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OXFORD

Original Article

Re-evaluation of the Early Cretaceous titanosauriform sauropod dinosaur *Triunfosaurus leonardii* from the Triunfo Basin, Brazil: implications for the initial radiations of Somphospondyli and Titanosauria

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ABSTRACT

Somphospondylan titanosauriforms have a rich, global fossil record. However, the early evolutionary history of this sauropod dinosaur clade, including that of the titanosaurian lineage, is poorly understood. Purported titanosaurs have been described from the earliest Cretaceous of South America and Eurasia, which would make them the stratigraphically oldest known representatives of this clade, with implications for early titanosaur biogeography. However, their remains are fragmentary and their phylogenetic affinities require further testing. Among these is *Triunfosaurus leonardii*, known from caudal vertebrae, haemal arches, and an ischium from the Berriasian–lower Hauterivian Rio Piranhas Formation, Triunfo Basin, north-eastern Brazil. We present a redescription of the holotype of *Triunfosaurus*, including a number of anatomical re-interpretations, which enables us to provide a new diagnosis. Its inclusion into the largest phylogenetic data matrix for eusauropods so far assembled, comprising 162 OTUs (including >100 titanosauriform species) scored for 576 characters, recovers *Triunfosaurus* as a somphospondylan that is either close to, or an early-diverging member of, the titanosaur radiation. Additional results of our phylogenetic analyses indicate that the contemporaneous Argentinean sauropod, *Ninjatitan zapatai*, is probably a non-titanosaurian somphospondylan, closely related to the late Early Cretaceous taxon *Chubutisaurus insignis*, but that it could alternatively be a diplodocoid or represent chimeric remains of both clades. The stratigraphically earliest known titanosaur with unequivocal phylogenetic support comes from the Valanginian of eastern Eurasia, with our analyses reinforcing the previously proposed eutitanosaurian affinities of *Tengrisaurus starkovi*. Non-titanosaurian somphospondylans from the latest Jurassic–earliest Cretaceous are rare, but include Gondwanan and Eurasian occurrences. With the possible exception of *Triunfosaurus*, the stratigraphically earliest known titanosaurs do not belong to the earliest diverging titanosaurian lineages; members of the latter, as well as their closest relatives (e.g. *Andesaurus delgadoi*, Diamantinasauria, and *Huabeisaurus allocotus*), are from the mid-Cretaceous and globally widespread. We would expect the first titanosaurs to be morphologically closer to these taxa, rather than displaying 'typical' titanosaurian features, such as strongly procoelous anterior caudal vertebrae. Collectively, this implies that we are yet to sample representatives of the initial titanosaur radiation. The biogeographic origins of both Somphospondyli and Titanosauria are, therefore, probably obscured by spatiotemporal sampling failure.

Keywords: Gondwana; Laurasia; Mesozoic; Rio Piranhas Formation; Titanosauria

INTRODUCTION

Somphospondylan titanosauriforms were the predominant sauropod dinosaurs in the Cretaceous (D'Emic 2012, Mannion *et al.* 2019a, in press, Bellardini *et al.* 2022, Mocho *et al.* 2024a). They include the diverse titanosaurian lineage, which gave rise to the largest animals to have ever walked on land (Bonaparte and Coria 1993, Carballido *et al.* 2017), members of which were the only sauropods alive at the time of the Cretaceous/Palaeogene mass extinction, 66 million years ago (Salgado *et al.* 1997, Upchurch *et al.* 2004a, Curry Rogers 2005). Somphospondylans have a rich,

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abundant, and global fossil record (Wilson and Upchurch 2009, Cerda *et al.* 2012, Mannion *et al.* 2013, in press, Poropat *et al.* 2017, 2022, Gorscak and O'Connor 2019, Wang *et al.* 2021, Carballido *et al.* 2022a, Mo *et al.* 2023, Han *et al.* 2024, Díez Díaz *et al.* 2025). However, their early evolutionary and biogeographic history, including that of titanosaurs, is poorly understood (Le Loeuff *et al.* 2013, Dal Sasso *et al.* 2016, Gorscak and O'Connor 2016, Wilson *et al.* 2016, Mannion *et al.* 2019a, in press, Mocho *et al.* 2019a, 2024a, Gallina *et al.* 2021, 2022, Carballido *et al.* 2022b, Bellardini *et al.* 2022, Averianov *et al.* 2026, Mayer *et al.* 2026).

Given that unequivocal representatives of the somphospondylan sister-clade, Brachiosauridae, are known from the early Late Jurassic (Mannion *et al.* 2017), Somphospondyli must also have originated by then. Putative pre-Cretaceous somphospondylans are currently restricted to two species. *Australodocus bohetii* Remes, 2007, from the Tithonian section of the Tendaguru Formation of Tanzania, is known only from two cervical vertebrae; it was originally described as a diplodocid (Remes 2007), before being re-interpreted as a titanosauriform (Whitlock 2011). Most recently, Mannion *et al.* (2019b) presented new evidence that supported somphospondylan affinities for *Australodocus*. Mocho *et al.* (2019b) erected *Oceanotitan dantasi* Mocho *et al.* 2019 from the upper Kimmeridgian Praia de Amoreira–Porto Novo Formation of Portugal, based on caudal vertebrae and fragmentary appendicular remains. One of their phylogenetic analyses supported somphospondylan affinities, which would make it the stratigraphically oldest known member of the clade, but a more recent analysis placed *Oceanotitan* outside of Titanosauriformes (Mocho *et al.* 2024a).

The stratigraphically oldest specimens known from relatively complete remains that can be unequivocally assigned to Somphospondyli come from Early Cretaceous deposits. These include the non-titanosaurian species *Phuwiangosaurus sirindhornae* Martin *et al.* 1994 from the upper Valanginian–lower Hauterivian Sao Khua Formation of Thailand (Martin *et al.* 1994, Tucker *et al.* 2022) and *Garumbatitan morellensis* Mocho *et al.* 2024 from the Barremian Arcillas de Morella Formation of Spain (Mocho *et al.* 2024a), as well as the titanosaurs *Malawisaurus dixeyi* Haughton, 1928 and *Tapuiasaurus macedoi* Zaher *et al.* 2011 from the Aptian Dinosaur Beds Formation of Malawi (Jacobs *et al.* 1993, Gomani 2005) and Quiricó Formation of south-eastern Brazil (Zaher *et al.* 2011, Wilson *et al.* 2016), respectively. *Euhelopus zdanskyi* Wiman, 1929, from the Berriasian–Valanginian Mengyin Formation of eastern China (Xu and Li 2015), probably represents a stratigraphically older non-titanosaurian somphospondylan (Wilson and Upchurch 2009), although it is possible that it is more closely related to non-neosauropod mamenchisaurids instead (Moore *et al.* 2020).

