle of the scapular and coracoid articular surfaces of glenoid, coracoid fossa much close to the scapular margin than to the glenoid margin, scapular acromion weakly developed and bearing no hook-like process.

Description

The specimen was excavated from a quarry, including three primarily articulated dorsal vertebrae, six caudal vertebrae, one anterior caudal neural spine, one nearly complete anterior chevron, three isolated metatarsals and two claws, complete left scapular and coracoid, one complete right fibula, proximal end of a tibia and some isolated dorsal rib fragments (Figs. 2, 3, 4 and 5, Tables S1, S2).

Dorsal vertebrae. Three dorsal vertebrae were naturally connected when being excavated but later on isolated due to improper storage. The dorsal vertebrae are medially opisthocelous. The anterior articular surface of the dorsal centrum is convex and elliptical in shape whilst the posterior articular surface is concave and pot-like in shape. The margin of the convex anterior articular surface and its dorsal centrum is clear and forms a ridge-like line. The height of each dorsal centrum is greater than its width as in other mamenchisaurids. The broken surface of the dorsal centrum shows typical grid structure and camerate of internal tissue texture (Fig. 3B3, C3), which is similar to those of the middle-posterior dorsal centra in *Mamenchisaurus youngi*³⁰. The ventral surface of the dorsal centrum bears no keel, and is transversely smooth and concave, which is similar to most sauropods like *Omeisaurus tianfuensis*, *Shunosaurus lii*, *Mamenchisaurus youngi*, and *Analong chuanjieensis*^{9,30–32}. The pleurocoel of the dorsal centrum is oval and located much anterodorsally. The pleurocoel of the dorsal centrum bears strong ventral margin, but its dorsal margin flushes into a lateral surface, which is similar to those of the middle dorsal centra in *Mamenchisaurus youngi* (ZDM 0083), but different from those clearly whole pleurocoel margin in *Omeisaurus tianfuensis* (ZDM 5002)^{9,30}. Moreover, the pleurocoel develops a further deep excavation which is divided by the vertically orientated internal laminae. But in other eusauropod dinosaurs like *Mamenchisaurus youngi* (ZDM 0083), *Shunosaurus lii* (ZDM 5008) and *Omeisaurus tianfuensis* (ZDM 5002), the laminae in the pleurocoel of the dorsal centra are absent^{8,30}. The neural arches of the dorsal vertebrae were artificially destroyed after excavation. Their neural spines are relatively positioned backward, and each extends nearly to the posterior end of its centrum. The dorsal neural spine is oriented vertically and slightly posterodorsally. The postzygapophyseal surface is relatively small and its lamina is less developed (Fig. 3D). In lateral view, the spinopostzygapophyseal lamina of the neural spine is thin and well developed. The prezygapophyses are lean and form an acute angle of about 60°, but the postzygapophyses are nearly horizontal. The head of the dorsal neural spine is coarse and weakly bifurcated. In posterior view, the coarse spinal ridge extends vertically along the midline and becomes bifurcated toward the base of the neural spine and further forms a clearly vertically oriented rhombic spinopostzygapophysial fossa (i.e. cen. sp-poz. f) (Fig. 3D1). Moreover, the base of the neural spine and the postogapophyses also form four lateral spinopostzygapophysial fossae which are divided by small laminae (i.e. med. sp-poz. f and lat. sp-poz. f) (Fig. 3D1). These fossae are symmetrically distributed on bilateral

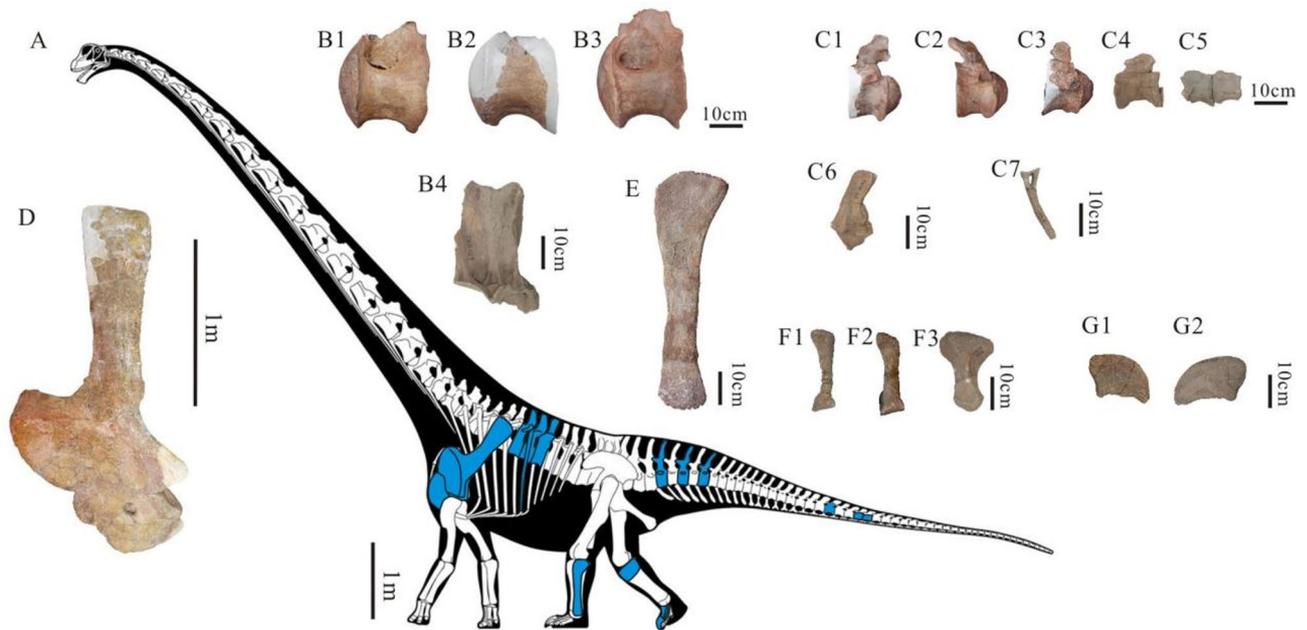


Fig. 2. Fossil remains of *Tongnanlong zhimingi* (TNM 0254). (A) Skeletal outlines showing recovered elements in blue color. The skeletal reconstruction is the proportional scaling of *Mamenchisaurus youngi* with copyright Scott Hartman (2022) (<https://www.skeletaldrawing.com/sauropods-and-kin>); (B1–B3) Dorsal vertebrae in lateral view; (B4) dorsal neural spine in posterior view; (C1–C5) Caudal vertebrae in lateral view; (C6) caudal neural spine in lateral view; (C7) chevron in lateral-posterior view; (D) Scapula and coracoid in lateral view; (E) Fibula in anterior view; (F1–F3) Metatarsals in dorsal view; (G1, G2) Claws in lateral view.

