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A New Titanosaurian Sauropod from the Upper Cretaceous of Jiangxi Province, Southern China

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ABSTRACT

Jiangxititan ganzhouensis gen. et sp. nov. is a new titanosaurian sauropod recovered from the Upper Cretaceous (Maastrichtian) Nanxiong Formation of Jiangxi Province, southern China. It is characterised by: (1) posterior cervical and anterior dorsal centra strongly compressed dorsoventrally; (2) accessory horizontal laminae present within the anterior dorsal pleurocoels; (3) posterior cervical and anterior dorsal neural arches low; (4) posterior cervical and anterior dorsal neural spines deeply bifurcated and widely separated; (5) inverted 'V' lamina formed by the left and right medial spinoprezygapophyseal laminae present at the anterior margin of the bifid point in posteriormost cervical and anteriormost dorsal neural spines; (6) triangular fossa formed by the metapophysis, medial and lateral spinoprezygapophyseal laminae present at the anterior margins of the posteriormost cervical and anteriormost dorsal neural spines; (7) postzygapophyses in the posterior cervical vertebrae fan-shaped; (8) medial and lateral spinopostzygapophyseal laminae present in the anterior dorsal vertebrae; and (9) anterior dorsal rib short and gracil. Our phylogenetic analysis places *Jiangxititan* within the deeply-nested titanosauriform clade Lognkosauria and the sympatric *Gannansaurus* in a much earlier-diverging lineage. This new discovery thus demonstrates the presence of both early-diverging and late-diverging titanosauriform sauropods in the Late Cretaceous Ganzhou dinosaur fauna.

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KEYWORDS
Titanosauria; Upper Cretaceous; Nanxiong Formation; Jiangxi Province; Jiangxititan ganzhouensis

Introduction

The Upper Cretaceous Nanxiong Formation of Jiangxi Province, southern China has yielded a diverse array of vertebrates in recent years, including theropods (Xu and Han 2010; Wang et al. 2013; Wei et al. 2013; Lü et al. 2013a, 2014, 2015, 2016, 2017; Mo and Xu 2015), ornithopods (Xing et al. 2021, 2022), crocodiles (Li et al. 2019), turtles (Tong and Mo 2010), lizards (Mo et al. 2010, 2012), and mammals (Jin et al. 2022), as well as a vast number of dinosaur eggs (Sato et al. 2005; Cheng et al. 2008; Ji 2009; Shao et al. 2014; Zhao et al. 2015; Wang et al. 2016; Jin et al. 2019; Bi et al. 2021; Fang et al. 2022). Only one sauropod taxon, *Gannansaurus sinensis*, has been recorded in this area (Lü et al. 2013b).

Here we decribed another new sauropod dinosaur taxon, *Jiangxititan ganzhouensis*, which consists of seven articulated posterior cervical and anterior dorsal vertebrae, some articulated cervical and dorsal ribs. The specimen was collected from the latest Cretaceous deposits (i.e. Nanxiong Formation) in Tankou Town, Nankang County, southwest of Ganzhou City, Jiangxi Province, which is about five kilometres away from Longling Town, the locality of *Gannansaurus* (Figure 1). The Nanxiong Formation, or its equivalents, is found across several provinces in southeastern China and represented by an extensive sequence of red mudstones, sandstones and conglomerates (Bureau of Geology and Mineral Resources of Guangdong Province 1988). The presence of *Truncatella maxima* and *Rubeyella carinate* suggests that the Nanxiong Formation was deposited towards the end of the Late Cretaceous (Maastrichtian) (Bureau of Geology and Mineral Resources of Jiangxi Province 1984; Wang et al. 2013). *Jiangxititan* preserves some distinct characters, such as neural spines deeply bifurcated, neural arches very low, centra strongly compressed dorsoventrally, etc, very different from some other Cretaceous of titanosauriforms from Asia. The discovery of the new taxon adds a new element not only to the poorly preserved sauropod dinosaurs in the Late Cretaceous of Jiangxi, but also to the diversity of titanosauriforms in the Late Cretaceous of Asia. Nomenclature of vertebral laminae and pneumatic fossae follows Wilson (1999) and Wilson et al. (2011).

Anatomical abbreviations

ACDL, anterior centrodiapophyseal lamina; CDF, centrodiapophyseal fossa; CeA, antepenultimate cervical vertebra; CeP, penultimate cervical vertebra; CeU, ultimate cervical vertebra; CPOL, centropostzygapophyseal lamina; CPRL, centroprezygapophyseal lamina; cr, cervical rib; D, dorsal vertebra; di, diapophysis; dr, dorsal rib; epi, epipophysis; EPRL, epipophyseal – prezygapophyseal lamina; hl, horizontal lamina; lSPOL, lateral spinopostzygapophyseal lamina; lSPRL, lateral spinoprezygapophyseal lamina; met, metapophysis; mSPOL, medial spinopostzygapophyseal lamina; mSPRL, medial spinoprezygapophyseal lamina; pa, parapophysis; PACD-F, parapophyseal centrodiapophyseal fossa; PCDL, posterior centrodiapophyseal lamina; pd, dorsolaterally facing platform of diapophysis; pl, pleurocoel; POCD-F, postzygapophyseal centrodiapophyseal fossa; PODL, postzygodiapophyseal lamina; POSD-F, postzygapophyseal spinodiapophyseal fossa; poz,

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postzygapophysis; PPDL, paradiapophyseal lamina; PRCD-F, prezygapophyseal centrodiapophyseal fossa; PRDL, prezygodiapophyseal lamina; PRPAD-F, prezygapophyseal paradiapophyseal fossa; PRPL, prezygoparapophyseal lamina; PRSD-F, prezygapophyseal spinodiapophyseal fossa; prz, prezygapophysis; SPDL, spinodiapophyseal lamina; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina; TPOL, intrapostzygapophseal lamina; TPRL, intraprezygapophyseal lamina.

Systematic palaeontology

Dinosauria Owen (1842)
Sauropoda Marsh (1878)
Neosauropoda Bonaparte (1986)
Somphospondyli Wilson & Sereno (1998)
Titanosauria Bonaparte and Coria (l993)

Jiangxititan ganzhouensis gen. et sp. nov. (Figures 2–9; Table 1)
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urn:lsid:zoobank.org:act:379B8F91–2396-40E6-9F8C-898D20B4C27E

Holotype

NHMG 034062, seven articulated vertebrae including three posteriormost cervicals and the first four dorsals (D1-D4), two articulated cervical ribs, three articulated dorsal ribs (Figures 2–9; Table 1). The specimen is housed in the Natural History Museum of Guangxi Zhuang Autonomous Region.

Etymology

The generic name *Jiangxi*, pinyin, is in reference to the fossil locality in Jiangxi Province, southern China, *titan*, in Greece, means giant dragon. The specific name *ganzhou*, pinyin, is from the fossil locality of Nankang County, Ganzhou City, Jiangxi Province.

Locality and horizon

The specimen was collected in Tankou Town, Nankang County, Ganzhou City, Jiangxi Province, southern China. Upper Cretaceous (Maastrichtian), Nanxiong Formation (Bureau of Geology and Mineral Resources of Jiangxi Province 1984; Bi et al. 2021).

Diagnosis

Jiangxititan ganzhouensis can be diagnosed on the basis of the following unique combination of character states: posterior cervical and anterior dorsal centra strongly compressed dorsoventrally; accessory horizontal laminae present within the anterior dorsal pleurocoels; posterior cervical and anterior dorsal neural arches low; posterior cervical and anterior dorsal neural spines deeply bifurcated and widely separated; inverted 'V' lamina present at the anterior margin of the bifid point in posteriormost cervical and anteriormost dorsal neural spines; both the EPRL and SPDL present in posterior cervical vertebrae; triangular fossa formed by the metapophysis, medial and lateral SPRLs present at the anterior margin of the posteriormost cervical and anteriormost dorsal neural spines; postzygapophyses in the posterior cervical vertebrae fan-shaped; medial and lateral SPOLs present in the anterior dorsal vertebrae; anterior dorsal rib short and gracil.

Ontogenetic assessment

The *Jiangxititan* specimen preserved seven articulated posterior cervical and anterior dorsal neural arches. The neural arches and centra are fully fused, some of the cervical and dorsal ribs are attached. The right side of the cervical rib in CeP is preserved, but is deformed and obscured by the rock. The left side of the cervical rib in CeU is partly fused with the parapophysis. The left sides of the dorsal ribs in D1, D3 and D4 are attached with the parapophyses and diapophyses. This indicates that *Jiangxititan* probably represents a morphologically mature individual (Wedel and Taylor 2013; Griffin et al. 2021).