Several fragmentary and highly incomplete specimens from the earliest Cretaceous that have been recently described as new species appear to also represent somphospondylans. Rather than being identified as early-diverging members, most of these have been assigned to Titanosauria. The Valanginian Murtoi Formation in eastern Russia has yielded *Tengrisaurus starkovi* Averianov and Skutschas, 2017, which is known from one cervical vertebra and a small number of caudal vertebrae and has been recovered as a lithostrotian titanosaur (Averianov and Skutschas 2017, Averianov *et al.* 2021, 2022, 2026). Wang *et al.* (2021) described *Hamititan xinjiangensis* Wang *et al.* 2021 for a series of seven articulated caudal vertebrae and chevrons from the Shengjinkou Formation of north-west China, dated to the upper Valanginian (Zheng *et al.* 2024, Song *et al.* 2025), which they recovered as a titanosaur. *Volgatitan simbirskiensis* Averianov and Efimov, 2018 is known from seven associated caudal vertebrae from an unnamed stratigraphic unit in western Russia, dated to the upper Hauterivian, and was recovered within Lithostrotia by Averianov and Efimov (2018). Gallina *et al.* (2021) erected *Ninjatitan zapatai* Gallina *et al.* 2021 for fragmentary axial and appendicular remains from the upper Berriasian–Valanginian Bajada Colorada Formation of North Patagonia, Argentina, with their phylogenetic analysis (and all subsequent analyses) supporting it as the earliest known titanosaur. Previously, *Triunfosaurus leonardii* Carvalho *et al.* 2017, known from caudal vertebrae, haemal arches, and an ischium from the Berriasian–lower Hauterivian Rio Piranhas Formation of north-eastern Brazil, was also described and recovered as a titanosaur (Carvalho *et al.* 2017), although Poropat *et al.* (2017: 571) argued that no clear titanosaurian features could be identified in these remains and suggested that *Triunfosaurus* could not be assigned beyond Somphospondyli (see also: Mannion *et al.* in press).

A number of these taxa have been central to arguments proposing either a Gondwanan or Laurasian origin for Titanosauria (e.g. Gallina *et al.* 2021, Averianov *et al.* 2026). However, the phylogenetic affinities of most of these stratigraphically early somphospondylans have not been independently tested. In particular, aside from a brief comment by Poropat *et al.* (2017), the affinities of *Triunfosaurus* have not been reconsidered and this taxon was not discussed in either the non-titanosaurian macronarian (Carballido *et al.* 2022a) or early titanosaurian (Gallina *et al.* 2022) chapters of a recent, otherwise comprehensive volume on South American sauropodomorph dinosaurs (Otero *et al.* 2022). Given that *Triunfosaurus* appears to represent one of the stratigraphically oldest somphospondylans, it remains an important, but neglected, taxon regardless of its titanosaurian affinities. To rectify this, here we present a detailed anatomical re-description of *Triunfosaurus*, including several re-interpretations of features documented in the original publication of Carvalho *et al.* (2017). We also re-evaluate the proposed titanosaurian affinities of an isolated fibula described by Ghilardi *et al.* (2016) that emanates from the same formation as *Triunfosaurus*. We re-examine the phylogenetic position of *Triunfosaurus*, alongside several other stratigraphically early purported titanosaurs, presenting a revised view of the initial radiation of the somphospondylan sauropod clade.

Institutional abbreviations: DGEO-CTG-UFPE, Departamento de Geologia, Centro de Tecnologia e Geociências, Universidade Federal de Pernambuco, Recife, Brazil; MSNM, Museo di Storia Naturale di Milano, Milan, Italy; NHMUK, Natural History Museum, London, UK; UFRJ-DG, Universidade Federal do Rio de Janeiro, Macrofossil Collection, Departamento de Geologia, Rio de Janeiro, Brazil.

SYSTEMATIC PALAEONTOLOGY

Sauropoda Marsh, 1878
Neosauropoda Bonaparte, 1986
Macronaria Wilson and Sereno, 1998

Titanosauriformes Salgado *et al.* 1997
Somphospondyli Wilson and Sereno, 1998

Triunfosaurus Carvalho, Salgado *et al.* 2017

Type species: Triunfosaurus leonardii Carvalho *et al.* 2017.

Holotype: UFRJ-DG 498 R, three articulated anterior caudal vertebrae (UFRJ-DG 498-k-R), three anterior caudal neural spines (UFRJ-DG 498-g-R, UFRJ-DG 498-h-R, UFRJ-DG 498-i-R), three proximal haemal arches (UFRJ-DG 498-b-R, UFRJ-DG 498-d-R, UFRJ-DG 498-f-R), and a right ischium (UFRJ-DG 498-a-R).

Locality and horizon: Areias Farm, Triunfo County, Paraíba State, north-eastern Brazil; Rio Piranhas Formation, Triunfo Basin, Berriasian–lower Hauterivian, Lower Cretaceous (Carvalho *et al.* 2017, Carvalho and Leonardi 2024).

Revised diagnosis: Triunfosaurus leonardii is characterized by the following three autapomorphies: (i) small tubercle close to distal end of lateral surface of anterior caudal prezygapophyses; (ii) anterior caudal neural spines strongly expanded anteroposteriorly, such that the dorsal third of the neural spine is approximately a third longer than the anteroposterior length at the base; and (iii) anteriormost haemal arch with ridges along lateral margins of proximal rami, forming flange-like processes as they continue onto the distal blade.

Additional comments: Other features listed by Carvalho *et al.* (2017) as diagnostic for *Triunfosaurus* are either more widespread amongst sauropods or are re-interpreted below. Poropat *et al.* (2017: 571) suggested that the ischium might be too large to belong to the same individual as the caudal vertebrae. However, the caudal centrum length to ischium length ratio (0.18) is comparable to that of the early-diverging titanosaur *Andesaurus delgadoi* Calvo and Bonaparte, 1991 (0.18; Mannion and Calvo 2011) and the non-titanosaurian somphospondylan *Tastavinsaurus sanzi* Canudo *et al.* 2008 (0.20; Canudo *et al.* 2008). Coupled with the close association of the remains assigned to *Triunfosaurus* (Carvalho *et al.* 2017), this supports the view that they likely represent a single individual.

Description and comparisons

Caudal vertebrae

Three articulated caudal vertebrae (UFRJ-DG 498-k-R) are preserved (Fig. 1; Table 1), as well as three additional, disarticulated, fragmentary partial caudal neural spines (UFRJ-DG 498-g-R, UFRJ-DG 498-h-R, and UFRJ-DG 498-i-R), that do not provide additional informative anatomical information. Of the articulated series, only the second vertebra preserves a substantial portion of the centrum, and this is incomplete ventrally and missing the right side, with a small anterior portion of the centrum of the third vertebra also preserved. Carvalho *et al.* (2017: 76) listed these as 'middle-anterior' caudal vertebrae in their diagnosis of *Triunfosaurus*, but otherwise described them as middle-posterior caudal vertebrae. Based on several features, including the presence of prominent caudal ribs and well-developed spinoprezygapophyseal laminae (SPRLs), we here re-interpret them as belonging to the anterior part of the caudal series instead (see also: Poropat *et al.* 2017), although they do not represent the anteriormost few caudal vertebrae.

Carvalho *et al.* (2017: 76) stated that the anterior surfaces of the centra are 'obliterated', but enough is preserved of the second vertebra to demonstrate that the centrum is anteriorly concave (Fig. 1); for example, the anterolateral margin is finished bone. Nevertheless, it is difficult to determine how deep this concavity was likely to have been because of deformation and incompleteness, and it is possible that the anterior articular surface was only mildly concave. The posterior articular surface of the centrum is essentially flat. As such, the caudal vertebrae of *Triunfosaurus* contrast with the procoelous condition that characterizes the anterior caudal centra of nearly all titanosaurs, including the early-diverging, early Late Cretaceous Argentinean taxon *Andesaurus* (Salgado *et al.* 1997). Within Titanosauria and its immediate outgroups, only the early Late Cretaceous Gondwanan clade Diamantinasauria (Poropat *et al.* 2020, 2023, Beeston *et al.* 2024), contemporaneous East Asian taxa (e.g. *Dongyangosaurus sinensis* Lü *et al.*, 2008, *Huabeisaurus allocotus* Pang and Cheng, 2000) (D'Emic *et al.* 2013, Mannion *et al.* 2019a), and possibly the mid-Cretaceous Tanzanian species *Mnyamawamtuka moyowamkia* Gorscak and O'Connor, 2019 (Gorscak and O'Connor 2019), retain the plesiomorphic condition that characterizes the anterior caudal centra of *Triunfosaurus*.