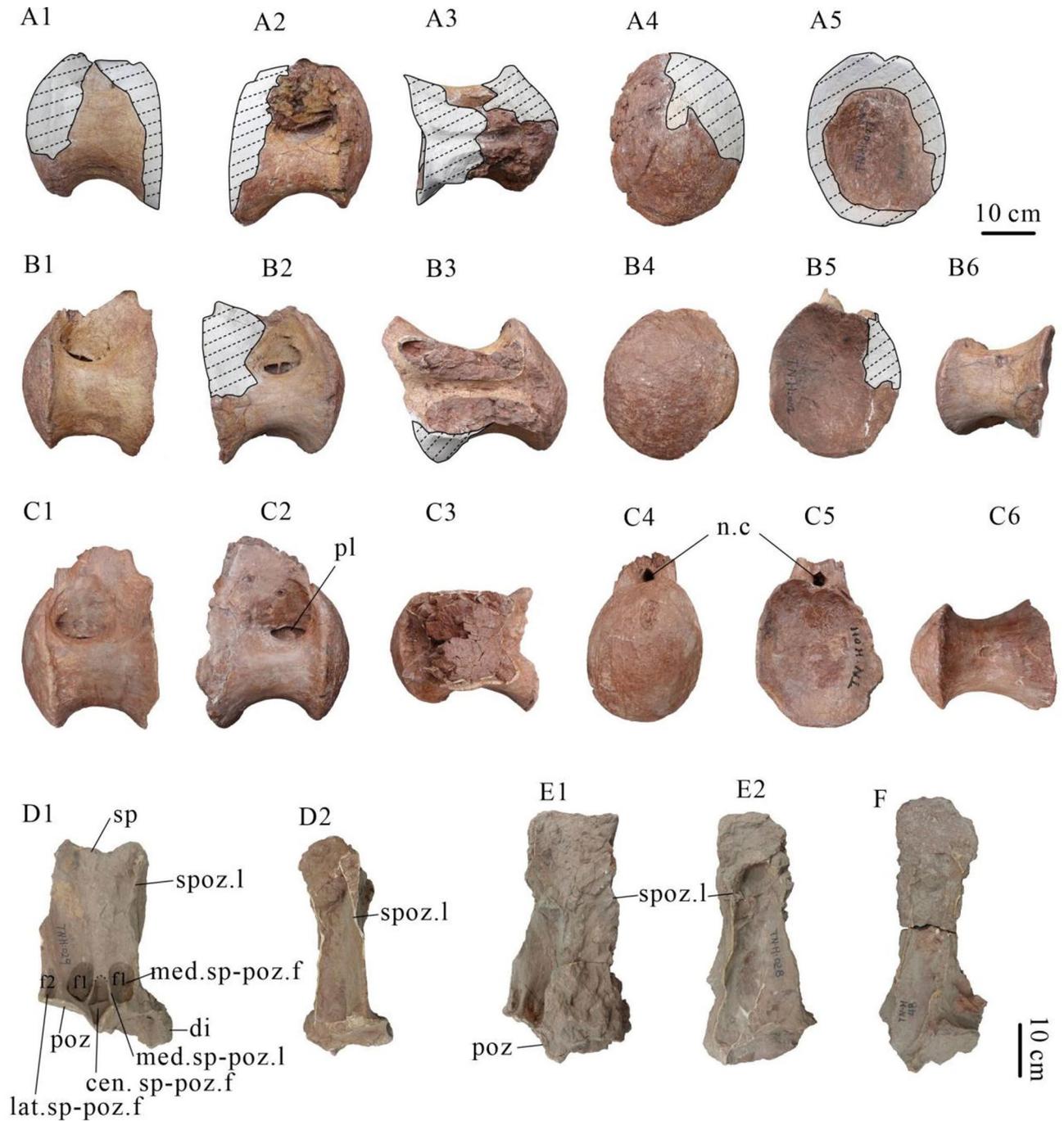


Fig. 3. Dorsal vertebrae of *Tongnanlong zhimingi*. (A–C) Dorsal centra, (1–6) in left lateral, right lateral, dorsal, anterior, posterior and ventral views; (D1–D3) Dorsal neural spine in posterior, lateral and dorsal views; (E1, E2) Dorsal neural spine in lateral-posterior and lateral views; (F) Dorsal neural spine in anterior-lateral views; Scale bar = 10 cm. cen.sp-poz.f, central spinopostzygapophysial fossa; pl, pleurocoel; lat.sp-poz.f (f1), lateral spinopostzygapophysial fossa; poz, postzygapophysis; di, diapophysis; med.sp-poz.f, medial spinopostzygapophysial fossa; med.sp-poz.l (f1), medial spinopostzygapophysial lamina; n.c, neural canal; sp, neural spine; spoz.l, suprapostzygapophysial lamina.

sides of the neural spinal ridge, and the medial ones (i.e. f1) are much bigger and deeper than the lateral ones (i.e. f2) (Fig. 3D1). The central spinopostzygapophysial fossa and medial spinopostzygapophysial fossae are divided by small, thin vertical laminae (i.e. med. sp-poz. l). The lateral spinopostzygapophysial fossae become shallow till missing when extending upward to the less lower half of the neural spine. The spinopostzygapophysial fossae and laminae structures are unique that never been seen in other eusauropods and mamenchisaurids such as in *Mamenchisaurus* and *Omeisaurus*^{8,30}. In lateral view, the neural canal is enclosed by pedicel that is partly located in its centrum rather than the whole neural arch. In posterior view, the neural canal forms a deep fossa