Description and comparisons

The holotype was recovered during construction work, with the first and the last vertebrae of the series being broken during the field work (Figures 2–4). The right side of the neural arches of the seven articulated vertebrae was relatively complete, whereas the left side was deformed during its fossilisation. The anterior dorsal pleurocoels are visible in ventral view, partly due to the deformation. For description, the three cervical vertebrae will be designated as CeA (antepenultimate cervical vertebra), CeP (penultimate cervical vertebra) and CeU (ultimate cervical vertebra), respectively, and the four dorsal vertebrae will be designated as D1-D4. The identification of the first dorsal vertebrate (D1) is based on the following features: the distal end of the articulated dorsal rib directs mainly laterally and slightly posteriorly (Figures 2 and 4); the capital and tubercular heads are nearly coplanar; the parapophysis is positioned at the anteroventral margin of the pleurocoel (Figure 3); the parapophysis is oval in shape, differs from that of the posteriormost cervical which is anteroposteriorly elongated; the lack of oblique septum within the pleurocoel, differs from that of the posteriormost cervical where three accessory laminae are present within the pleurocoel; the length of centrum in D1 decreases dramatically than that of the posterior most cervical (Table 1).

The CeA preserves its posterior half of the centrum and fragmentary postzygapophysis, while the fourth dorsal vertebra (D4) preserves its anterior part of the centrum and some neural arch. The cervical vertebrae CeP and CeU have fused cervical ribs, while D1, D3 and D4 have articulated dorsal ribs. All the cervical and dorsal ribs are incomplete.

Posterior cervical vertebrae (Figures 2–6; Table 1)

Centra

The centra in CeP and CeU are nearly complete, the anterior part of the centrum in CeA is missing. The centra are strongly opisthocoelous, with a convex anterior articulation and corresponding concave posterior articulation, as indicated by the exposed margins of some intercentrum articulations (Figures 3 and 4). The centrum is relatively elongated in CeP, and decreases in length in CeU (Table 1). In lateral view, the ventral surfaces of the cervical centra are concave anteroposteriorly. In ventral view, the ventral surfaces of the cervical centra in CeP and CeU are markedly constructed transversely, posterior to the parapophyses (Figure 4). The ventral surfaces of the cervical centra in CeP and CeU are slightly concave transversely between the parapophyses, no ventral ridges or excavations present at the ventral surfaces. The camellate internal structures can be seen from the broken ventral surfaces of the centra. The centra in CeP and CeU are strongly compressed dorsoventrally

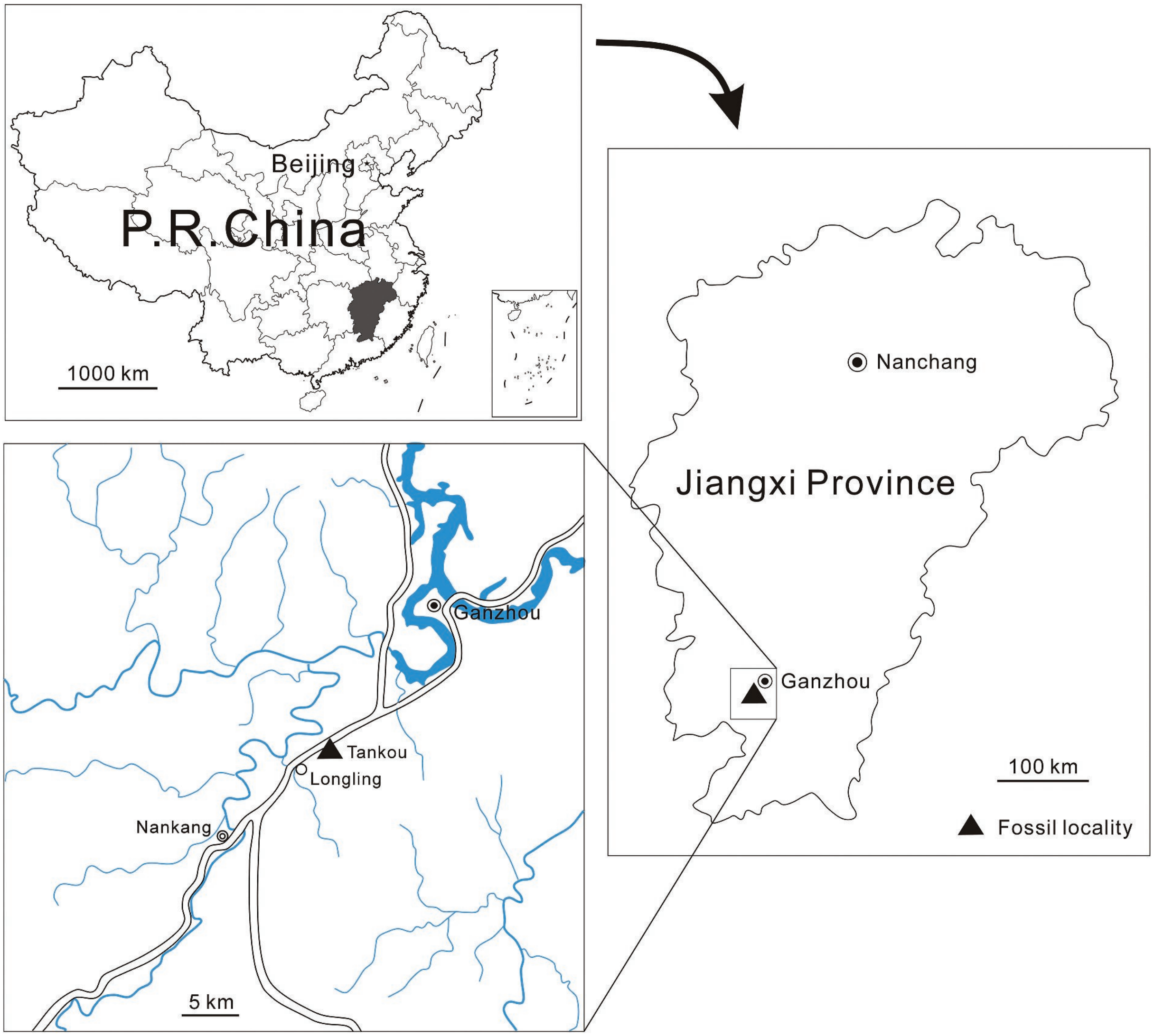

Figure 1. Map showing the fossil locality of the holotype of *Jiangxititan ganzhouensis* (NHMG 034062).

(Table 1), with the ratio of mediolateral width to dorsoventral height of posterior articular surfaces being greater than 2.3, similar to *Mendozasaurus neguyelap* (González Riga et al., 2018).

The pleurocoels are preserved in CeA-CeU, though the anterior part of the pleurocoel in CeA is broken (Figure 3). The cervical pleurocoels in CeP and CeU are deep and large, occupying almost their lateral surfaces of the centra, and are divided into numerous separate chambers by subvertical laminae. All the pleurocoels have deep excavations that ramify into the centra.

The parapophyses are preserved in CeP and CeU (Figure 3). They lie at the anteroventral margins of the centra, projecting ventrolaterally. The parapophyses are anteroposteriorly elongated, similar to some derived titanosaurs, such as *Malawisaurus*, *Saltasaurus*, and *Alamosaurus* (D'Emic 2012). The parapophyses extend posteriorly and reach nearly the midlength of the centra. They project primarily laterally, and slightly ventrally. No excavations present on the dorsal surfaces of the parapophyses.

Neural arches

The neural arches in CeP and CeU are preserved, with the anterior part of CeP being damaged (Figure 2). The neural arch is low, with the upper margin of the neural canal being level with the TPRL or TPOL (Figures 6 and 7), although the neural canal is obscured due to the preservation and preparation, similar to the conditions in *Ligabuesaurus*, *Rukwatitan*, *Mendozasaurus*and other titanosaurs (Bonaparte et al. 2006; Gorscak et al. 2014; Gonzàlez Riga et al. 2018). The total heights of the cervical vertebrae are less than 30 cm due to the low neural arches and the laterally directed metapophyses (Table 1). The ratio of the posterior cervical neural arch (arch height measured from dorsal surface of the centrum to base of prezygapophyses) to centrum dorsoventral height is less than 0.5, similar to other titanosaurs, such as *Malawisaurus*, *Saltasaurus*, and *Alamosaurus* (Mannion et al. 2013, 2019a).