The lateral surface of the centrum is strongly concave anteroposteriorly and Carvalho *et al.* (2017: 76) listed 'posterior half of the centrum with lateral faces strongly concave having a small pleurocoels [sic]' in their diagnosis of *Trinfosaurus*. Based on Carvalho *et al.* (2017: fig. 4), Poropat *et al.* (2017: 571) commented that this morphology indicates that 'the ventrolateral surface of the centrum appears to be deeply excavated'. However, this concavity is situated on the dorsal two-thirds of the centrum (the ventral part is not preserved). It is not a distinct fossa or 'pleurocoel' and lacks sharp-lipped margins; instead it results from the natural transverse waisting (i.e. narrowing) of the centrum. With the floor of the neural canal held horizontally, the anterior and posterior margins of the centrum slope forward slightly in lateral view. However, this is not the prominent inclination seen in the anterior-middle caudal centra of some titanosaurs, including the late Early Cretaceous French species *Normanniasaurus genceyi* Le Loeuff *et al.* 2013 (Le Loeuff *et al.* 2013), as well as several latest Cretaceous lineages, such as South American aeolosaurines (Franco-Rosas *et al.* 2004, Santucci and Arruda-Campos 2011), the Spanish taxon *Qunkasaura pintiquiniestra* Mocho *et al.* 2024 (Mocho *et al.* 2024b), and the Malagasy species *Rapetosaurus krausei* Curry Rogers and Forster, 2001 (Curry Rogers 2009).

The neural arch is restricted to the anterior two-thirds of the centrum, extending up to the anterior margin of the latter. Prezygapophyses are robust and project anterodorsally. Carvalho *et al.* (2017: 76) described them as 'short' in their diagnosis of *Triunfosaurus*, but the prezygapophyses extend beyond the anterior margin of the centrum for approximately two-thirds of a centrum length. This is comparable to the anterior caudal vertebrae of most somphospondylans, whereas the prezygapophyses are typically shorter in other sauropods, irrespective of the position of the neural arch relative to the centrum (González Riga 2003,

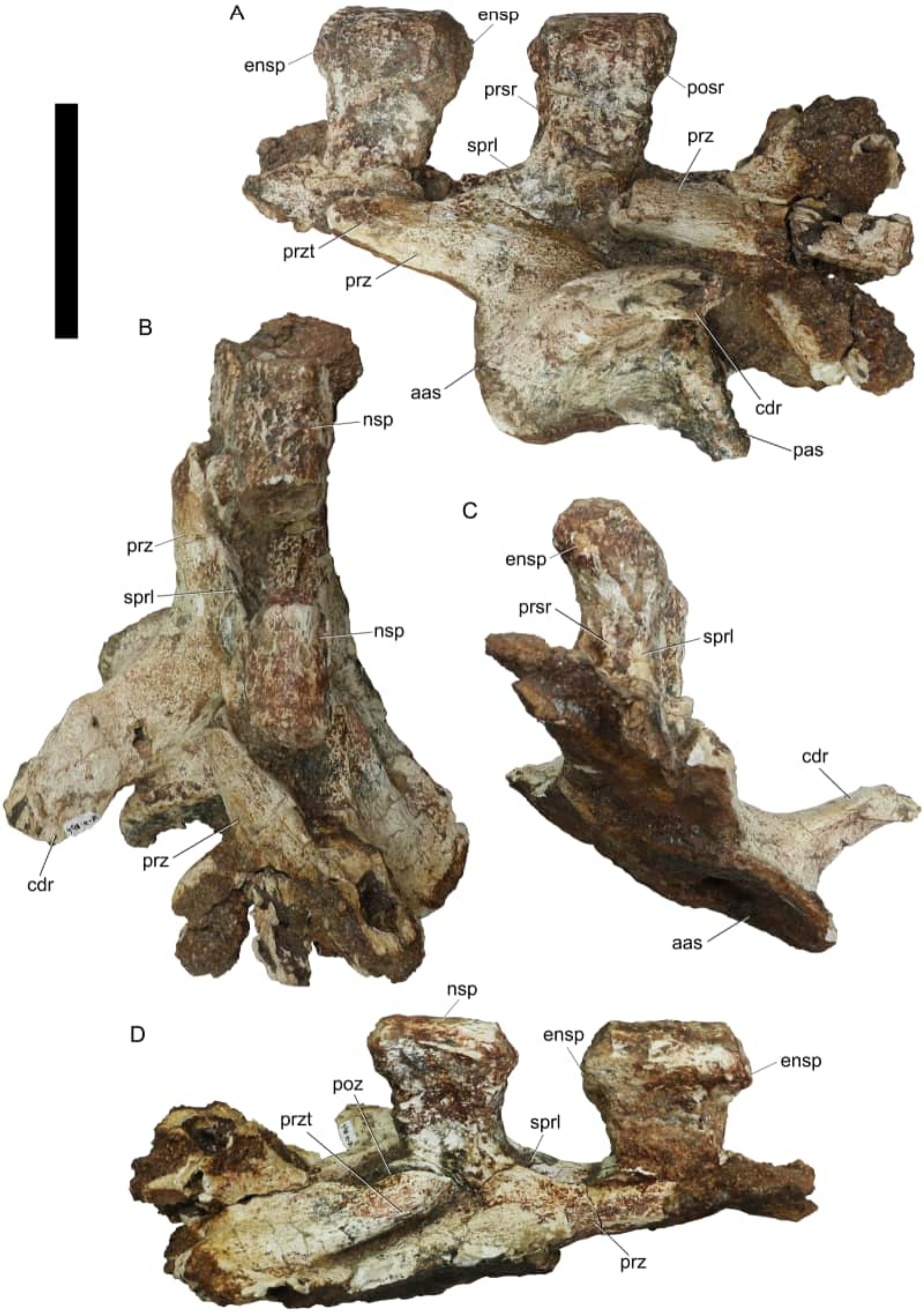

Figure 1. Photographs of articulated anterior caudal vertebrae of *Triunfosaurus leonardii* (UFRJ-DG 498-k-R) in: A, left lateral; B, dorsal (anterior towards top); C, anterior; and D, right lateral views. Abbreviations: aas, anterior articular surface; cdr, caudal rib; ensp, expanded neural spine; nsp, neural spine; pas, posterior articular surface; posr, postspinal rugosity; poz, postzygapophysis; prsr, prespinal rugosity; prz, prezygapophysis; przt, prezygapophyseal tuberosity; sprl, spinoprezygapophyseal lamina. Scale bar equals 100 mm.