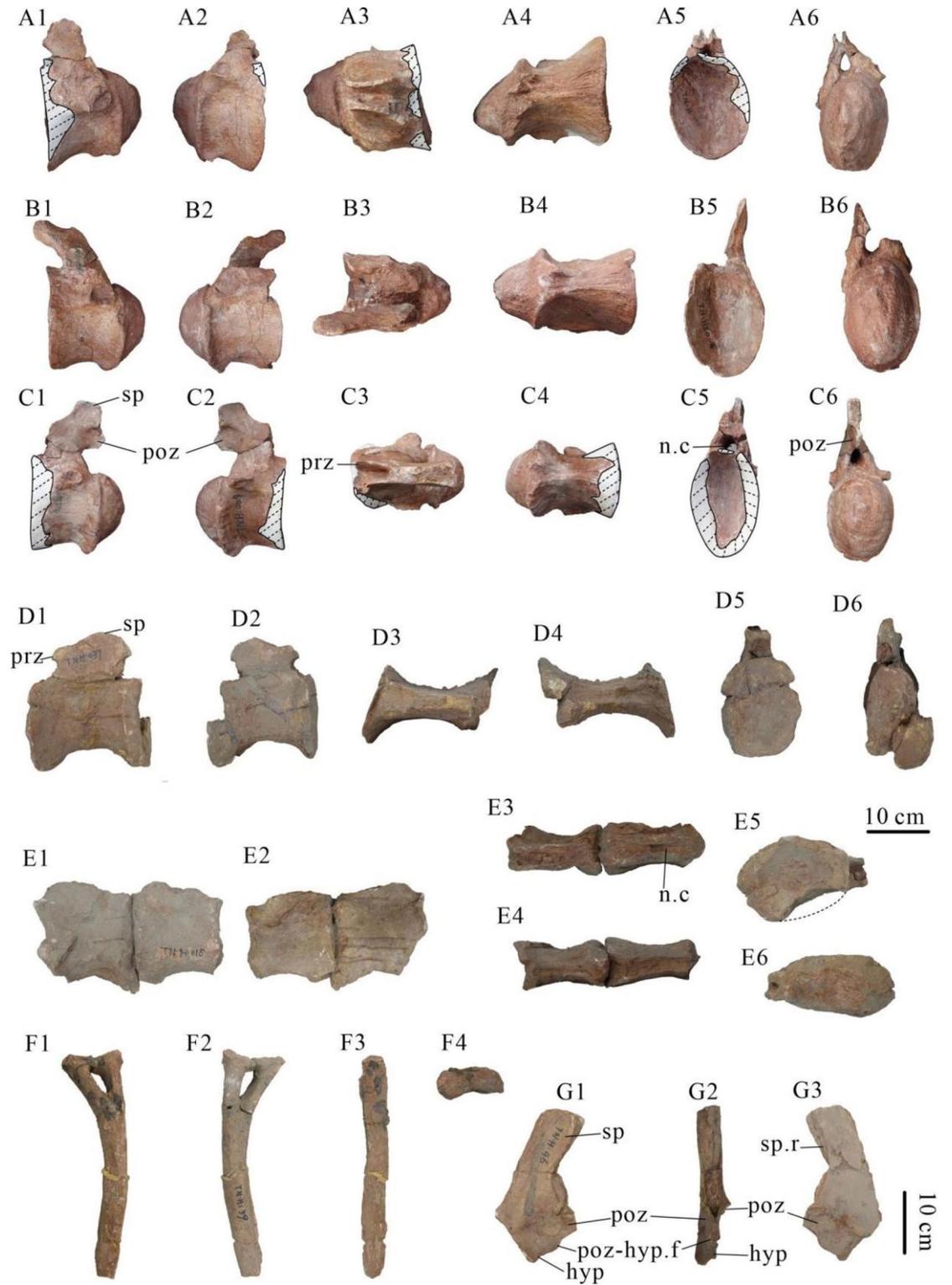


Fig. 4. Caudal vertebrae and chevron of *Tongnanlong zhimingi*. (A-E) Caudal vertebrae, (1–6) in left lateral, right lateral, dorsal, ventral, anterior and posterior views; (F1–F4) Chevron in anterior-lateral, posterior-lateral, lateral and top views; (G1–G3) Caudal neural spine in left lateral, posterior, right lateral and dorsal views. (A–G) with scale bar = 10 cm. hyp, hyposphene; n.c, neural canal; poz, postzygapophysis; prz, prezygapophysis; sp, neural spine; sp.r, ridge of neural spine; poz-hyp.f, postzygapophysis-hyposphene fossa.

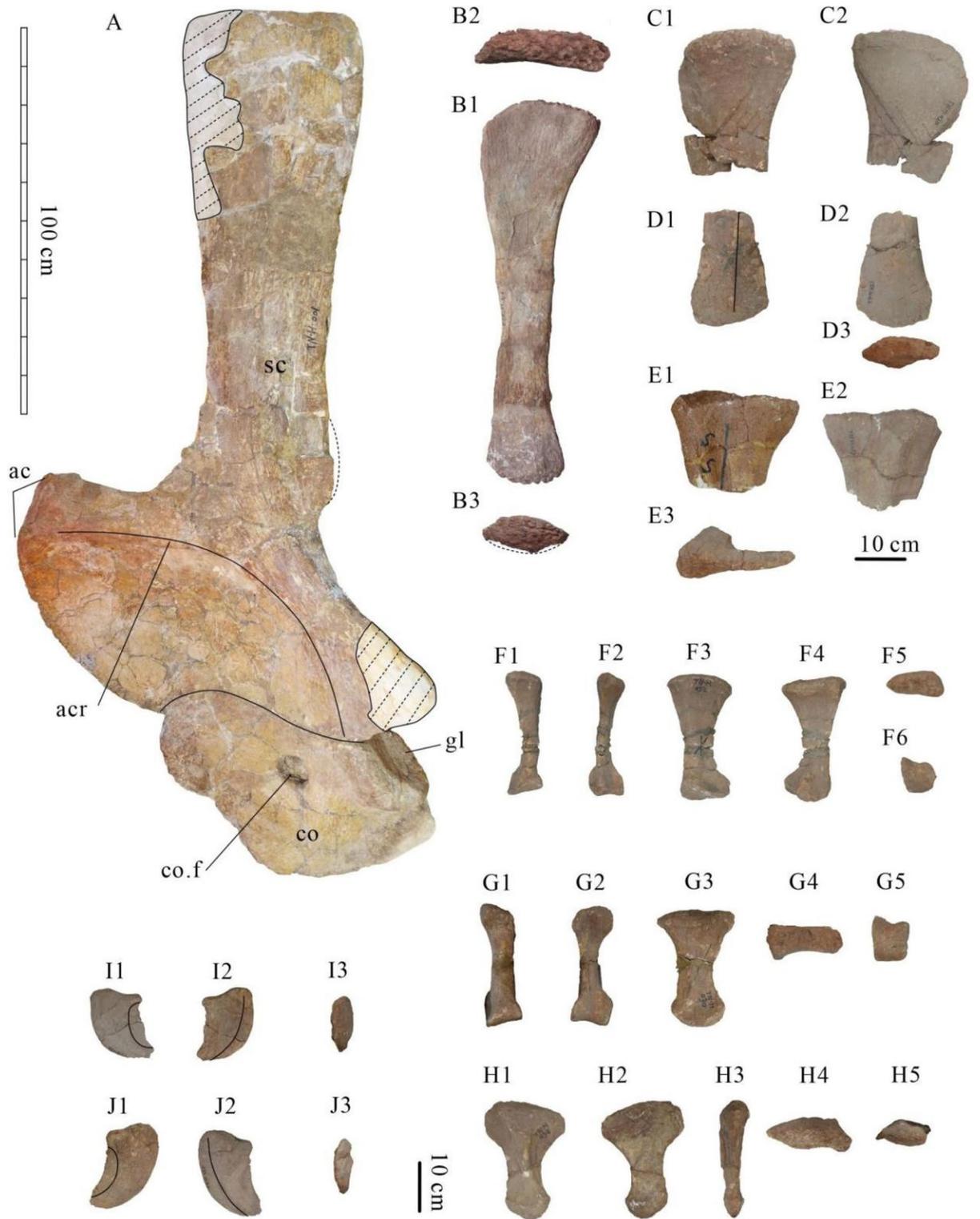


Fig. 5. Shoulder girdle and hindlimb bones of *Tongnanlong zhimingi*. (A) Left scapula and coracoid in external view; (B1–B3) right fibula in anterior, proximal and distal views; (C1, C2) proximal end of left fibula in anterior and posterior views; (D1–D3) distal end of the left fibula in anterior, posterior and distal views; (E1–E2) proximal end of the left tibia in anterior, posterior and proximal views; (F1–F6) Metatarsal III in dorsal, ventral, dorsal-lateral, ventral-lateral, proximal and distal views; (G1–G6) Metatarsal IV in dorsal, ventral, lateral, proximal and distal views; (H1–H5) Metatarsal V in dorsal, ventral, lateral, proximal and distal views; (I1–J3) Claws in internal, external and proximal views. (A) with scale bar = 100 cm; (B–J) with scale bar = 10 cm. Abbreviations: ac, acromion; acr, acromial ridge; co, coracoid; cof, coracoid fossa; gl, glenoid; sc, scapular blade.

with a vertically oval-shaped outline (Fig. 3C5). The height ratio of the neural canal to its centrum is only about 14% (5 cm and 33 cm, respectively). The neural arch is partly preserved and positioned relatively high, and the transverse process is above the horizontal level of the neural canal, which indicates that the dorsal vertebrae belong to the middle part of the dorsal series.