Diapophyses

The diapophyses are preserved in CeP and CeU, with the right side of the diapophyses being preserved better than the left side (Figures 2–4; Table 1). The diapophyses direct laterally, rather than dorsolaterally. The articular surfaces of the diapophyses are rugose, pointing ventrally, and slightly laterally (Figure 4). In ventral view, the articular surface of the diapophysis is subtriangular in outline. The diapophysis is low in CeU, nearly level with the ventral margin of the centrum. The camellate internal structures can be seen from the broken surfaces of the diapophyses. Muscle scars are

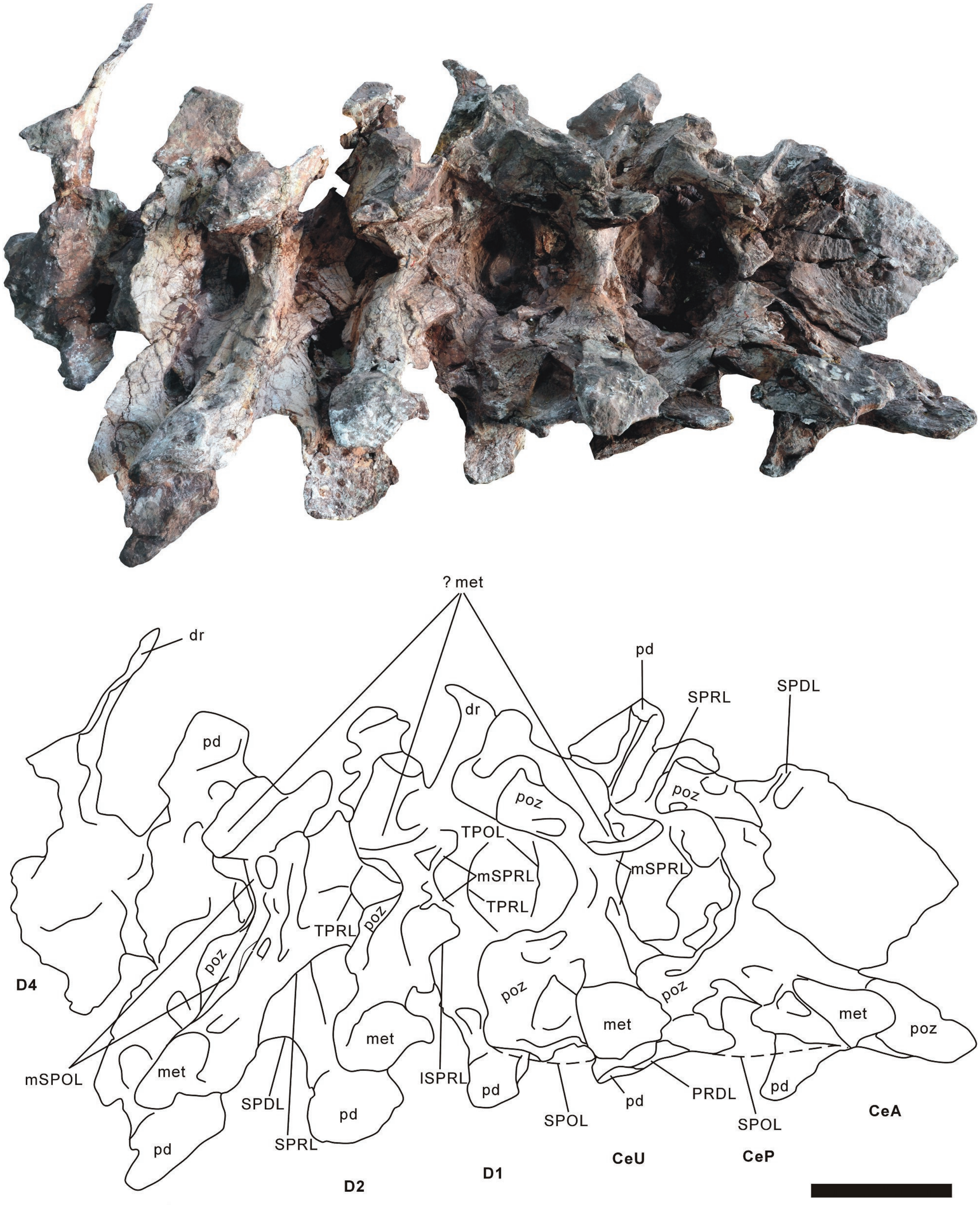

Figure 2. Holotype of *Jiangxititan ganzhouensis* (NHMG 034062) in dorsal view with interpreted outline below. Abbreviations: CeA, antepenultimate cervical vertebra; CeP, penultimate cervical vertebra; CeU, ultimate cervical vertebra; D, dorsal vertebra; dr, dorsal rib; lSPRL, lateral spinoprezygapophyseal lamina; met, metapophysis; mSPOL, medial spinopostzygapophyseal lamina; mSPRL, medial spinoprezygapophyseal lamina; pd, dorsolaterally facing platform of diapophysis; PODL, postzygodiapophyseal lamina; poz, postzygapophysis; PRDL, prezygodiapophyseal lamina; SPRL, spinoprezygapophyseal lamina; TPOL, intrapostzygapophseal lamina; TPRL, intraprezygapophyseal lamina. Scale bar equals 20 cm.

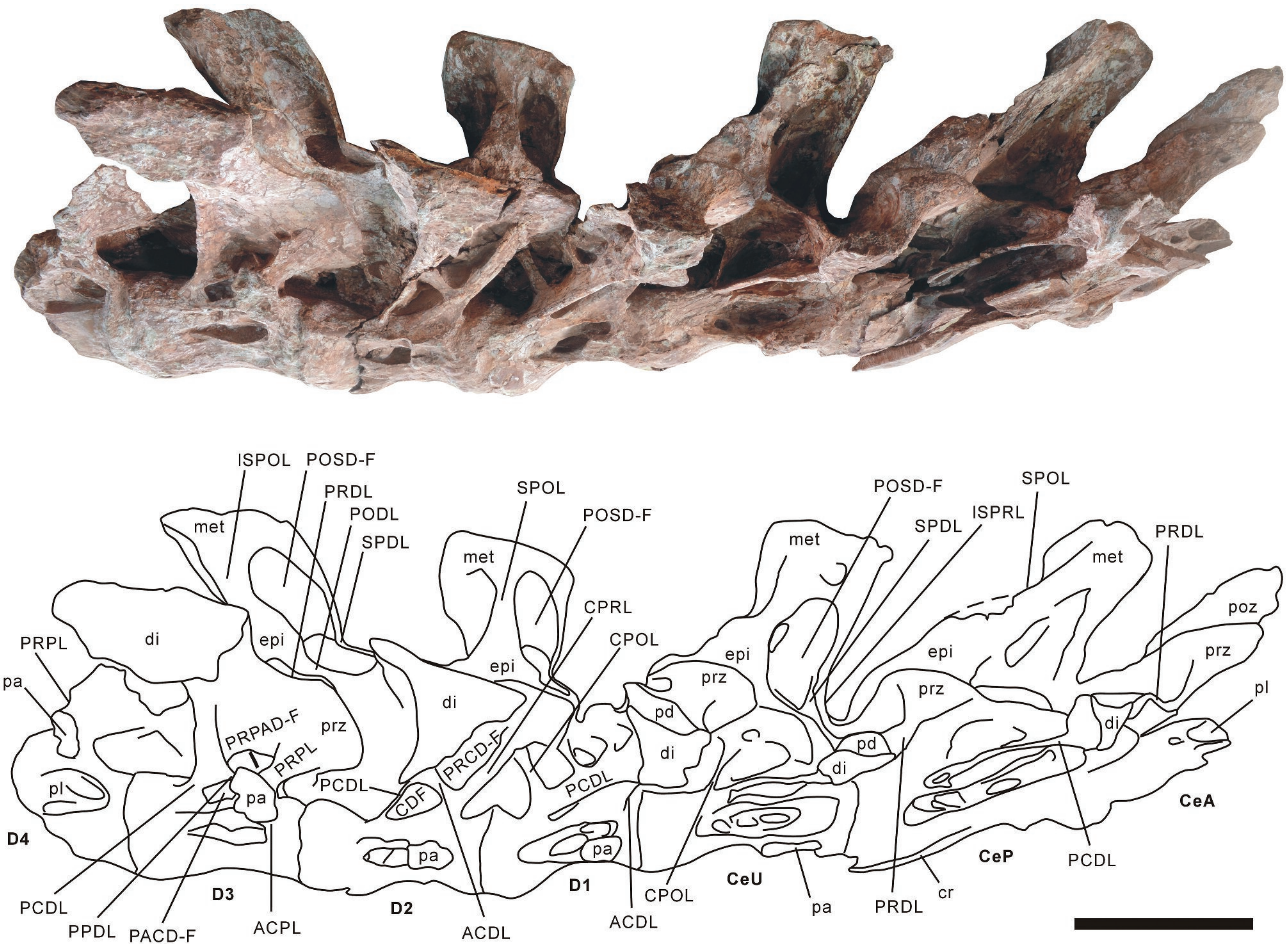

Figure 3. Holotype of *Jiangxititan ganzhouensis* (NHMG 034062) in right lateral and slightly ventral view, with interpreted outline below. Abbreviations: ACDL, anterior centrodiapophyseal lamina; CeA, antepenultimate cervical vertebra; CeP, penultimate cervical vertebra; CeU, ultimate cervical vertebra; CPOL, centropostzygapophyseal lamina; CPRL, centroprezygapophyseal lamina; cr, cervical rib; D, dorsal vertebra; di, diapophysis; dr, dorsal rib; epi, epipophysis; ISPOL, lateral spinopostzygapophyseal lamina; ISPRL, lateral spinoprezygapophyseal lamina; met, metapophysis; pa, parapophysis; PACD-F, parapophyseal centrodiapophyseal fossa; PCDL, posterior centrodiapophyseal lamina; pd, dorsolaterally facing platform of diapophysis; pl, pleurocoel; PODL, postzygodiapophyseal lamina; POSD-F, postzygapophyseal spinodiapophyseal fossa; poz, postzygapophysis; PRCD-F, prezygapophyseal centrodiapophyseal fossa; PRDL, prezygodiapophyseal lamina; PRPAD-F, prezygapophyseal paradiapophyseal fossa; PRPL, prezygoparapophyseal lamina; prz, prezygapophysis; SPDL, spinodiapophyseal lamina; SPOL, spinopostzygapophyseal lamina. Scale bar equals 20 cm.