Mannion *et al.* 2013, Mocho *et al.* 2024b). Unlike some aeolosaurines (Santucci and Arruda-Campos 2011), the prezygapophyses do not curve downwards at their distal ends. The prezygapophyseal articular surfaces face primarily medially. Although the outer surface is encrusted with matrix, there is a small tubercle on the lateral surface of the prezygapophysis, a short distance from the distal end. This is present on the left prezygapophysis of the second caudal vertebra and the right prezygapophysis of the third caudal vertebra (the other prezygapophyses are incomplete/concealed in the relevant region, rather than this feature being absent),

Table 1. Measurements of the first and second elements of the three articulated anterior caudal vertebrae of *Triunfosaurus leonardii* (UFRJ-DG 498-k-R).

Dimension	1st	2nd
Centrum anteroposterior length		97
Neural arch dorsoventral height		~32
Distance from anterior margin of centrum to distal tip of prezygapophysis		59
Neural spine dorsoventral height	120	108
Neural spine mediolateral width (at base)	33	26
Neural spine maximum mediolateral width	46	37
Neural spine anteroposterior length (at base)	53	54
Neural spine maximum anteroposterior length	77	71

Measurements in millimetres.

and is regarded as a newly identified autapomorphy of *Triunfosaurus*.

Postzygapophyses are large, flat facets that face mainly laterally, and slightly ventrally. Their anterior margin is roughly level with the centrum midlength, and their posterior margin extends slightly beyond that of the neural spine. It is not possible to observe the region ventral to the postzygapophyses, although it seems that there was little space between them and the posterior neural canal opening, with no possibility for the presence of a hyposphene. The absence of a hyposphene in anterior caudal vertebrae is consistent with the condition in most titanosaurs, as well as several somphospondylans that might lie just outside of this clade (Upchurch 1998, Mannion *et al.* 2013), including *Dongyangosaurus* and *Huabeisaurus* (D'Emic *et al.* 2013, Mannion *et al.* 2019a), in addition to *Tastavinsaurus* (Canudo *et al.* 2008).

Of the articulated caudal series, only the second vertebra preserves a caudal rib. This left rib is missing its distal end, but, based on a preserved disarticulated caudal rib of similar size (UFRJ-DG 498-j-R), there is probably not much material missing. The caudal rib curves posterolaterally, extending at least to the posterior margin of the centrum; as preserved, it is unclear if it extended beyond the posterior margin. Carvalho *et al.* (2017: 76) regarded upwardly inclined caudal ribs as an autapomorphy of *Triunfosaurus*, but, with the floor of the neural canal held horizontally, there is only a subtle dorsal deflection of the rib. The caudal rib is a fairly simple structure, with a flattened dorsal surface and anteroposteriorly convex ventral surface. Both its anterior and posterior margins form sharp ridges, but neither of these ridges extends on to the neural arch. Distally, the anterior ridge demarcates the flat dorsal surface of the caudal rib and a slightly ventrally tilted, small anterior surface. No tubercles or raised areas are present on the dorsal surface of the caudal rib. This contrasts with the condition in many titanosaurs (and several other eusauropods), in which there is a tubercle on the dorsal surface at approximately midlength, although this is sometimes restricted to the anteriormost caudal vertebrae (Kellner *et al.* 2005, D'Emic *et al.* 2013, Poropat *et al.* 2016). Other than the ridges on the anterior and posterior margins of the caudal rib, there is no lamina that would be described as a prezygodiapophyseal lamina (i.e. the anterior ridge does not continue up to the prezygapophysis) and no evidence for a postzygodiapophyseal lamina. However, these laminae are often present only on the anteriormost caudal vertebrae (Mannion *et al.* 2013).

The neural spine projects dorsally, with a very subtle posterior inclination. At its base, it is anteroposteriorly longer than mediolaterally wide. SPRLs are prominent structures that extend at least until the midheight of the neural spine, at which point they appear to fade out. They are restricted to the anterolateral margins of the neural spine. There is no SPRL process (*sensu* D'Emic 2012). A midline prespinal rugosity is present throughout the neural spine height, increasing in anteroposterior prominence dorsally. The posterior margins of the neural spines are not well preserved, but a comparable postspinal rugosity is also apparent, which increases in anteroposterior extent dorsally. Distinct prespinal and postspinal ridges primarily characterize the anterior caudal neural spines of titanosaurs, as well as taxa such as *Huabeisaurus*, although they are also present in some unequivocal non-titanosaurian titanosauriforms (e.g. *Giraffatitan brancai* Janensch, 1914 and *Phuwiangosaurus*), as well as other eusauropods (Mannion *et al.* 2013). In lateral view, the neural spine has subparallel anterior and posterior margins, but is strongly expanded anteroposteriorly along its dorsal third as a result of the prespinal and postsprinal rugosities. The degree of this expansion, in which the dorsal third of the neural spine is approximately a third longer than the anteroposterior length at the base (Table 1), is regarded as a newly identified autapomorphy of *Triunfosaurus*. There is no lamina or excavation on the lateral surface of the neural spine, but there is a slight transverse expansion at the apex, at the same point at which the spine expands anteroposteriorly. The dorsal surface of the neural spine is flat anteroposteriorly and transversely convex.

Haemal arches

Two fairly complete haemal arches (UFRJ-DG-498-b-R and UFRJ-DG-498-d-R), as well as the distal blade of a third haemal arch (UFRJ-DG-498-f-R), are preserved (Fig. 2; Table 2). UFRJ-DG-498-b-R was originally identified as coming from the middle caudal vertebral series (Carvalho *et al.* 2017), but is more likely to represent the anteriormost haemal arch of the tail, based on comparisons with other titanosauriforms for which this element is preserved (Mannion and Calvo 2011, Mannion *et al.* 2013). It is also only slightly dorsoventrally shorter than UFRJ-DG-498-d-R, which is undoubtedly from the anterior region of the tail.

Although not completely planar, UFRJ-DG-498-b-R is anteroposteriorly thin, with a generally flat anterior surface and an overall transversely convex posterior surface. It is proximally unbridged, with the rami well-separated from one another. In this regard, the haemal arches of *Triunfosaurus* are consistent with those of nearly all macronarians (Calvo and Salgado 1995, Upchurch 1998), with the exception of a small number of East Asian somphospondylans, including *Daxiatitan binglingi* You *et al.* 2008 and *Xianshanosaurus shijiagouensis* Lü *et al.* 2009 (Mannion *et al.* 2013). The proximal articular surfaces of UFRJ-DG-498-b-R are flat for most of their extent, without any groove, although they become anteroposteriorly convex at their very posterior ends. The absence of a proximal groove distinguishes *Triunfosaurus* from several somphospondylans, including some euhelopodids (D'Emic 2012), the early Late Cretaceous Argentinean titanosaurs *Epachthosaurus sciuttoi* Powell, 1990 (Poropat *et al.* 2016) and *Mendozasaurus neguyelap* González Riga, 2003 (González Riga *et al.* 2018), aeolosaurines (Powell 2003, Santucci and