Caudal vertebrae. Six caudal vertebrae are preserved with three of them belonging to the anterior portion and the other three belonging to the middle-posterior portion. The three anterior caudal centra are procoelous. The posterior articular process of the anterior caudal centrum is medially convex and forms a marked condyle. The condyle length is about one third of its centrum (with length of 6 cm and 19 cm, respectively) (Fig. 4B). The margin of the posterior articular process and its centrum is clear and forms an oval ridge-like outline. The anterior caudal centra are taller than wide. The lateral surfaces of the caudal centra are smooth and shrunk inwardly, and bear no lateral fossa. The ventral surface of the caudal centrum bears a shallow longitudinal hollow along its midline. The caudal rib is low and situated wholly on the centrum, much closer to the posterior articular process than to the anterior one (Fig. 4A1, B1, C1). The hyposphenal ridge of the neural arch is present and slender (Fig. 4G2). The postzygapophysis extends less to the posterior articular surface of its centrum. The anterior neural spine is posterodorsally oriented and blade-like in shape, with a width/length ratio of about 20% (1.4 cm and 6.5 cm, respectively) (Fig. 4G). The anterodorsal margin of the neural spine is situated anteriorly and does not extend to the postzygapophyses. In anterior view, the spinoprezygapophyseal lamina is clearly developed and positioned near to the base of the neural spine. In posterior view, the spinopostzygapophyseal lamina is weakly developed, which makes the posterior surface of the neural spine vertically concave with a central ridge dividing the concavity into two parts (i.e. sp.r in Fig. 4G3). The postzygapophyses are much more vertical and their faces form a small acute angle of about 30°. In posterior view, a dorsoventrally elongated fossa is present between the postzygapophyses and hyposphene (i.e. poz-hyp. f in Fig. 4G1, G2), which is a unique character that differs from the absence of fossa in the anterior caudal vertebrae of other eusauropods like *Mamenchisaurus* and *Omeisaurus*^{1,8,30}.

An isolated caudal vertebra is partly preserved but clearly different from the three anterior caudals (Fig. 4D), which belongs to the middle-posterior part of the caudal series. Its centrum is weakly amphicoelous. Both the anterior and posterior articular surfaces are ellipse-shaped. The ventral surface bears a clear concavity on the midline. Its prezygapophysis is weakly developed, extending anteriorly no more than the articular surface. The neural spine is low and extends posteriorly more than the posterior articular surface. Another two naturally articulated posterior caudal centra are preserved (Fig. 4E). Their length is clearly greater than their height and width (16 cm, 14 cm and 10 cm, respectively), which makes the centra laterally compressed in shape. Both centra are weakly amphicoelous. Both the anterior and posterior articular surfaces are oval in outline. The ventral surface of each centrum bears a clear anteroposteriorly elongated vascular groove. The neural canal is situated wholly above its centrum.

Chevron. The proximal end of the preserved chevron is bridged dorsally by a bone bar (Fig. 4F). The proximal end also bears a deep haemal canal, and its shaft below the canal curves slightly backward, which indicates that it belongs to an anterior chevron.

Ribs. The dorsal ribs are broken. One nearly complete dorsal rib is more than 150 cm long. In proximal view, the capitulum and tuberculum are both robust, forming an acute angle. The plate-like process is developed anteriorly to the tuberculum, which indicates that it is an anterior dorsal rib.

Scapula. The left scapula and coracoid are completely preserved (Fig. 5A). The scapula is relatively large, and its blade is long and straight. The ratio of the maximal dorsoventral height to the total anteroposterior length of the scapula approaches about 60% (109 cm and 182 cm, respectively), this ratio only reaches 50% in that of *Mamenchisaurus youngi* (ZDM 0126)³⁰. The proximal end of the scapula is extremely extended whilst the distal end is only weakly extended dorsoventrally. The highest point of the dorsal margin of the blade is clearly lower than the dorsal margin of the proximal end. The cross section of the scapular blade at the base is D-shaped, with the lateral surface strongly convex dorsoventrally and medial surface flat, which is similar to that in *Analong chuanjieensis*³¹ *Dashanpusaurus dongi*⁶ *Bellusaurus sui*³³ but different from the rectangular shape in *Shunosaurus lii* (ZDM 5007)⁶. The scapular proximal plate develops a strong acromial ridge, extending dorsally from the margin of the proximal plate and ventrally to the margin of the glenoid. The area of the anterior acromial ridge forms a distinct concavity, which is similar to that in *Mamenchisaurus youngi* (ZDM 0126)³⁰. The acromion is well-developed on the dorsal end of the proximal plate and forms a rounded outline other than a posteriorly directed hook-like process, which is similar to that in *Mamenchisaurus jingyanensis*³⁴. The suture of scapula and coracoid is S-shaped other than nearly straight as those in other eusauropods like *Mamenchisaurus youngi* (ZDM 0126) and *Omeisaurus tianfuensis* (ZDM 5002). Also, the suture and the scapular blade midline forms a broad obtuse angle (about 110°) other than nearly perpendicular as in that of *Mamenchisaurus youngi* (ZDM 0126). The glenoid is thick mediolaterally. Its scapular and coracoid articular surfaces form a broad obtuse angle (about 110°), differing from the right angle (nearly 90°) in that of *Mamenchisaurus youngi* (ZDM 0126)³⁰ and neosauropods like *Ruyangsaurus*³⁵.

Coracoid. The coracoid is relatively quadrilateral in shape with a dorsoventral height greater than anteroposterior length (about 68 cm and 46 cm, respectively). In lateral view, the dorsal margin of the coracoid lies below the level of the scapular proximal plate and separates the latter by a broad V-shaped notch. The glenoid articular surface of the coracoid is weakly concave. The lateral surface of the coracoid develops a convex notch that attaches the biceps. The coracoid fossa is big and subcircular (with a diameter of about 9 cm), which is located much closer to the scapular margin of the coracoid than to the glenoid margin of the coracoid (with distances of 7 cm and 18 cm, respectively).

Fibula and tibia. The right fibula is completely preserved (Fig. 5B). The fibula is slender with a shaft length of about 103 cm. The fibular proximal end is extremely extended, and its proximal margin is relatively straight (Fig. 5B2). The distal end is more extended anteroposteriorly than mediolaterally. Both the proximal and distal

articular surfaces of the fibular are coarse. The cross-section of the middle shaft of fibula is D-shaped. The left fibula only preserves the proximal and distal ends (Fig. 5C, D). The anterior surface of the distal end of the fibular shaft bears a clear longitudinal ridge that separates the anterior surface into two parts.