Table 1. Measurements (in cm) of the vertebrae in the holotype of *Jiangxititan ganzhouensis* (NHMG 034062).

Vertebra	Centrum length (without convex)	Centrum posterior width	Centrum posterior height	Width across diapophyses	Width of right metapophysis	Total height
CeA	20+	23	10	?	?	10+
CeP	27	24	10	46+	29	25
CeU	22	23	9	59+	31	27
D1	18	22	10	60+	31	28
D2	19	21	11	63+	32	29
D3	18	21	12	65+	?	23+
D4	13+	?	?	?	?	18+

Width of right metapophysis: measured from the distal end of the right metapophysis to the notch; '+' denotes a measurement based on an incomplete element.

developed on the dorsolateral end of the diapophysis, forming a distinct platform (Figures 2 and 3).

Zygapophyses

The prezygapophyses and postzygapophyses in CeP and CeU, and the right side of the postzygapophysis in CeA are preserved (Figures 2 and 3). The medial margins of the postzygapophyses are relatively complete, while the lateral and dorsal margins are broken away during the fieldwork (Figure 2). The prezygapophyses are positioned slightly beyond the anterior margin of the anterior convex articulation. The postzygapophysis extends posteriorly and slightly ventrally well beyond the posterior margin of the centrum to contact the prezygapophysis of the succeeding vertebrate. In dorsal view, the postzygapophysis in CeU is large and fan-shaped, with a transverse width of 17 cm, and an anteroposterior length of 14 cm, respectively, though the postzygapophsis is somewhat broken. Fan-shaped postzygapophysis is also present in CeP, with the width of 14 cm, and the length of 17 cm, respectively. The left and

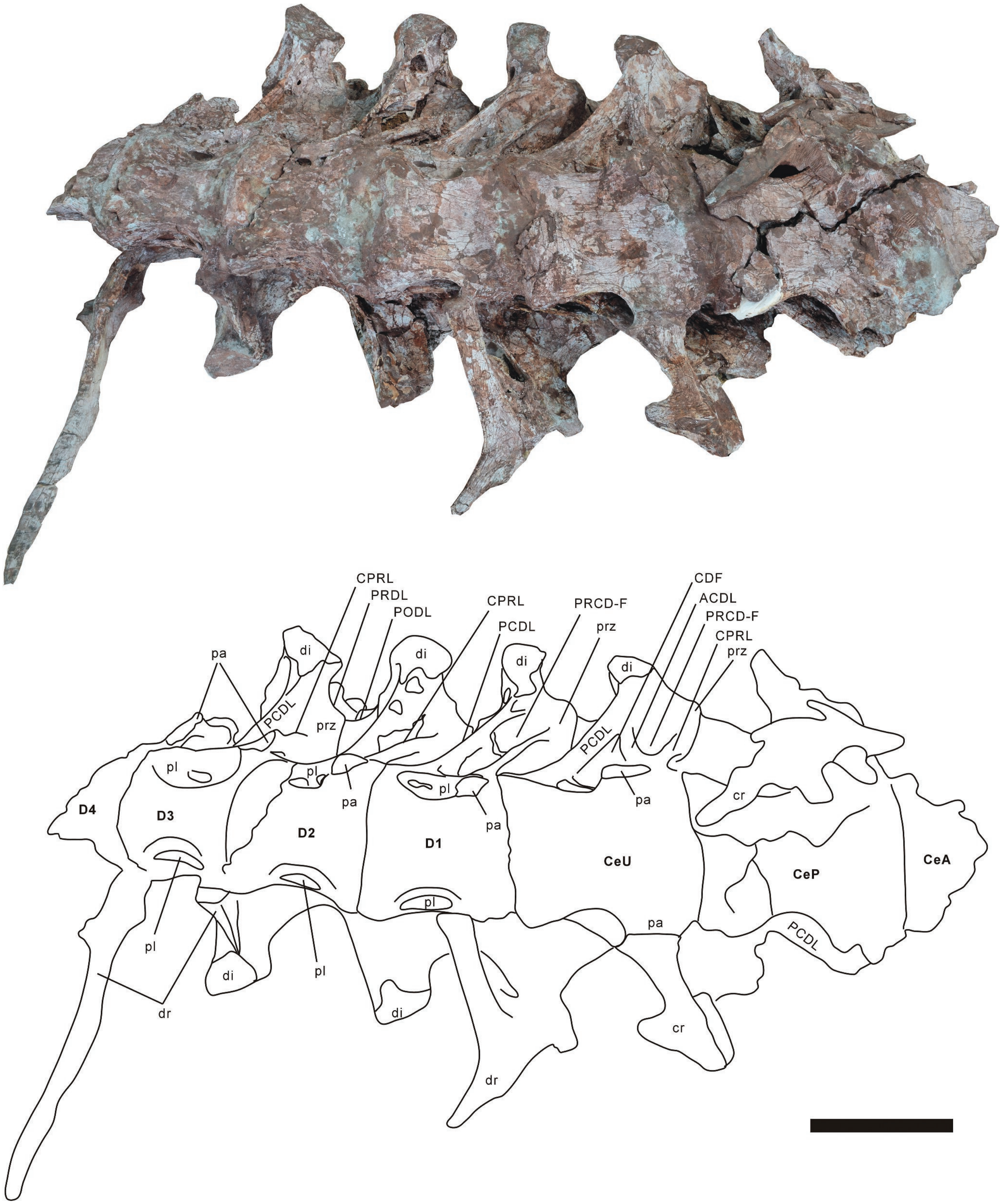

Figure 4. Holotype of *Jiangxititan ganzhouensis* (NHMG 034062) in ventral view with interpreted outline below. Abbreviations: ACDL, anterior centrodiapophyseal lamina; CDF, centrodiapophyseal fossa; CeA, antepenultimate cervical vertebra; CeP, penultimate cervical vertebra; CeU, ultimate cervical vertebra; CPRL, centroprezygapophyseal lamina; cr, cervical rib; D, dorsal vertebra; di, diapophysis; dr, dorsal rib; pa, parapophysis; PCDL, posterior centrodiapophyseal lamina; pl, pleurocoel; PODL, postzygodiapophyseal lamina; PRCD-F, prezygapophyseal centrodiapophyseal fossa; PRDL, prezygodiapophyseal lamina; prz, prezygapophysis. Scale bar equals 20 cm.

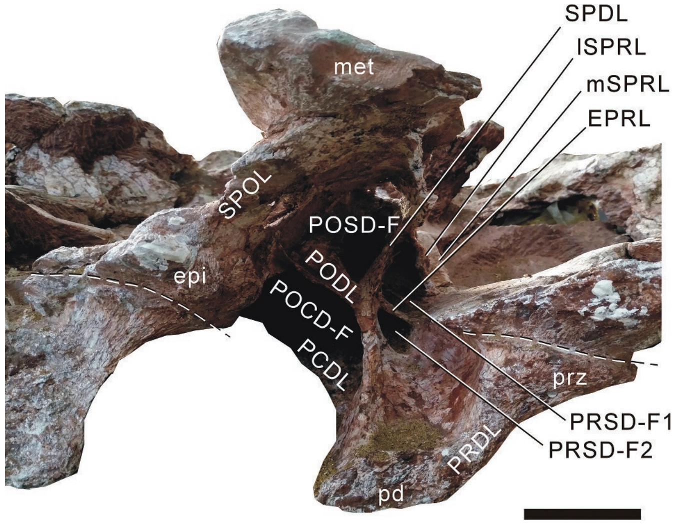

Figure 5. The neural arch of the posterior most cervical vertebra (CeU) of *Jiangxititan ganzhouensis* (NHMG 034062) in right lateral view. Abbreviations: EPRL, epipophyseal – prezygapophyseal lamina; lSPRL, lateral spinoprezygapophyseal lamina; met, metapophysis; mSPRL, medial spinoprezygapophyseal lamina; PCDL, posterior centrodiapophyseal lamina; pd, dorsolaterally facing platform of diapophysis; POCD-F, postzygapophyseal centrodiapophyseal fossa; PODL, postzygodiapophyseal lamina; POSD-F, postzygapophyseal spinodiapophyseal fossa; PRDL, prezygodiapophyseal lamina; PRSD-F, prezygapophyseal spinodiapophyseal fossa; prz, prezygapophysis; SPDL, spinodiapophyseal lamina; SPOL, spinopostzygapophyseal lamina. Scale bar equals 5 cm.

right sides of the pre- and postzygapophyses are widely positioned from each other, well exceeding the width of the centrum, similar to the basal titanosaur *Rukwatitan* in which the interprezygapophyseal distance is approximately twice the width of the centrum (Gorscak et al. 2014). For example, the distance between the lateral margins of the left and right postzygapophyses in CeP is greater than 48 cm, though the left postzygapophysis is incomplete. The epipophyses are present in CeA-CeU, which protrude the lateral margins of the postzygapophyses (Figures 3 and 5), unlike most of other sauropods such as *Euhelopus* (Wilson and Upchurch 2009), *Silutitan* (Wang et al. 2021), in which the epipophyses primarily protrude the posterior margin of the postzygapophyses.