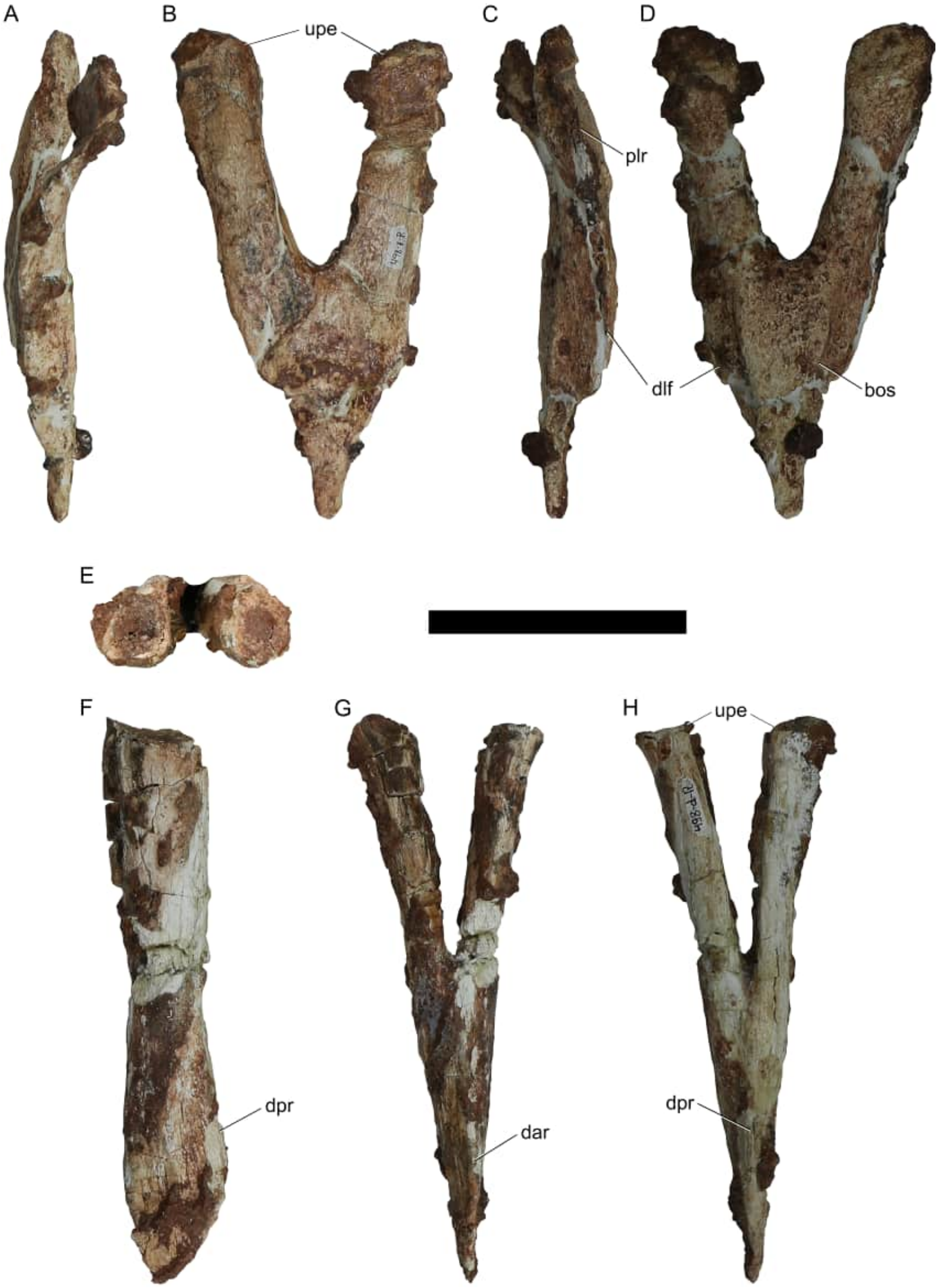

Figure 2. Photographs of anterior chevrons of *Triunfosaurus leonardii*. UFRJ-DG 498-b-R in: A, left lateral; B, anterior; C, right lateral; and D, posterior views; UFRJ-DG 498-d-R in: E, proximal; F, left lateral; G, anterior; and H, posterior views. Abbreviations: bos, break-of-slope; dar, distal anterior ridge; dlf, distal lateral flange; dpr, distal posterior ridge; plr, proximal lateral ridge; upe, unbridged proximal end. Scale bar equals 100 mm.

Arruda-Campos 2011), and the latest Cretaceous Spanish titanosaur *Lohuecotitan pandafilandi* Díez Díaz *et al.* 2016 (Díez Díaz *et al.* 2016), as well as *Oceanotitan* (Mocho *et al.* 2019b). With the flat proximal articular surfaces held horizontally, the UFRJ-DG-498-b-R haemal arch projects primarily posteriorly, with a ventral deflection. The proximal rami have a D-shaped cross-section, with sharp ridges along their lateral margins, which continue on to the distal blade as flange-like processes. These are

Table 2. Measurements of the haemal arches of *Triunfosaurus leonardii* (UFRJ-DG 498-b-R and UFRJ-DG 498-d-R).

Dimension	UFRJ-DG 498-b-R	UFRJ-DG 498-d-R
Total dorsoventral height of haemal arch	189	221*
Dorsoventral height of haemal canal	97	95
Maximum transverse width of haemal arch	108	76

An asterisk denotes an incomplete measurement. Measurements in millimetres.

most clearly seen in posterior view, where there is a distinct break in slope between them and the anteroposteriorly thicker central part of the distal blade. We regard them as a newly identified autapomorphy of *Triunfosaurus*. There are no further ridges or grooves on the haemal arch. The distal blade is dorsoventrally short, and narrows to a point along its distal half.

UFRJ-DG-498-d-R is straight, with no curvature of the distal blade: with the articular surface held horizontally, the haemal arch projects primarily ventrally, with a slight posterior deflection. UFRJ-DG-498-d-R is proximally unbridged and the articular surface of each ramus is gently concave anteroposteriorly, forming a single facet. Although missing its very distal tip, the haemal canal is >40% of the total proximodistal height of the haemal arch, which is a feature of most titanosauriforms (Curry Rogers and Forster 2001, Wilson 2002, Mannion *et al.* 2013). There are no ridges or flanges on the proximal rami, but there is a midline proximodistal ridge on the posterior surface of the distal blade, and an anterior ridge appears to develop close to the preserved distal end. These ridges result from the transverse narrowing of the shaft at this point, which becomes blade-like. It is not possible to unequivocally determine whether the distal blade expanded anteroposteriorly, although this was unlikely to have been a prominent expansion.

Ischium

A right ischium (UFRJ-DG-498-a-R) is preserved, missing its distal end, as well as much of the anteroventral margin of the distal blade (Fig. 3; Table 3). There is no iliac 'neck' and no evidence for a tubercle on the lateral surface of iliac peduncle, although the bone is broken at the very proximal end. The articular surface of the iliac peduncle is comma-shaped, pinching out at its anteromedial margin, where it merges into the medial margin of the acetabulum. The latter transversely narrows towards its anterior end, and the acetabular surface slopes to face dorsolaterally, as a result of the flange of bone that extends from the anteromedial corner of the iliac peduncle. A similar flange has been described in the East Asian somphospondylans *Huabeisaurus* and *Sonidosaurus saihangaobiensis* Xu *et al.* 2006 (D'Emic *et al.* 2013), as well as '*Ornithopsis eucamerotus*' Hulke, 1882 from the Early Cretaceous of the UK (Upchurch *et al.* 2011), which potentially represents an additional member of Somphospondyli. There is no upturned anterodorsal corner of the acetabulum in the ischium of *Triunfosaurus*, contrasting with the condition in most titanosaurs and close relatives, including early-diverging members such as *Andesaurus*, *Diamantinasaurus matildae* Hocknull *et al.* 2009, and *Dongyangosaurus*, although *Huabeisaurus* also lacks this anterodorsal projection (D'Emic 2012, D'Emic *et al.* 2013, Mannion *et al.* 2013, 2019a). The acetabular line [i.e. a straight line from the anterodorsal corners of the iliac and pubic peduncles (Carballido *et al.* 2012)] forms an approximate right angle with the long axis of the shaft. The latter passes through the upper part of the pubic articulation.