Only the proximal end of the left tibia is preserved (Fig. 5E). In posterior view, the tibial lateral surface is thinner and greater than its medial surface, which further form a clear vertical crest as those in other eusauropods¹.

Pes. Three metatarsals are completely preserved (Fig. 5F, G, H). The metatarsals are smooth laterally with the middle shafts shrunk inwardly. The metatarsal V is well preserved and dorsoventrally compressed (Fig. 5H). Its proximal end is extremely extended mediolaterally while the distal end weakly extended dorsoventrally. The distal articular surface is fan-shaped. The maximal transverse width of the distal end of the metatarsal V is only half of its proximal end (8 cm and 16 cm, respectively). The ratio of the shaft length to the proximal transverse width of metatarsal V is about 1.4 (23 cm and 16 cm, respectively), which is less than 1.5 as in other eusauropods¹. The dorsal surface of the shaft of metatarsal V bears a ridge along the midline. Another two metatarsals are relatively slender and only slightly longer than the metatarsal V (Fig. 5F, G). Their proximal ends are mediolaterally expanded with clear articular surfaces developed on the medial and lateral sides, which indicate they belong to middle metatarsals and possibly metatarsal III or IV.

Pedal ungual. Two unguals were discovered (Fig. 5I, G). They are almost identical in shape but different in size. The ventral margins of unguals are only slightly curved but dorsal margins strongly curved. These unguals are strongly compressed mediolaterally and their tips are not that sharp. The lateral surface of each ungual bears a shallow groove. Their proximal articular surfaces are slightly concave. The ventral margin of each ungual develops a tuberosity along its distal half portion. In sauropod dinosaurs, the manus only bears one ungual in digit I and hoof-like bones in digits II-V; the pes bears claws I-V, and these unguals are similar in shape with the first pedal ungual being the biggest and unguals II-V being smaller in size, for example, the pedal ungual I is twice as large as the pedal ungual II in *Omeisaurus tianfuensis*^{9,36}. Thus, we infer that the two unguals belong to the pes.

Comparative discussion

The phylogenetic analysis placed *Tongnanlong* as a derived eusauropod dinosaur stably located in the clade of Mamenchisauridae. *Tongnanlong* has a closer relationship to *Jingiella*, *Mamenchisaurus* and *Chuanjiesaurus* than to *Omeisaurus*. Phylogenetic result also supports Mamenchisauridae as a stable group in Eusauropoda (Fig. 6, Fig. S1).

Tongnanlong shares some characters with *Mamenchisaurus hochuanensis*²⁹, *Mamenchisaurus youngi*³⁰, *Mamenchisaurus anyuensis*⁹ and *Omeisaurus tianfuensis*³⁶ which supports the assignment to Mamenchisauridae: the ratio of scapular total length/blade minimal width of more than 6, the dorsal margin of the scapular acromion within a rounded outline, the opisthocoelous dorsal vertebrae and procoelous anterior caudal centra, pneumatic structures and bifurcated neural spine of dorsal vertebrae, dorsal centra anteroposteriorly longer than dorsoventrally tall, anterior caudal central height greater than its width, lateral pleurocoels on dorsal centra.

Tongnanlong differs from other mamenchisaurids for bearing the following unique combination of characters, which support the erection of a new genus and species other than assigning it to known mamenchisaurids: complex spinopostzygapophysial laminae and fossae of the dorsal vertebrae (also in *Xinjiangtitan shanshanensis*), small vertical laminae dividing the lateral pleurocoels on dorsal centra, the suture of scapula and coracoid curved into S-shaped (also in *Tienschanosaurus chitainensis*), a fossa well-developed between the postzygapophysies and hypophene of the anterior caudal neural spine. Moreover, *Tongnanlong* has the following differences compared to other eusauropods, particularly the mamenchisaurid taxa from the adjacent regions in southwestern China, especially the Sichuan Basin and Yunnan Province.

Tongnanlong differs from *Mamenchisaurus anyuensis*^{9,23} in various aspects. Due to the brief description of *M. anyuensis* in published literature, the following comparisons are based on firsthand, personal observation of its holotype (AL 001). The distal end of scapular blade is only slightly extended and its exterior surface is concave in *Tongnanlong* but relatively extended with a flat lateral surface in *M. anyuensis*. The hook-like process of the scapular acromion is absent in *Tongnanlong* but developed in *M. anyuensis*. The acromial ridge is curved and extends dorsally above the glenoid in *Tongnanlong* but it is straight and extends posteriorly to the glenoid in *M. anyuensis*. The scapular proximal plate is much extended dorsoventrally in *Tongnanlong* than that in *M. anyuensis*. The coracoid outline is relatively quadrilateral in *Tongnanlong* but regularly subrounded in *M. anyuensis*. The exterior surface of coracoid is slightly concave in *Tongnanlong* while convex in *M. anyuensis*. The sizes of dorsal vertebrae, scapula and coracoid of *Tongnanlong* are all bigger than those of *M. anyuensis*, which indicates that *Tongnanlong* is a larger mamenchisaurid individual than *M. anyuensis* (Fig. S2).

Tongnanlong differs from *Mamenchisaurus youngi* (ZDM 0083)³⁰ in various aspects, such as less extended distal end of scapular blade than that in *M. youngi*, rounded outline and absent hook-like process of the scapular acromion whereas straight outline with weakly hook-like process in *M. youngi*; coracoid fossa less close to the scapular suture than that in *M. youngi*, and irregularly quadrilateral of coracoid but regularly oval in *M. youngi*.

Tongnanlong differs from *Mamenchisaurus hochuanensis*²⁹ by having lateral pleurocoels on dorsal centra that are much developed than that in *M. hochuanensis*. The caudal neural spine is blade-like in *Tongnanlong* whilst rod-like in *M. hochuanensis*. The metatarsal V of *Tongnanlong* is much slenderer with a ratio of the proximal width to its shaft length about 50% (16 cm and 24 cm, respectively), but the ratio reaches to 83% (15 cm and 18 cm, respectively) in *M. hochuanensis*. Also, the scapular distal end in *Tongnanlong* is less extended than that in *M. hochuanensis* (ZDM 0126)³⁷.

Tongnanlong differs from the *Mamenchisaurus jingyanensis*³⁴ in that it bears well developed lateral pleurocoels on dorsal centra, but pleurocoels are absent in *M. jingyanensis*. The articular surface of middle caudal centrum