Neural spines

The most striking feature of the cervicals is their deeply bifurcated neural spines and widely positioned metapophyses (Figure 2). The right sides of the metapophyses are well-preserved in CeP and CeU, while the left sides suffered from deformation. The transverse width of the metapophysis (width from the bifid point to the distal margin of metapophysis) well exceeds its centrum width or centrum height (Table 1). The metapophyses are relatively straight and direct laterodorsally, forming an angle of about 30 degree to the horizontal level, with the distal ends of the metapophyses well beyond the lateral margins of the centra, differing from *Opisthocoelicaudia* in which the metapophyses direct dorsally (Borsuk-Bialynicka 1977). The dorsal surface of the notch separating the metapophyses in CeP is smooth, and somewhat flat in CeU, no median tubercles are positioned between the metapophyses, differing from *Euhelopus* which has trifid posterior cervical neural spines. The dorsal surfaces of the distal parts of the metapophyses are rugose, directing dorsally, slightly medially. Large internal concavities can be seen from the broken surfaces of the metapophyses. The deep bifurcation of the posterior cervical neural spines in *Jiangxititan* is much more developed than in *Euhelopus*, *Phuwiangosaurus*, *Dongbeititan* (Wang et al. 2007), and other titanosauriforms with bifid neural spines from Asia, but less than most dicraeosaurids, such as *Dicraeosaurus hansemanni* from Africa (Janensch 1929).

Cervical laminae and fossa system

The cervical laminae and fossae are well developed, although some of them are damaged during the fieldwork, especially in their left sides.

The ACDL is well preserved in CeU. It projects anteromedially from the diapophysis to contact the anterolateral margin of the centrum, and is across between the nearly paralleled PCDL and CPRL, resulting in two subtriangular fossae in front and behind it, naming PRCD-F and CDF respectively, at the lateral aspect of the diapophysis (Figure 4). The CPRL seems bifurcated, with marked excavation present at the posterior margin of it.

The PCDLs are present in CeP and CeU. The right side of the PCDL in CeU is complete, projects posteromedially from the diapophysis to contact the lateral margin of the centrum, exceeding the posterior margin of the pleuroceol (Figure 4).

The CPOL can be seen in CeU, while it is broken in CeP (Figure 3). It extends medioventrally from the postzygapophysis to contact the posterior part of the PCDL.

The PRDLs are present in CeP and CeU, and are relatively complete in their right sides (Figure 3). In lateral view, the PRDL is oriented posteroventrally from the prezygapophysis to contact the diapophysis. The length of the PRDL in CeU is shorter than that of CeP, but is more robust than the latter.

The PODLs are present in CeP and CeU (Figures 3 and 5). The right side of the PODL in CeU is relatively complete. It is oriented posterodorsally from the diapophysis to contact the SPDL, then keep extending posterodorsally to contact the anterior margin of the postzygapophysis (Figure 5), forming the POSD-F and POCD-F above and below the PODL, respectively.

An EPRL is present in CeU, projecting posterodorsally from the prezygapophysis to contact the SPDL and merge with the upper part of the PODL, resulting two deep fossae, naming PRSD-F1 and PRSD-F2, respectively (Figure 5). The EPRL is oblique, unlike *Euhelopus* and *Silutitan* in which the EPRL is nearly horizontal. The EPRL is unknown in the preceding cervical due to the preservation.

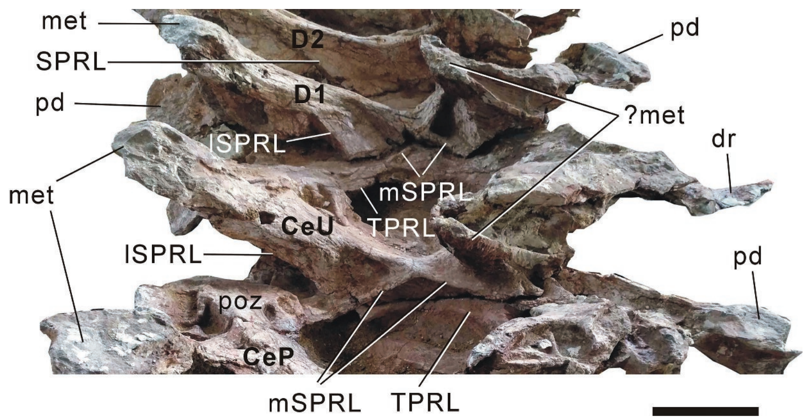

Figure 6. The CeP-D2 of *Jiangxititan ganzhouensis* (NHMG 034062) in anterodorsal view. Abbreviations: CeP, penultimate cervical vertebra; CeU, ultimate cervical vertebra; D, dorsal vertebra; dr, dorsal rib; lSPRL, lateral spinoprezygapophyseal lamina; met, metapophysis; mSPRL, medial spinoprezygapophyseal lamina; pd, dorsolaterally facing platform of diapophysis; poz, postzygapophysis; SPRL, spinoprezygapophyseal lamina; TPRL, intraprezygapophyseal lamina. Scale bar equals 10 cm.

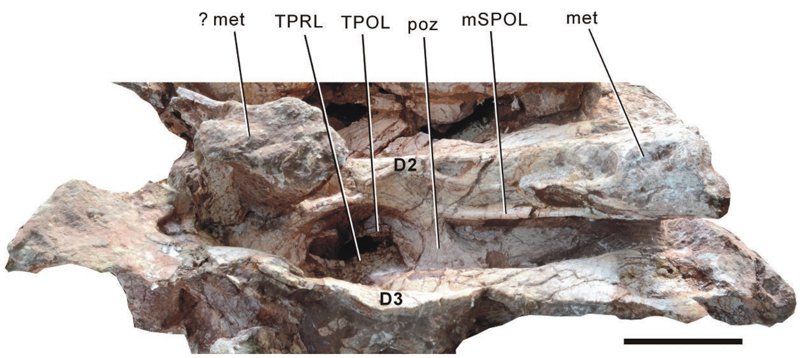

Figure 7. The second dorsal vertebra (D2) of *Jiangxititan ganzhouensis* (NHMG 034062) in posterodorsal view. Abbreviations: D, dorsal vertebra; met, metapophysis; mSPOL, medial spinopostzygapophyseal lamina; poz, postzygapophysis; TPOL, intrapostzygapophseal lamina; TPRL, intraprezygapophyseal lamina. Scale bar equals 10 cm.

The SPDLs are present in CeP and CeU, though some of them are broken away. The SPDL is complete in CeU (Figure 5), extending dorsally from the diapophysis to contact the anterior margin of the metapophysis, although the dorsal part of the SPDL is somewhat broken.

The SPRLs are present in CeP and CeU, though some of them are broken. The SPRL in CeU is divided into two laminae: lateral SPRL and medial SPRL (Figures 2, 5 and 6). The lateral SPRL projects dorsolaterally from the lateral margin of the prezygapophysis to contact the anterior margin of the metapophysis, while the medial SPRL projects dorsomedially from the medial margin of the prezygapophysis to contact its partner, forming an inverted 'V' lamina at the anterior margin of the bifid point (Figure 6). This inverted V-shaped lamina is not seen in CeP, in which only lateral SPRL is present. The prespinal and postspinal laminae are absent.

The SPOLs are present in CeP and CeU (Figures 2, 3 , and 5). The SPOL extends posteroventrally from the posteroventral margin of the metapophysis to contact the posterolateral margin of the postzygapophysis. In lateral view, the SPOL is long in CeP, and relatively short in CeU, though they are somewhat broken during the fieldwork.

Cervical ribs

The right side of the cervical rib in CeP and the left one in CeU are preserved, but are damaged during the field work (Figure 4). In ventral view, the rib shaft in CeU points posteriorly, though its distal shaft is broken.

Anterior dorsal vertebrae (Figures 2,3–4, and 6 –9; Table 1)

Centra

The centra of the dorsal vertebrae are opisthocoelous. The length of the centrum decreases compare to the preceding cervical (Table 1). In lateral view, the ventral surfaces of the dorsal centra are markedly concave anteroposteriorly. In ventral view, the ventral surfaces of the dorsal centra are slightly constricted and somewhat flat transversely between the parapophyses (Figure 4). The dorsal centra are strongly compressed dorsoventrally as in the preceding cervical centra (Table 1), with the ratio of mediolateral width to dorsoventral height of posterior articular surfaces of the anteriormost dorsal centra (D1-D3) being greater than 1.90, compare to *Ligabuesaurus*, *Mierasaurus*, and *Opisthocoelicaudia* which are 2.22, 1.80, and 1.48, respectively (Mannion et al. 2019a). This ratio is much less in *Yongjinglong* and *Dongbeititan* (Wang et al. 2007; Li et al. 2014).