The dorsoventral height of the pubic articulation greatly exceeds the anteroposterior length of the proximal plate, as is the case in nearly all macronarians (Salgado *et al.* 1997, Carballido *et al.* 2012, Mannion *et al.* 2019b). The lateral tubercle for *m. flexor tibialis internus III* is a prominent, rounded process that is not set within a fossa. This morphology characterizes most titanosauriforms (D'Emic 2012, Poropat *et al.* 2016, Mannion *et al.* 2019b). Unlike the processes in the somphospondylans *Huabeisaurus* and *Wintonotitan wattsi* Hocknull *et al.* 2009 (D'Emic *et al.* 2013, Poropat *et al.* 2015), the tubercle is not visible in medial view.

It is not possible to unequivocally determine whether the proximal part of the distal blade was emarginated, although based on the orientation of the small portion of the anteroventral margin that is preserved it seems unlikely that it would have been. The absence of an emarginated ischium characterizes titanosaurs (Upchurch 1998, Wilson 2002) and a small number of somphospondylan taxa that might lie just outside of the clade, i.e. *Dongyangosaurus* and *Huabeisaurus* (D'Emic *et al.* 2013, Mannion *et al.* 2019a). The distal blade is transversely thicker along its posterodorsal, rather than anteroventral, surface, but it is fairly plate-like throughout. Although incomplete distally, it is extremely unlikely that the distal end would have been subtriangular and it also does not appear likely that there was much dorsoventral expansion of the blade at its distal end. Distally, the ischium is twisted, such that the conjoined ischial blades would be closer to the coplanar condition that characterizes most macronarians (Upchurch 1998, Wilson and Sereno 1998).

Ontogenetic stage

The caudal neural arches and ribs are fully fused with their respective centra, with sutures obliterated. This has traditionally been regarded as a good indicator of skeletal maturity in fossil archosaurs, but Griffin *et al.* (2021) demonstrated that the timing of fusion can vary along the vertebral column in dinosaurs. Without osteohistological data, body size is also not a robust indicator of ontogenetic status (Griffin *et al.* 2021), although the caudal vertebrae and ischium are relatively small (Table 1) compared with other somphospondylans, approximately 75%–90% the length of equivalent elements in *Andesaurus* and *Tastavinsaurus* (Canudo *et al.* 2008, Mannion and Calvo 2011). As such, we suggest that the known remains of *Triunfosaurus* might represent a subadult individual, but they are unlikely to pertain to a juvenile individual.

Affinities of DGEO-CTG-UFPE 7517

Ghilardi *et al.* (2016) described a fibula (DGEO-CTG-UFPE 7517) from the Sousa Basin, also emanating from the Rio Piranhas Formation, that they referred to Titanosauria. They highlighted two features in support of this referral. The first feature, the sigmoidal shape of the fibula, also characterizes the non-titanosaurian somphospondylan, *Tastavinsaurus* (Canudo *et al.* 2008), as noted by Ghilardi *et al.* (2016). It also characterizes numerous additional

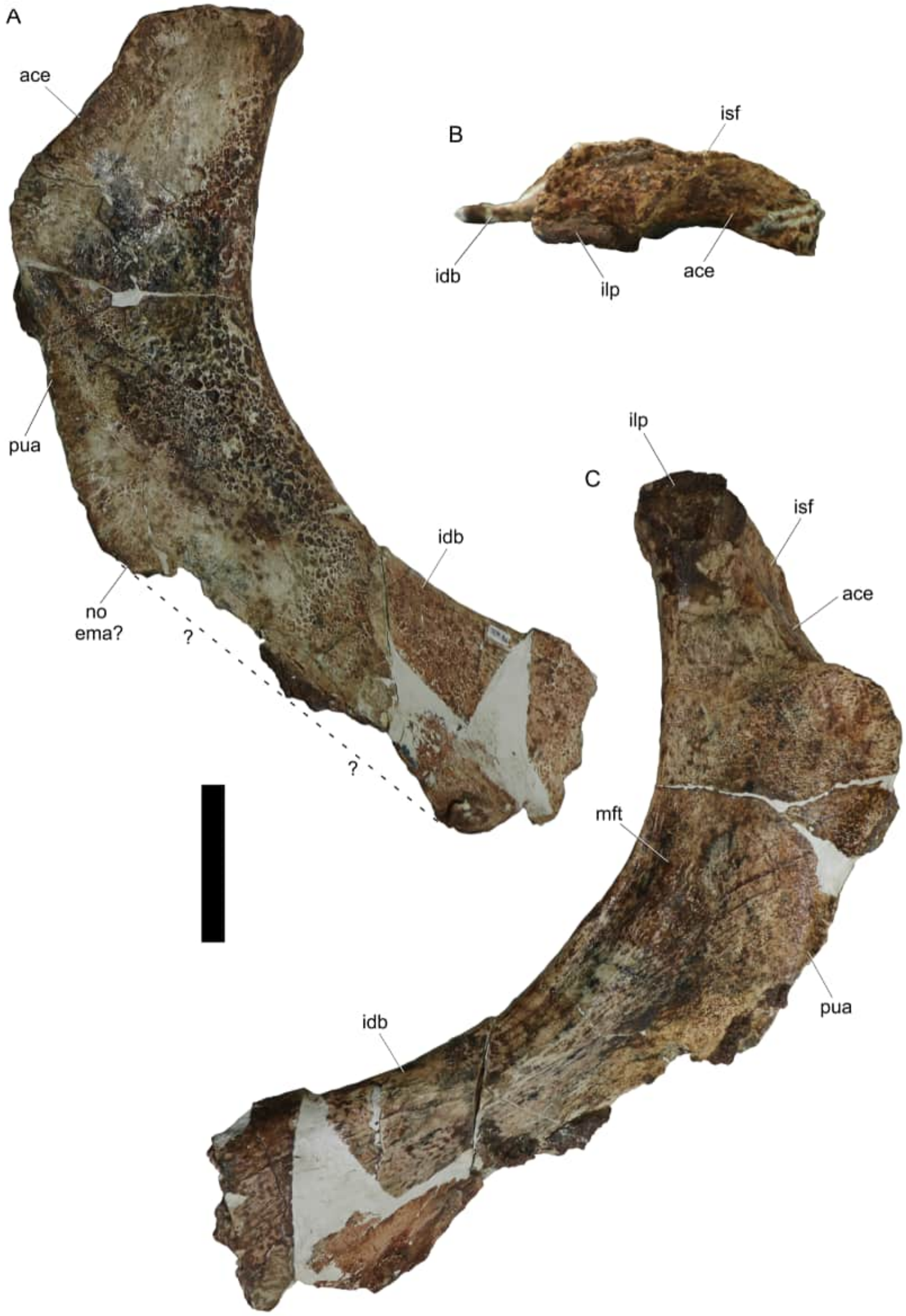

Figure 3. Photographs of right ischium of *Triunfosaurus leonardii* (UFRJ-DG 498-a-R) in: A, medial; B, proximal; and C, lateral views. Abbreviations: ace, acetabulum; ema, emargination; idb, ischiadic distal blade; ilp, iliac peduncle; isf, ischiadic flange; mft, *m. flexor tibialis internus III* attachment; pua, pubic articulation. Dashed line represents inferred anteroventral margin of blade if ischium lacks emargination distal to the pubic articulation. Scale bar equals 100 mm.

non-titanosaurian somphospondylans (D'Emic 2012, Mannion *et al.* 2013). The second feature corresponds to the triangular shape of the distal end, which does appear to be a morphology restricted to titanosaurs (Canudo *et al.* 2008, Poropat *et al.* 2016). However, the shape of the eroded distal end of the fibula described by Ghilardi *et al.* (2016: fig. 3f) is closer to the semicircular outline that characterizes many eusauropods (Poropat *et al.* 2016). As such, we re-interpret DGEO-CTG-UFPE 7517 as an

Table 3. Measurements of the right ischium of *Triunfosaurus leonardii* (UFRJ-DG 498-a-R).