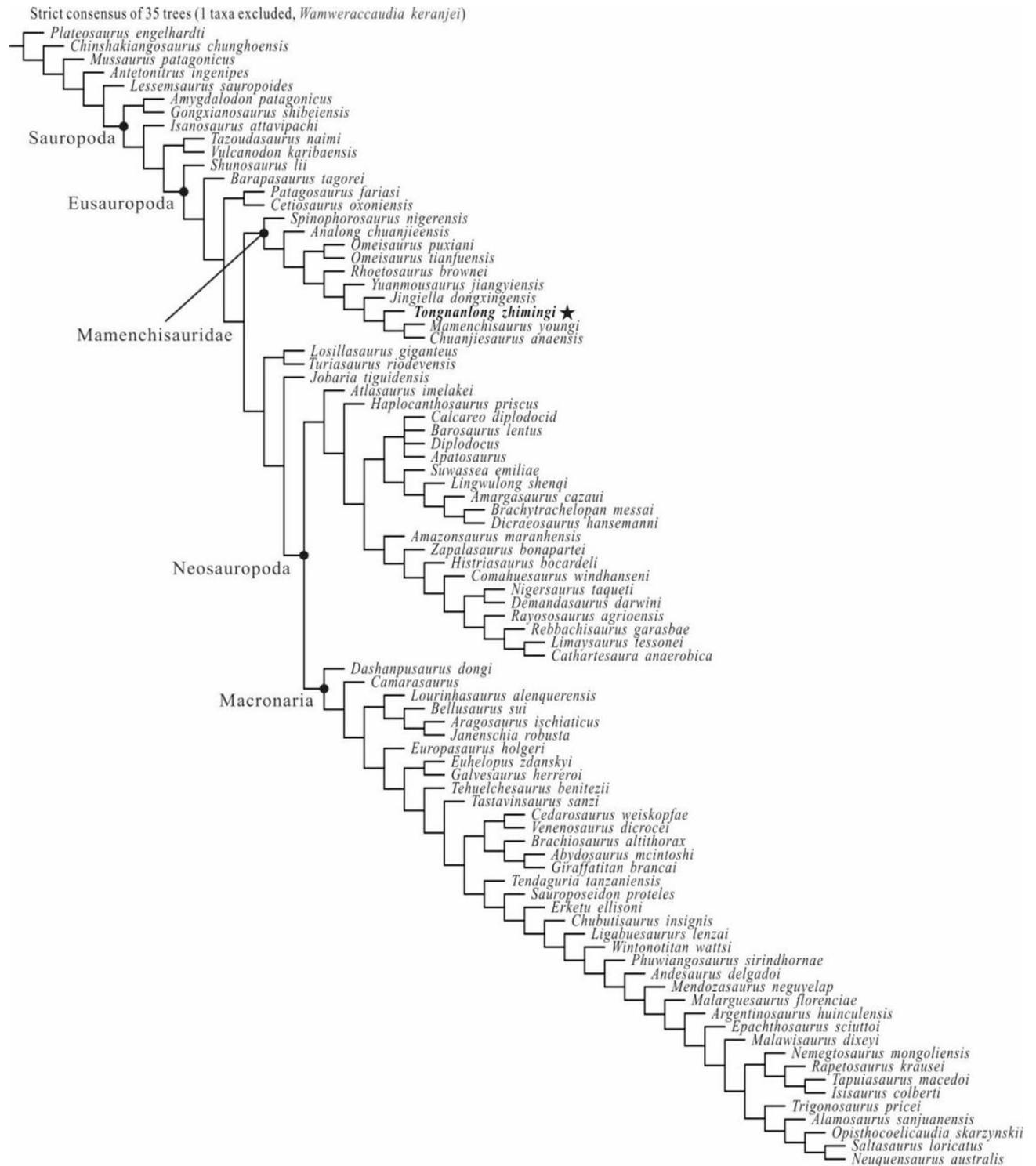


Fig. 6. The strict consensus of the 35 most parsimonious trees showing the systematic position of *Tongnanlong zhimingi* among sauropod dinosaurs (with consistency index = 0.335 and retention index = 0.685).

of *Tongnanlong* is oval and laterally compressed but circular in *M. jingyanensis*. The scapular proximal plate is much extended dorsally in *Tongnanlong* than that in *M. jingyanensis*. The scapular blade and proximal plate form a nearly right angle on the dorsal margin in *Tongnanlong*, but it is a broad obtuse angle in *M. jingyanensis*. The suture of scapula and coracoid is curved and S-shaped, but it is almost straight in *M. jingyanensis*.

Tongnanlong differs from the *Omeisaurus tianfuensis* (ZDM 5002)³⁶ in that the head of the dorsal neural spine is weakly bifurcated of *Tongnanlong* while not bifurcated in *O. tianfuensis*. The lateral pleurocoels of dorsal centra only had clear ventral margin in *Tongnanlong* whilst a wholly sub-rounded margin in *O. tianfuensis*.

The pleurocoel of dorsal centrum in *Tongnanlong* is shallower than that in *O. tianfuensis* which is extremely developed and almost pokes through the dorsal centrum.

Tongnanlong differs from the *Zigongosaurus fuxiensis* (ZDM 00251; CQMNH CV 025011)^{8,38} in that the height of scapular proximal plate is smaller than the length of scapular blade in *Tongnanlong*, whereas the proximal plate height is greater than its blade in *Z. fuxiensis*. The shape of the coracoid is irregular in *Tongnanlong* but regularly oval in *Z. fuxiensis*.

Tongnanlong differs from the *Shunosaurus lii* (IVPP V 9065)^{8,32,39} in that the dorsal centra are opisthocoelous but weakly amphicoelous in *S. lii*. The dorsal pleurocoels strongly developed in *Tongnanlong* whilst weakly developed in *S. lii* (ZDM 5008). The scapular proximal plate is less extended in *S. lii* (ZDM 5003) than that in *Tongnanlong*.

Tongnanlong differs from *Analong chuanjieensis*³¹ in that the neural canals are nearly circular-shaped but considerably slot-shaped in *A. chuanjieensis*. The centrum is taller than wide in *Tongnanlong* while conversely in *A. chuanjieensis*. The neural spine of anterior caudal vertebrae is plate-like in *Tongnanlong* whilst rod-like in *A. chuanjieensis*.

Tongnanlong differs from *Qijianglong guokr*¹⁰ in some aspects even though some similarities are present in their morphology, for example the strongly opisthocoelous dorsal centra, and they were both yielded from the Suining Formation. The articular surfaces of dorsal and caudal centra are anteroposteriorly shorter than dorsoventrally tall in *Tongnanlong* while conversely in *Q. guokr*. In dorsal view, the dorsal neural spine forms a clear midline groove in *Q. guokr* but absent in *Tongnanlong*. The dorsal neural spine is thinner anteroposteriorly in *Q. guokr* than those in *Tongnanlong*. Also, the pleurocoels on the dorsal centrum is smaller and bears no vertical laminae in *Q. guokr* compared to those in *Tongnanlong*. The sizes dorsal centra are bigger in *Tongnanlong* than those in *Q. guokr*, which indicates a much huger individual than the latter. However, it is difficult to make further detailed comparison due to the fragmentary nature of the bones or the lack of overlapping bones, such as the partly preserved anterior caudal centra in *Tongnanlong* and the nearly complete mid-distal caudal vertebrae in *Q. guokr*.

Tongnanlong differs from *Yuanmousaurus jiangyiensis*⁴⁰ in that the dorsal and caudal centra are clearly taller than wide whilst nearly equal in *Y. jiangyiensis*. The scapular proximal plate is much extended in *Tongnanlong* than that in *Y. jiangyiensis*, which shows a ratio of proximal plate width/blade length of scapular about 0.91 in *Tongnanlong* but only 0.69 in *Y. jiangyiensis*. Also, the sizes of scapula and coracoid are greater in *Tongnanlong* than that in *Y. jiangyiensis*, which indicates that *Tongnanlong* is a much larger individual than the 17 m long *Y. jiangyiensis*.