The pleurocoels are preserved in D1-D4, though the posterior margin of the pleurocoel in D4 are broken (Figure 3). The posterior margins of the dorsal pleurocoels are acute, as in most other macronarians (Upchurch 1998; Mannion et al. 2013). The pleurocoels in D1–3 are large, pointing ventrolaterally, and are visible in ventral

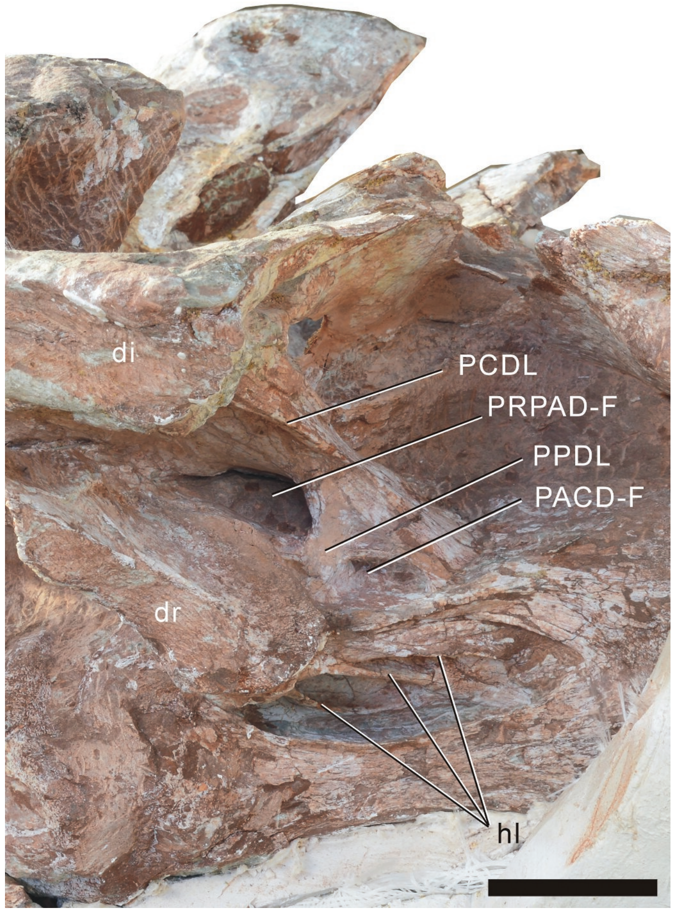

Figure 8. The third dorsal vertebra (D3) of *Jiangxititan ganzhouensis* (NHMG 034062) in left lateral view, showing the horizontal laminae within the pleurocoel. Abbreviations: di, diapophysis; dr, dorsal rib; hl, horizontal lamina; PACD-F, parapophyseal centrodiapophyseal fossa; PCDL, posterior centrodiapophyseal lamina; PPDL, paradiapophyseal lamina; PRPAD-F, prezygapophyseal paradiapophyseal fossa. Scale bar equals 5 cm.

view (Figure 4). These pleurocoels are set within the fossae, similar to most other titanosaurs (Upchurch et al. 2004). Accessory horizontal laminae are present within the pleurocoel in D3 (Figure 8).

The paraphyses are preserved in D1-D4 (Figure 3). From D1 to D4, the positions of the parapophyses vary. It positioned at the anteroventral corner of the pleurocoel in D1, and located on the anterior margin of the pleurocoel in D2, then lie slightly dorsally to the pleurocoels in D3 and D4. The parapophyses are elliptical in outline, though the posterior part of the parapophysis in D4 is broken.

Neural arches

The neural arches in D1-D3 are preserved, with the posterior part of D3 being damaged. The neural arches are low as in the preceding cervicals, with the upper margins of the neural canals being level with the TPRLs (Figure 6), although the neural canals are obscured due to the preservation. The total heights of the dorsal vertebrae are less than 30 cm due to the low neural arches and the laterally directed metapophyses, as in the preceding cervical (Table 1).

Diapophyses

The diapophyses are preserved in D1-D4, with the right side of the diapophyses being preserved better than the left side (Figures 2–4; Table 1). The diapophyses direct slightly dorsally in the dorsal vertebrae, other than laterally as in the cervical series. The articular surfaces of the diapophyses are rugose, pointing ventrally, and slightly laterally as in the preceding cervical. In ventral view, the articular surfaces of the diapophyses are subtriangular in outline, increasing in diameter from 7 cm in CeU to 13 cm in D3. The diapophyses are positioned slightly dorsally to those of the preceding cervicals, and nearly to the level of upper margin of the centrum in D3. As in the proceeding cervicals, the diapophyses of the dorsals developed a dorsally, slightly laterally facing platform (Figure 2).

Zygapophyses

The prezygapophyses and postzygapophyses in D1 and D2, and the prezygapophyses in D3 are preserved, though some of them are broken (Figures 2–4). The prezygapophyses and postzygapophyses are relatively complete in their right sides, while their left sides are damaged. As in the preceding cervicals, the left and right sides of the pre- and postzygapophyses are widely positioned from each other, well exceeding the width of the corresponding centrum. The anterior margin of the prezygapophysis in D1 and D2 is well beyond the anterior margin of the corresponding centrum, and slightly beyond the anterior margin in D3. In ventral view, the transverse width of the articular surface of the prezygapophysis in CeP to D3 increases backward (10 cm in CeP and 16 cm in D3). Accordingly, the transverse width of the articular surface of the postzygapophysis in CeP to D2 increases backward (14 cm in CeP and 20 cm in D2). In dorsal view, the distance between the medial margins of the left and right postzygapophyses in CeP to D2 decrease backward (22 cm in CeP and 9 cm in D2). The

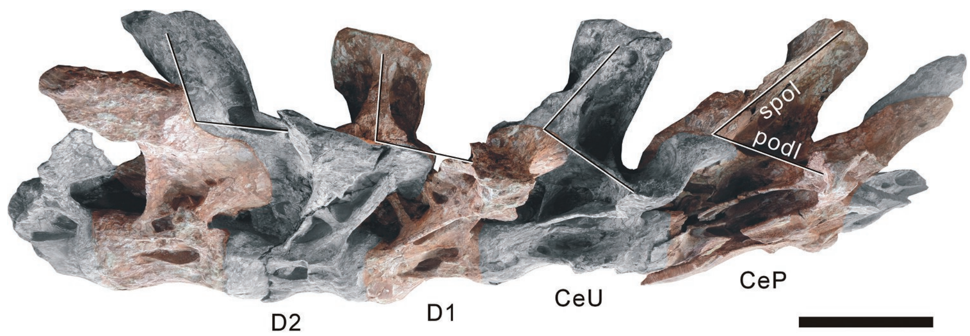

Figure 9. Holotype of *Jiangxititan ganzhouensis* (NHMG 034062) in right lateral and slightly ventral view, showing the variation of the angle between the SPOL and PODL along the cervical and dorsal series. Abbreviations: SPOL, spinopostzygapophyseal lamina; PODL, postzygodiapophyseal lamina. Scale bar equals 20 cm.

Table 2 Phylogenetic coding for *Jiangxititan* and *Gannansaurus*

Jiangxititan(40/556)
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epipophyses are present in D1 and D2, and protrude the lateral margins of the postzygapophyses as in the cervical series.

Neural spines

The dorsal neural spines are deeply bifurcated as in the preceding cervicals (Figure 2). They are well preserved in the right sides of D1 and D2, while their left sides suffered from deformation. In lateral view, the metapophysis inclines slightly posteriorly, rather than anteriorly as in the cervical series. The dorsal surfaces of the bifid points are smooth as in the preserved cervical, no median tubercles are positioned between the metapophyses. In dorsal view, the dorsal surface of the bifid point in D1 is U-shaped, with a concave posterior margin. The dorsal surfaces of the distal parts of the metapophyses are rugose, directing dorsally, slightly medially. As in the cervical series, the deep bifurcation of the neural spines is much more developed than in those of titanosauriforms (*Opisthocoelicaudia*, for example) with bifid neural spines from Asia, but less than that of *Dicraeosaurus hansemanni* from Africa.

Dorsal laminae and fossa system

The dorsal laminae and fossae are well developed as in the preceding cervical. Because the left lateral sides of the dorsal neural arches are incompletely preserved, the descriptions of the laminae and fossae are mainly based on the right lateral, dorsal, and ventral aspects.

The ACDLs are present in D1 and D2, and is absent and replaced by the rudimentary PPDL and very short but robust ACPL in D3 (Figure 3). The ACDLs in D1 and D2 are acrossed between the nearly paralleled PCDL and CPRL, resulting two fossae in front and behind it, naming PRCD-F and CDF, respectively (Figures 3 and 4). There are also two fossae in the lateral aspect of the diapophysis in D3, naming PRPAD-F and PACD-F above and below the rudimentary PPDL, respectively (Figure 3). The PACD-F is relatively small, and is positioned at the posterior margin of the parapophysis. The PRPAD-F is large, shallow dorsally and deep ventrally, with a weakly developed, anteroventrally oblique bony strut and two resulting concavities present at the ventral part of the PRPAD-F.

The PCDLs are present in D1-D3, but less developed than those in the cervical series (Figures 3 and 4). They oriented posteromedially, and slightly ventrally from the diapophyses to contact the posterolateral margins of the centra.

The CPOLs can be seen in D1, and obscured in D2 and D3 (Figure 3). The CPOL in D1 is robust, directing anteromedially and ventrally from the postzygapophysis to contact the posterior part of the PCDL.