Dimension	Measurement
Maximum proximodistal length	545*
Iliac peduncle maximum anteroposterior length	78
Iliac peduncle maximum mediolateral width	65
Anteroposterior length of proximal plate	143
Dorsoventral height of pubic articulation	255
Maximum anteroposterior length of blade	130*

An asterisk denotes an incomplete measurement. Measurements in millimetres.

indeterminate somphospondylan (see also: Poropat *et al.* 2017: 570–71; Averianov *et al.* 2026: 11). It is possible that DGEO-CTG-UFPE 7517 is referrable to *Triunfosaurus leonardii*, although such an attribution must await the discovery of a specimen that preserves a fibula and overlaps anatomically with the holotype of this species.

PHYLOGENETIC APPROACH AND RESULTS

Phylogenetic dataset

We added *Triunfosaurus* to the phylogenetic data matrix presented in Díez Díaz *et al.* (2025). This is the most recent iteration of a dataset originally published by Mannion *et al.* (2013), with major additions in terms of numbers of taxa and characters presented in Poropat *et al.* (2016) and Mannion *et al.* (2019a, b). As well as *Triunfosaurus*, we incorporated four additional Early Cretaceous sauropods that have been recovered as early-diverging titanosaurs in previous studies: (i) *Ninjatitan zapatai*, from the Bajada Colorada Formation of Argentina, was scored based on the description of Gallina *et al.* (2021); (ii) *Tengrisaurus starkovi*, from the Murtoi Formation of Russia, was scored based on the descriptions presented in Averianov and Skutschas (2017) and Averianov *et al.* (2021); (iii) *Hamititan xinjiangensis*, from the Shengjinkou Formation of China, was scored based on the description provided by Wang *et al.* (2021); and (iv) *Volgatitan simbirskiensis*, from an unnamed stratigraphic unit in Russia, was scored based on the description in Averianov and Efimov (2018). We also incorporated the revised information on diamantinasaurians from Beeston *et al.* (2024), comprising: (i) the five specimen-level OTUs added by those authors (AODF 0032, AODF 0590, AODF 0665, and AODF 2296, and the holotype of '*Australotitan cooperensis*'); (ii) the revisions to character scores of the type specimen OTUs of *Diamantinasaurus matildae* and *Wintonotitan wattsi* (see Appendix); (iii) the revision to character 176 (restricting the identification of camellae in anteriormost caudal vertebrae to the centrum) (see Appendix); and (iv) four of their newly added characters. Additionally, we included two further characters. The six characters added herein to the data matrix of Díez Díaz *et al.* (2025) are numbered 571–576:

C571. Anteriormost caudal neural arches, camellate internal tissue structure: absent (0); present (1) (Beeston *et al.* 2024).
C572. First caudal centrum, ventral midline keel: absent (0); present (1) (Upchurch *et al.* 2004b, Tschopp *et al.* 2015; modified here; note that the derived state is scored if a keel is present in the anteriormost caudal vertebra preserved).
C573: Humerus, ridge extends medially from deltopectoral crest, then turns to extend proximally, creating a fossa lying medial to the dorsal part of the deltopectoral crest on the anterior face: absent (0); present (1) (Beeston *et al.* 2024).
C574: Ulna, prominent interosseous ridge on distal anterior surface: absent (0); present (1) (Beeston *et al.* 2024).
C575. Ischium, prominent flange extends anteromedially from the margin of the acetabulum on the section formed by the iliac peduncle: absent (0); present (1) (new character based on: Upchurch *et al.* 2011, D'Emic *et al.* 2013).
C576: Tibia, double ridge extending distally from lateral projection of proximal articular area, with fossa posterolateral to ridges containing a lower tuberosity and an upper deep pit: absent (0); present (1) (Beeston *et al.* 2024).

Finally, we revised some character scores for the titanosauriforms *Lusotitan atalaiensis* and *Tastavinsaurus sanzi* following proposals by Mocho *et al.* (2024a), which we document in the Appendix. The revised data matrix consists of 162 OTUs scored for 576 characters. The NEXUS and TNT files, along with the full Character List, are provided as Supplementary Information.

Phylogenetic analysis

Phylogenetic analyses under a parsimony framework were run in TNT v.1.6 (Goloboff *et al.* 2008, Goloboff and Morales 2023). Following the most recent iteration of this data matrix (Díez Díaz *et al.* 2025), 17 of the 574 characters were treated as ordered (characters 11, 14, 15, 27, 40, 51, 104, 147, 148, 195, 205, 259, 297, 426, 435, 472, and 510) and eight OTUs that had previously been identified as highly unstable were excluded *a priori* to facilitate our analyses (*Astrophocaudia*, *Australodocus*, *Brontomerus*, *Fukuititan*, *Fusuisaurus*, *Liubangosaurus*, *Malarguesaurus*, and *Mongolosaurus*). Two versions of the analysis were run: one in which equal character weighting (EQW) was applied, and a second in which extended implied weighting (EIW) was implemented (Goloboff 2014), using a *k*-value of 9 (see: Mannion *et al.* 2019a). As with recent iterations of this data matrix (Poropat *et al.* 2023, Díez Díaz *et al.* 2025), eight further OTUs identified as unstable (the 'Cloverly titanosauriform', *Arrudatitan*, *Caieiria*, *Paralititan*, *Puertasaurus*, *Ruyangosaurus*, *Shingopana*, and *Trigonosaurus*) were excluded *a priori* from the EQW analysis, although they were retained in the EIW analysis. Starting with a 'New Technology Search' for both the EQW and EIW analyses, we used the 'Stabilize Consensus' option with sectorial searches, drift, and tree fusing all selected. After five rounds of consensus stabilizing, the resultant trees were used as the starting topologies for a 'Traditional Search', utilizing tree bisection–reconnection.