Tongnanlong differs from *Chuanjiesaurus ananensis*⁴¹ in that the caudal centra are taller than wide while almost equal in *C. ananensis*. The coracoid fossa is positioned much further away from the glenoid margin of coracoid in *C. ananensis* than that in *Tongnanlong*. The scapula-coracoid suture is clear in *Tongnanlong* but almost fused in *C. ananensis*. The size of scapula and coracoid are greater in *Tongnanlong* than that in *C. ananensis*, which indicates that *Tongnanlong* is much bigger than *C. ananensis*.

Tongnanlong differs from *Jingiella dongxingensis*⁴² in that the anterior caudal centra are typically procoelous but generally amphicoelous in the latter. Also, the sizes of anterior caudal centra in *Tongnanlong* are much larger than those in *J. dongxingensis*. The dorsal neural spines are much higher than wide in *Tongnanlong* but transversely compressed in *J. dongxingensis* though this might be caused by their different positions. Complex fominae and laminae above the postzygapophyses of the dorsal vertebrae are well-developed in *Tongnanlong* but absent in *J. dongxingensis*. The ventral mid-keel on the anterior caudal centra is present in *J. dongxingensis* but absent in *Tongnanlong*.

Moreover, *Tongnanlong* displays differences from the Middle-Late Jurassic mamenchisaurids that lived in northwestern China, especially the mamenchisaurids from Xinjiang Province, such as *Tienshanosaurus chitaiensis*, *Xinjiangtitan shanshanensis*, *Klamelisaurus gobiensis*, *Hudiesaurus sinojapanorum* and *Mamenchisaurus sinocanadorum*.

Tongnanlong differs from *Tienshanosaurus chitaiensis*⁴³ in that the sizes of dorsal and anterior caudal vertebrae, scapula and coracoid are bigger than those of the latter, which indicates a much larger individual of the former. Due to the limited description of *T. chitaiensis* in published literature, it is difficult to make further vertebrate comparisons between the two taxa. Even though both display a S-shaped suture of scapula and coracoid, it is much curved dorsally in *Tongnanlong* but ventrally in *T. chitaiensis*. The acromial ridge is obtuse, curved and extends dorsally above the glenoid in *Tongnanlong* but nearly straight and only extends further posteriorly to than the glenoid in *T. chitaiensis*. Ventrally, the ratio of the lower border width to glenoid surface length in the coracoid is approximately 0.6 in *Tongnanlong* but nearly 1.2 in *T. chitaiensis*.

Tongnanlong differs from *Xinjiangtitan shanshanensis* in many aspects though they both came from the Late Jurassic and have many anatomical similarities^{44,45}. Although both of them bear complex spinopostzygapophysial fossae and laminae structures, the spinopostzygapophysial fossae are much deeper and their number reaches five (two lateral and two medial fossae separately, and one central fossa) in *Tongnanlong* but shallow and three fossae (two lateral fossae within a vertical ridge seeing in dorsal 6 and one central fossa seeing in dorsal 3, 6, 9, 11) in *X. shanshanensis*. The spinopostzygapophysial laminae is much narrower and blade-like in shape in *Tongnanlong* but broad, ridge-like in shape (seeing dorsal 3, 6, 9, 11) in *X. shanshanensis*. Also, the dorsal neural spine is much higher dorsally and thinner anteroposteriorly in *Tongnanlong* than those in *X. shanshanensis*. Although both pleurocoels on the dorsal centra are deep, there are small vertical laminae dividing the pleurocoels in *Tongnanlong* but absent in *X. shanshanensis*.

Tongnanlong differs from the *Klamelisaurus gobiensis*⁴⁶ in that the dorsal neural spine is higher than the latter. The shape of the anterior caudal neural spine is blade-like in *Tongnanlong* but claviform in *K. gobiensis*. In dorsolateral view, the acromial ridge is located closer to the posterior margin of the proximal portion of the scapula in *K. gobiensis* than that in *Tongnanlong*. Regarding the partially reconstructed dorsal junction between

the scapula and coracoid, their suture is S-shaped in *Tongnanlong* but straight in *K. gobiensis*. The coracoid is irregularly quadrilateral in outline in *Tongnanlong* but slightly trapezoidal in *K. gobiensis*. The lateral surface of the coracoid is concave anteroposteriorly in *Tongnanlong* but gently convex in *K. gobiensis*. The sizes of the dorsal centra, coracoid, fibula and proximal tibia are much larger in *Tongnanlong* than those in *K. gobiensis*, which indicates a much larger individual of the former.

Given the difficulties in identifying the precise position of the isolated dorsal vertebra of *Hudiesaurus sinojapanorum*⁴⁷ comparisons could only show that the ventral surfaces of the dorsal centra bear no midline ridges in *Tongnanlong*, while the midline ridge is well-developed in *H. sinojapanorum*, and the outline of the posterior articular surface of the dorsal centrum is much rounded in *H. sinojapanorum* but oval in *Tongnanlong*. Moreover, it is challenging to make comparisons between *Tongnanlong* and *Mamenchisaurus sinocanadorum* due to their non-overlapping skeletal parts, as only the lower jaw and cervical series were preserved in the latter⁴⁸.

Diversity of Mamenchisauridae in the Sichuan Basin

The Jurassic strata in the Sichuan Basin has yielded abundant sauropod dinosaurs since the first dinosaur discovery in 1915, and is now well-known and represented by Jurassic sauropod dinosaurs like *Shunosaurus*, *Omeisaurus* and *Mamenchisaurus*^{1,8}. The Jurassic dinosaurs from the Sichuan Basin are divided into three dinosaur faunas: (1) the Early Jurassic *Lufengosaurus* Fauna with basal sauropodmorphs predominately represented by *Lufengosaurus*, (2) the Middle Jurassic *Shunosaurus* Fauna with sauropods predominately represented by *Shunosaurus* and *Omeisaurus*, and (3) the Late Jurassic *Mamenchisaurus* Fauna with sauropods predominately represented by *Mamenchisaurus*². Since the family Mamenchisauridae was established based on the fossils from the Upper Shaximiao Formation in the Sichuan Basin²⁹ the validity and evolutionary relationships of this family have experienced several controversies¹. It was originally considered as a junior synonym of the family Euhelopodidae⁴⁹ then it was abandoned based on the following phylogenetic analyses^{50,51}. The clade including *Omeisaurus* and *Mamenchisaurus* from China was assigned to a new family Omeisauridae instead of Mamenchisauridae⁵². Some studies treated the Mamenchisauridae as a clade of Asian eusauropod taxa from the Middle Jurassic to the earliest Cretaceous^{8,30,53}. Mamenchisauridae is now mainly supported to be a valid clade that includes the Middle-Late Jurassic eusauropods *Omeisaurus*, *Mamenchisaurus* and closely related forms^{6,42,52}.