The PRDLs are present in D1-D3 (Figure 3). In lateral view, the PRDL is short and robust in D1, and is relatively elongated in D2 and D3. It is oriented posteroventrally, and slightly laterally from the prezygapophysis in D1, and posterolaterally in D2 and D3 to contact the diapophysis.

The PODLs are present in D1 and D2 (Figure 3). The PODL is oriented posteriorly and gradually dorsally to contact the anterior margin of the postzygapophysis, as the diapophysis raised up dorsally in the dorsal vertebrae. POSD-F is also developed in D1 and D2, as in the preceding cervical (Figure 3).

The PRPLs are only present in D3 and D4 (Figure 3), in which the parapophyses are positioned at the neural arches. The PRPL in D3 is complete, and is incomplete in D4 due to the preservation.

The SPDLs are present in D1 to D3, though most of them are broken. The SPDL projects posterodorsally from the diapophysis to contact the anterior margin of the metapophysis.

The SPRLs are present in D1 to D3, though some of them are broken. The SPRLs in D1 are divided into two laminae: lateral SPRL and medial SPRL (Figures 2 and 6). The lateral SPRL projects posterolaterally and dorsally from the posterolateral margin of the prezygapophysis to contact the anterior margin of the metapophysis, while the medial SPRL projects dorsomedially and posteriorly from the medial margin of the prezygapophysis to contact its partner, forming an inverted 'V' lamina at the anterior margin of the bifid point, as in CeU (Figure 6). This inverted V-shaped lamina is not seen in D2 and D3, in which only lateral SPRL is present. The TPRL is formed between the medial margins of the prezygapophysis, and the TPOL is formed between the medial margins of the postzygapophysis (Figures 2, 6 and 7).

The SPOLs are developed in D1 and D2 (Figure 3). They are oriented almost vertically from the metapophysis to contact the postzygapophysis, unlike in the preceding cervical in which the SPOLs are oriented posteroventrally. The length of the SPOLs of D1 and D2 are much shorter than those of CeU and CeP. There are lateral SPOL and medial SPOL present in D2 (Figures 2, 3 and 7), the lateral SPOL projects ventrally from the distal end of the metapophysis to contact the lateral margin of the postzygapophysis, while the medial SPOL projects from the medial margin of the postzygapophysis to contact the posterior margin of the metapophysis. As the postzygapophysis in CeP to D2 gradually migrates to the ventral aspect of the corresponding metapophysis backward, the angles between the SPOL and the PODL increased from acute angle in CeP to obtuse angle in D2 (Figure 9).

Dorsal ribs

The dorsal ribs are only preserved in D1, D3 and D4.The rib of D1 is incompletely preserved, with its distal end broken during the field work (Figures 2 and 4). The broken distal end is elliptical in shape, with a diameter of 1.5 cm. Unlike its preceding cervical rib, the distal shaft of this dorsal rib points laterally, and somewhat posteriorly. The dorsal rib in D3 only preserved its proximal end (Figure 8). The articulated left dorsal rib in D4 is relatively well-preserved, just missing some proximal part and its distal end (Figures 2 and 4). Its preserved length is 43 cm. The capitulum is articulated with the parapophysis, while the tubercle is broken. The midshaft is comma in cross section, and become flattened distally. The broken distal end is 3 cm and 0.7 cm in diameter, indicating that this rib is gracile and relatively short, differs from *Opisthocoelicaudia* in which the rib of D4 have a length of 153 cm, with the diameters of the midshaft being 10.5 cm and 3.5 cm, respectively. It is not known whether the rib of D4 possesses the pneumatic foramina in the proximal end due to the preservation.

Phylogenetic analysis

We ran phylogenetic analysis of a matrix modified from the Poropat et al. (2023) matrix with *Jiangxititan* and the sympatric *Gannansaurus* added in. Eighteen characters were ordered following Poropat et al. (2023) but no taxon was excluded *a priori*. The matrix was analysed with equally weighted parsimony using TNT v. 1.5 (Goloboff et al. 2008; Goloboff and Catalano 2016). It was first analysed using a 'New technology search' with default settings except changing 'Random additional sequences' from 1 to 1000 and applying the Ratchet and Drift during tree search. Then the resultant most parsimonious trees were subjected to an additional round of tree bisection and reconnection (TBR) branch swapping, which finally resulted 27,720 most parsimonious trees each with a tree length of 2738 steps, a CI of 0.214, and a RI of 0.588 (we set the maximum number of trees in memory to 150,000). We calculated Bremer support and bootstrap values for the recovered clades, which are in general very low. The strict consensus of the 27,720 most parsimonious trees places *Jiangxititan* deeply within the Titanosauriformes but the sympatric *Gannansaurus* in a much earlier-diverging lineage forming a large basal polytomy near the base of the Titanosauriformes (Figure 10). More specifically, *Jiangxititan* has been recovered as a lognkosaur but *Gannansaurus* as a titanosauriform outside the late-diverging clade comprising the Diamantinasauria and Lithostrotia.

Discussions

Jiangxititan displays some features suggesting a titanosaurian affinity. The presence of acute posterior margins of pleurocoels in anterior dorsal centra and plank-like cross-sectional shape of anterior dorsal rib indicate that *Jiangxititan* is a macronarian (Mannion et al. 2013). Within Macronaria, *Jiangxititan* is more similar to Somphospondyli in displaying features such as presence of somphospondylous vertebral pneumaticity and posteriormost cervical vertebrae with low infrazygapophyseal region (region between centrum and prezygapophyses shorter than centrum height) (D'Emic 2012). Futhermore, *Jiangxititan* possesses a titanosaurian feature: the presence of an elongate parapophysis in posterior cervical vertebrae (D'Emic 2012). Finally, a feature that the posterior cervical neural arch to centrum dorsoventral height ratio less than 0.5 only present in *Jiangxititan* and the titanosaurians *Malawisaurus*, *Rapetosaurus*, *Saltasaurus*, and *Alamosaurus* (Mannion et al. 2013). Thus, we refer *Jiangxititan* to Titanosauria, which is supported by our phylogenetic analysis.

At present, as many as 15 titanosauriforms are known from the Late Cretaceous of China (Xu et al. 2022), including *Huabeisaurus*, *Zhuchengtitan*, *Gannansaurus*, *Sonidosaurus*, *Borealosaurus*, *Baotianmansaurus*, *Dongyangosaurus*, *Jiangshanosaurus*, *Qingxiusaurus*, *Qinlingosaurus*, *Xianshanosaurus*, *Yunmenglong*, *Ruyangosaurus*, *Huanghetitan ruyangensis*, and *Jiutaisaurus* (Xue et al. 1996; Pang and Cheng 2000; Tang et al. 2001; You et al. 2004; Wu et al. 2006; Xu et al. 2006; Lü et al. 2007, 2008, 2009a, 2009b, 2013a, 2013b; Mo et al. 2008, 2017; Zhang et al. 2009; Mannion et al. 2019b). In addition, some fragmentary fossils recovered from the Upper Cretaceous of China have been identified as titanosauriform dinosaurs (Han et al. 2017, 2019; Mo et al. 2018). Other titanosauriforms from the Late Cretaceous of Asia include *Opisthocoelicaudia*, *Nemegtosaurus*, *Abdarainurus*, *Quaesitosaurus* (Nowinski 1971; Borsuk-Bialynicka 1977; Kurzanov and Bannikov 1983; Averianov and Lopatin 2020). Among these Late Cretaceous titanosauriforms, only *Opisthocoelicaudia*, *Ruyangosaurus*, *Yunmenglong*, *Baotianmansaurus*, *Dongyangosaurus* and *Huabeisaurus* are represented by fossils preserving overlapping elements with *Jiangxititan*.

Jiangxititan is similar to the titanosaur *Opisthocoelicaudia* in several features present in posterior cervical and anterior dorsal vertebrae, such as spongy bone in centra and neural arches (neural spines, prezygapophyses, postzygapophyses, etc.), centra compressed dorsoventrally, neural arches low, neural spines deeply bifurcated. However, *Jiangxititan* is markedly different from *Opisthocoelicaudia* by the following features: the ratio of mediolateral width to dorsoventral height of posterior articular surfaces of anteriormost dorsal centra (D1–3) is greater than 1.90 in *Jiangxititan*, while it is 1.48 in *Opisthocoelicaudia*; the neural spines are higher and the bifurcations are more developed in *Jiangxititan* than in *Opisthocoelicaudia*.