Present studies supports that the clade Mamenchisauridae consists of more than fifteen genera in China (i.e. *Tongnanlong*, *Mamenchisaurus*, *Omeisaurus*, *Zigongsaurus*, *Abrosaurus*, *Qijianglong*, *Chuanjiesaurus*, *Yuanmousaurus*, *Eomamenchisaurus*, *Jingiella*, *Tienschanosaurus*, *Klamelisaurus*, *Hudiesaurus*, *Xinjiangtitan*, *Huangshanlong* and *Anhuilong*) from the Middle-Late Jurassic strata, which are commonly widespread geographically in southwestern China (Sichuan, Yunnan, Guangxi provinces)^{8,40,42,54}, northwestern China (Gansu and Xinjiang provinces)^{29,55} and central China (Anhui Province)⁵⁶. Among these mamenchisaurid taxa, the genera *Mamenchisaurus* and *Omeisaurus* have higher species diversities than other taxa. The reported *Mamenchisaurus* includes six species: *M. constructus*⁵⁷ *M. hochuanensis*, *M. youngi*³⁰ *M. anyuensis*⁹ *M. jingyanensis*³⁴ *M. sinocanadorum*⁵⁸ and the genus *Omeisaurus* includes eight species: *O. junghsiensis*⁵⁹ *O. changshouensis*⁶⁰ *O. tianfuensis*, *O. fuxiensis*, *O. luoquanensis*³⁶ *O. maoianus*⁶¹ *O. jiao*⁶² and *O. puxian*⁶³. Although the validity of some species of *Omeisaurus* and *Mamenchisaurus* were debated, they still indicate an extremely high mamenchisaurid diversity in China. Moreover, the Late Jurassic stratum in Tanzania has yielded the sauropod dinosaur *Wamweracaudia keranji*, which belongs to Mamenchisauridae⁴. It suggests that Mamenchisauridae had a wide geographical distribution not only limited to East Asia but also Africa during the Late Jurassic. Mamenchisaurids were also reported from the earliest Cretaceous (controversial era, ?Late Jurassic) Phu Kradung Formation in northeastern Thailand which is not far away from the Sichuan Basin in southwestern China⁴² supporting that the genus *Mamenchisaurus* existed from the Middle Jurassic till the earliest Cretaceous. It is noteworthy that the sauropod dinosaurs in the Sichuan Basin had attained a high diversity, and the Sichuan Basin was an ideal habitat for sauropod dinosaurs compared to other contemporaneous mainlands in North America, Europe and Africa during the Middle-Late Jurassic period.

Body size of *Tongnanlong zhimingi*

Tongnanlong preserves complete scapular, coracoid and fibula bones but only partial limbs and vertebrate series, which makes the estimation of body size difficult. However, the length comparisons of scapula, coracoid and fibula with other eusauropods could provide some indications. Length comparisons of scapula and fibula show that *Tongnanlong* is observably greater than those in *Mamenchisaurus* and *Omeisaurus* which had a body length of about 20 m. Based on the ratio of fibula to body length of *Mamenchisaurus youngi* (ZDM 0083), *Mamenchisaurus hochuanensis* (ZDM 0126) and *Omeisaurus tianfuensis* (ZDM 5002), which had nearly complete individuals preserved, the estimated body length of *Tongnanlong* probably reaches about 23 ~ 26 m, and based on the ratio of scapula length to body length, the estimated body length *Tongnanlong* could be up to 24.5 ~ 28 m. It is noteworthy that the body length of *Tongnanlong* could reach 33 m based on the scapular data of *Mamenchisaurus jingyanensis*, but this data is uncertain for the inaccurate body length of *Mamenchisaurus jingyanensis*. *Mamenchisaurus jingyanensis* is known from an incomplete individual without complete vertebrate series and limbs, and its body length of 20 m was estimated by considering it to be similar to *Mamenchisaurus hochuanensis* (ZDM 0126)³⁴. Herein, we cautiously estimated that *Tongnanlong* probably achieved a body length of about 25 ~ 26 m, representing a huge-sized mamenchisaurid dinosaur and might be the biggest individual by owning the biggest scapula so far. Some studies suggested that huge-bodied reptiles could reduce death risks during predation and thus gained competitive advantages within the dinosaur fauna^{42,64,65} which might be a driving factor that facilitated the mamenchisaurids to gradually dominate the dinosaur fauna in Late Jurassic.

Conclusion

Mamenchisauridae was distributed globally in the Late Jurassic rather than an endemic fauna which was previously considered limited to East Asia. *Tongnanlong zhimingi* gen. et sp. nov. from the Upper Jurassic Suining Formation of Chongqing area in the Sichuan Basin is assigned to Mamenchisauridae based on its more complex structures of dorsal and anterior caudal vertebrae compared to those of other mamenchisaurid dinosaurs. The large size of scapula and fibula also implies that it is a gigantic mamenchisaurid individual and might be the biggest one so far. The dorsal vertebrae of *Tongnanlong* provides additional information to help us understanding the skeletal changes of sauropods in Eastern Asia. The newly reported *Tongnanlong* enriches the diversity of eusauropods and provides new information on the understanding of the sauropod diversity and evolutionary trend from the Middle Jurassic to the Late Jurassic when their bodies became larger.

Methods

Anatomy

Anatomical descriptions and comparisons in this study followed the Romerian nomenclature and orientation instead of standardized terms (e.g. using anterior/posterior instead of cranial/caudal). Measurements of the specimen were taken using a caliper and photographed with a Nikon D7000 camera.

Phylogenetic analysis

We conducted a phylogenetic analysis to determine the systematic position of *Tongnanlong* using the data matrix of Ren et al. (2023, 2024)^{6,42}. With the addition of *Tongnanlong* in the matrix, 87 taxa and 400 characters were analyzed (see in the Supplementary). We first analyzed the data matrix under the “New Technology” search options using sectorial search, ratchet, tree drift, and tree fuse options with default parameters (10000 maximum trees and 1000 random seeds). Then the “Traditional Search” was applied under the tree bisection reconnection branch (TBR) swapping algorithm (10000 random seeds, 10000 replicates, 100 trees saved per replication and 10000 maximum trees, consistency index=0.335 and retention index=0.685). Phylogenetic analysis yields 35 most parsimonious trees with 1407 steps. The strict consensus of 35 most parsimonious trees excludes the taxon *Wamweracaudia keranjei* as it was actively relocated in different clades of the 35 most parsimonious trees. Phylogenetic analysis was performed using TNT version 1.6 under maximum parsimony⁶⁶ and character mapping was carried out using Mesquite version 3.81⁶⁷.

Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in ZooBank. The LSIDs of this publication is EF21F164-0723-4F9A-AA6E-A7531CFC35F7 for this publication, 941C1474-8944-4197-B508-E66041A9418B for the genus *Tongnanlong*, and 25ED5383-9D83-4633-93F2-9F9727B14BDA for the species *Tongnanlong zhimingi*.

Data availability

Data is provided online freely within the supplementary information files and available on request. Correspondence and requests for supplementary materials should be addressed to X.W.

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Author contributions

X.W described the specimen and wrote the main manuscript. Y.T, J.D and L.L prepared Figs. 1, 2, 3, 4 and 5 and tables. X.W, Y.L and Y. L measured the specimen. G.W, D.L, G.P and S.Z prepared figure 6 and supplementary information. C.L refined the MS, checked and polished the English expressions, and gave constructive suggestions on dealing with the reviewers' opinions. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to X.W.

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