A further comparison with *Ruyangosaurus*, *Yunmenglong*, *Baotianmansaurus*, *Dongyangosaurus* and *Huabeisaurus* which preserved overlapping elements with *Jiangxititan* suggests that *Jiangxititan* is a distinct taxon. For example, *Jiangxititan* differs from *Huabeisaurus, Ruyangosaurus*, *Yunmenglong*, and *Baotianmansaurus* in the following features: (1) posterior cervical and anterior dorsal centra strongly compressed dorsoventrally; (2) pleurocoels of the posterior cervical vertebrae complex and divided by bony septa; (3) neural spine height of the posterior cervical and anterior dorsal vertebrae greater than centrum height; (4) both the eprl and spdl present in posterior cervical vertebra; (5) inverted 'V' lamina present at the anterior margin of the bifid point in posteriormost cervical and anteriormost dorsal neural spines; (6) postzygapophyses in the posterior cervical vertebrae fan-shaped; (7) both the lateral and medial

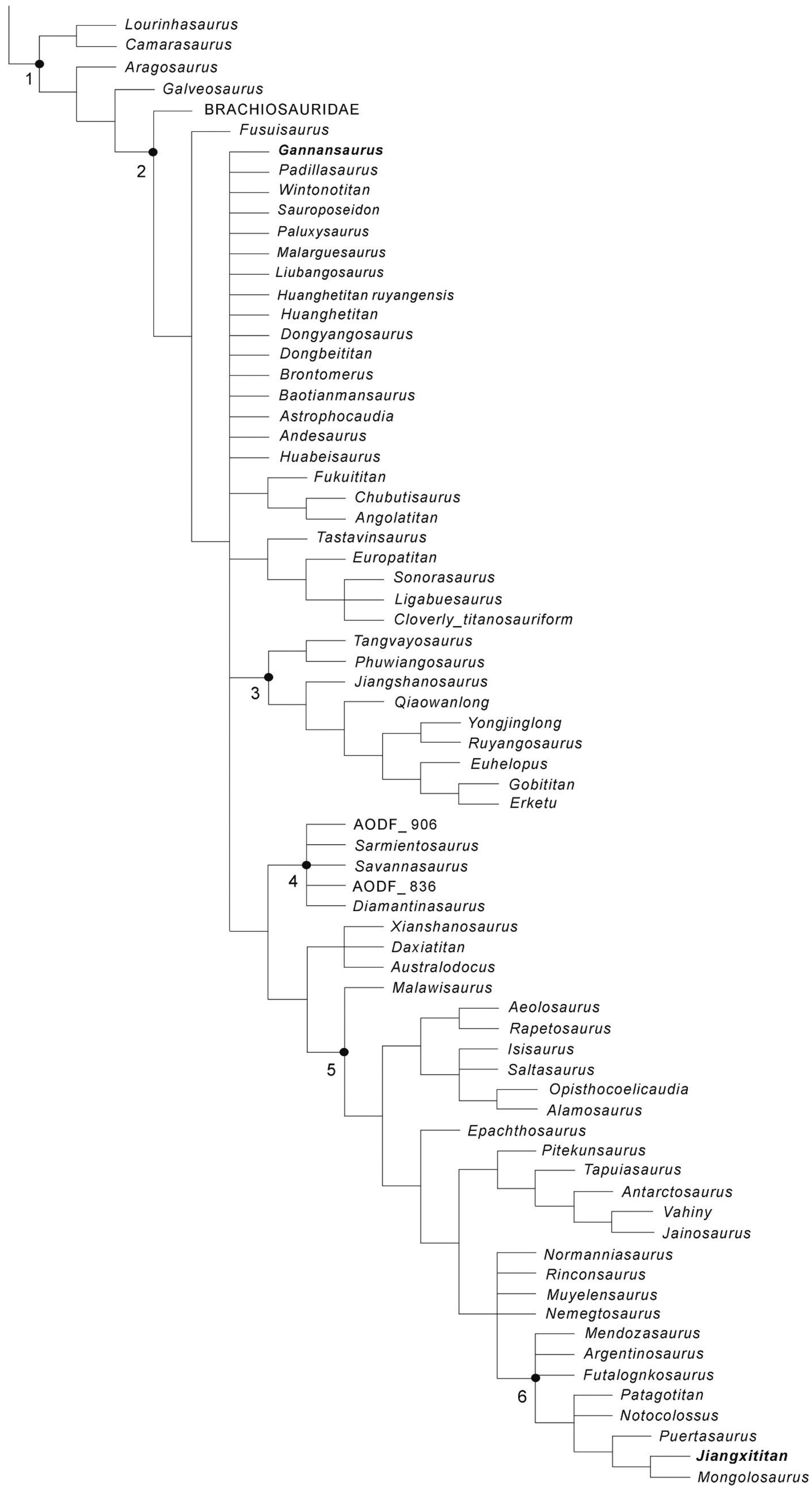

Figure 10. Phylogenetic analysis of *Jiangxititan ganzhouensis* (NHMG 034062). The data matrix follows Poropat et al. (2023), with the addition of *Jiangxititan* and *Gannansaurus* (see Table 2). Brachiosauridae has been collapsed into a single lineage. Nodes numbers indicate the clades retrieved: 1, Macronaria; 2, Titanosauriformes; 3, Euhelopodidae; 4, Diamantinasauria; 5, Lithostrotia; 6, Lognkosauria.

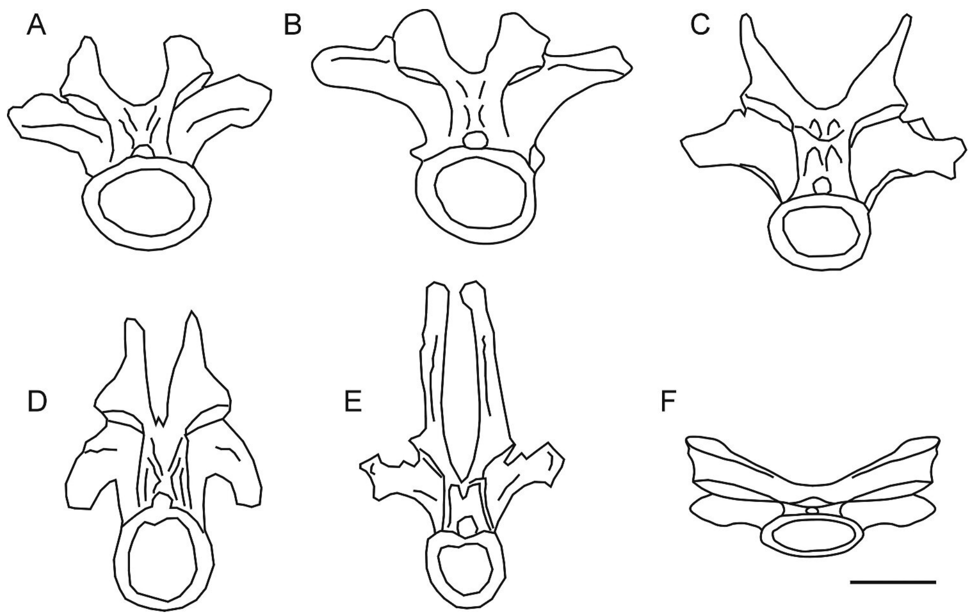

Figure 11. Comparison of the anterior dorsal vertebrae in posterior view (modified from Upchurch et al. 2004). A, *Opisthocoelicaudia*; B, *Camarasaurus*; C, *Apatosaurus*; D, *Diplodocus*; E, *Dicraeosaurus*; F, *Jiangxititan* (NHMG 034062). Scale bar equals 20 cm.

spinopostzygapophyseal laminae present in the anterior dorsal vertebrae; (8) anterior dorsal rib short and gracil.

Jiangxititan represents the second sauropod from the Upper Cretaceous Nanxiong Formation of Jiangxi Province. The first reported sauropod *Gannansaurus* is similar to *Euhelopus* in many features and thus was suggested to be closely related to the latter (Lü et al. 2013b). *Jiangxititan* displays features indicating a later-diverging position than *Gannansaurus*, and more specifically, *Jiangxititan* has been recovered as a lognkosaur but *Gannansaurus* as a titanosauriform outside the late-diverging clade comprising the Diamantinasauria and Lithostrotia, as indicated by our phylogenetic analysis. Consequently, although *Jiangxititan* does not have overlapping elements with *Gannansaurus*, we are confident that *Jiangxititan* is a distinct species from *Gannansaurus*.

Jiangxititan is distinguished from all other known sauropods by possessing the very high, deeply bifurcated and widely separated neural spines present in the posterior cervical and anterior dorsal vertebrae. Although similar conditions are present in the anterior dorsal vertebrae of *Opisthocoelicaudia*, *Camarasaurus*, *Diplodocus*, *Apatosaurus*, and *Dicraeosaurus* (Figure 11), the deep bifurcation is less developed in *Jiangxititan* than in *Dicraeosaurus*, but more developed than in *Opisthocoelicaudia*, *Camarasaurus*, *Diplodocus*, and *Apatosaurus* (Hatcher 1901; Osborn and Mook 1921; Gilmore 1936; Borsuk-Bialynicka 1977). In addition, the bifurcated neural spines direct laterally in *Jiangxititan*, very different from *Opisthocoelicaudia*, *Camarasaurus*, *Diplodocus*, *Apatosaurus*, and *Dicraeosaurus*, in which the anterior dorsal neural spines directed dorsally, rather than laterally.

Conclusions

Jiangxititan ganzhouensis is erected based on a partial skeleton from the upper Cretaceous Nanxiong Formation of Jiangxi Province, southern China. It displays some features suggesting a titanosaurian affinity. *Jiangxititan* is unique among the Asian titanosauriforms by possessing the deeply bifurcated posterior cervical and anterior dorsal neural spines, and the dorsoventrally compressed posterior cervical and anterior dorsal centra. The discovery of *Jiangxititan* increased the diversity of the titanosaurians in the Late Cretaceous of Asia.

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Disclosure statement

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