Phylogenetic results

Analysis under EQW resulted in >999999 most-parsimonious trees (MPTs) of length 3053 steps [consistency index (CI) = 0.198, retention index (RI) = 0.611]. Much of the topology is poorly resolved (Fig. 4) and Bremer supports are typically low across the tree, with values of 1 for most clades, including those containing the five newly added OTUs (Table 4). *Volgatitan* is recovered as a mamenchisaurid, forming a polytomy with *Mamenchisaurus* and

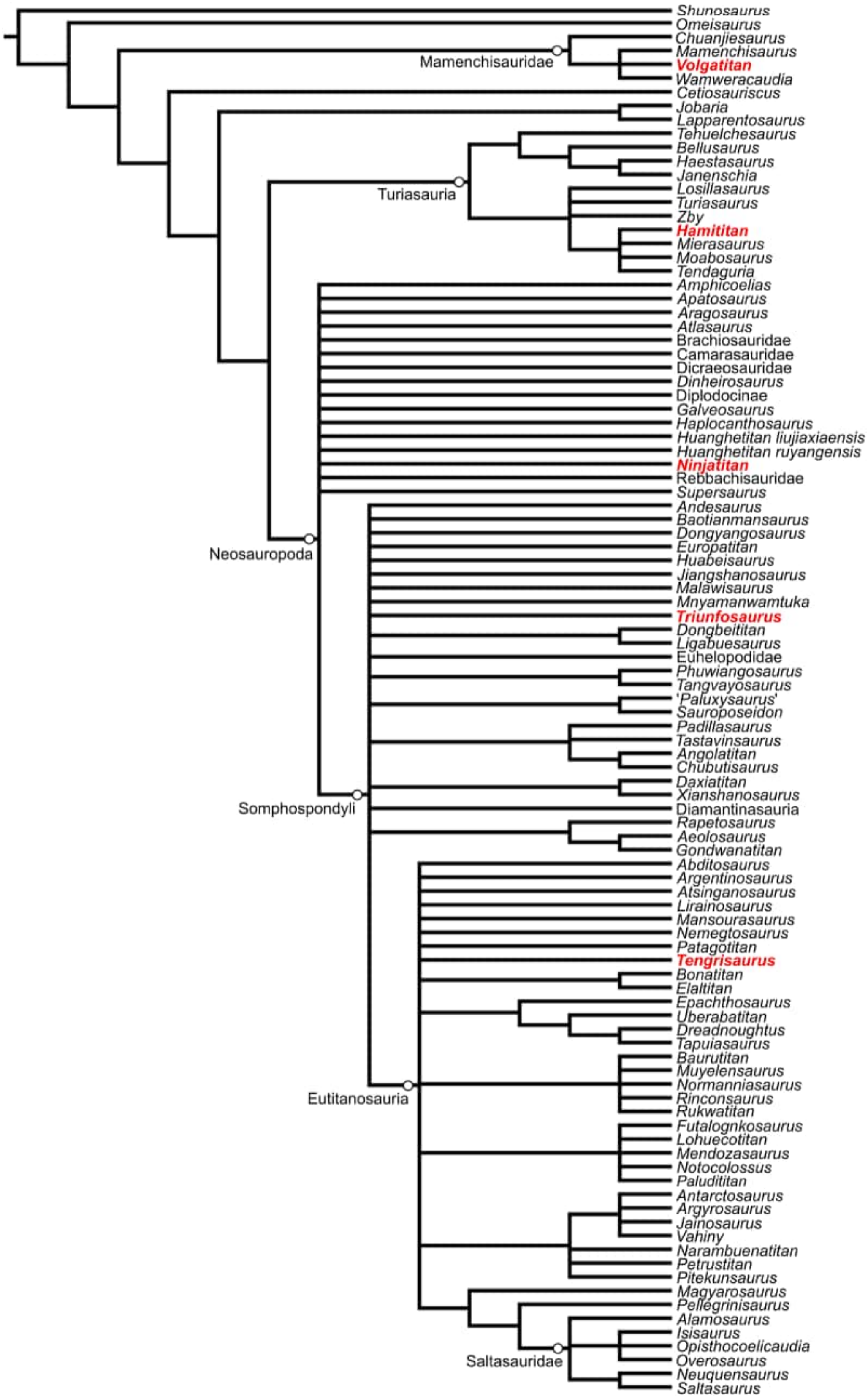

Figure 4. Strict consensus tree resulting from phylogenetic analysis using equal weighting (EQW). The five newly incorporated taxa (*Hamititan*, *Ninjatitan*, *Tengrisaurus*, *Triunfosaurus*, and *Volgatitan*) are highlighted in emboldened red font. Some clades are collapsed and the positions of some nodes are approximate.

Table 4. Summary of the phylogenetic position of the five putative titanosaurian taxa newly added to the data matrix under equal (EQW) and extended implied weighting (EIW) strategies.

Taxon	EQW	EIW
Triunfosaurus leonardii	Non-titanosaurian somphospondylan	Non-lithostrotian titanosaur
Ninjatitan zapatai	Diplodocid diplodocoid	Non-titanosaurian somphospondylan
Tengrisaurus starkovi	Eutitanosaurian lithostrotian	Colossosaurian eutitanosaur
Hamititan xinjiangensis	Turiasaurian eusauropod	Non-saltasaurid saltasauroid
Volgatitan simbirskiensis	Mamenchisaurid eusauropod	Mamenchisaurid eusauropod

Wamweracaudia. *Hamititan* is a turiasaurian eusauropod, forming a polytomy with *Mierasaurus*, *Moabosaurus*, and *Tendaguria*. The relationships of *Ninjatitan*, *Tengrisaurus*, and *Triunfosaurus* are difficult to determine from the strict consensus tree and, along with *Hamititan*, these are identified as among the most unstable OTUs. *Ninjatitan* is part of a large polytomy of non-somphospondylan neosauropods, *Triunfosaurus* is a non-lithostrotian somphospondylan, and *Tengrisaurus* is a lithostrotian titanosaur. Via exploration of the effects of *a posteriori* pruning of individual unstable OTUs and re-running the analysis excluding four out of five of the newly added OTUs *a priori* (for memory limitation reasons), our MPTs recover *Ninjatitan* as a diplodocid, *Triunfosaurus* as a non-titanosaurian somphospondylan, and *Tengrisaurus* as an early-diverging eutitanosaurian lithostrotian.

Analysis under EIW resulted in >999999 MPTs of length 123.8 steps (CI = 0.190, RI = 0.591). The topology (Fig. 5) is much more resolved than in the EQW analysis and is broadly congruent with that of recent iterations of this matrix (Beeston *et al.* 2024, Díez Díaz *et al.* 2025). The positions of the five newly incorporated taxa are also more readily identifiable than in the EQW analysis (Table 4). *Volgatitan* is once again recovered as a mamenchisaurid, in a polytomy with *Mamenchisaurus* and *Wamweracaudia*. *Ninjatitan* is recovered as a non-titanosaurian somphospondylan, the sister-taxon of the late Early Cretaceous Argentinean taxon, *Chubutisaurus*. *Triunfosaurus* is the sister-taxon to the Late Cretaceous Chinese sauropod, *Huabeisaurus*, recovered as an early-diverging non-lithostrotian titanosaurian clade. *Tengrisaurus* is a eutitanosaurian lithostrotian, forming a clade (Colossosauria *sensu* Carballido *et al.* 2022b) with mid-Cretaceous Gondwana taxa. *Hamititan* is an early-diverging non-saltasaurid saltasauroid, forming a polytomy with Late Cretaceous Gondwanan taxa. The full versions of the strict consensus tree for both the EQW and EIW analyses are provided as Supplementary Information.

DISCUSSION

Phylogenetic affinities of *Triunfosaurus leonardii*

Utilizing the data matrix presented by Carballido and Sander (2014), the only previous study to incorporate *Triunfosaurus* into a phylogenetic analysis recovered this taxon as a titanosaur, although just two additional steps were required to place it outside of Titanosauria (Carvalho *et al.* 2017). Our analyses of the phylogenetic placement of *Triunfosaurus* in an independent data matrix are unable to fully resolve this, with a position either just outside Titanosauria (EQW), or as an early-diverging non-lithostrotian titanosaur (EIW), depending on the character-weighting strategy. Under EIW, *Triunfosaurus* clusters with the Late Cretaceous East Asian taxon *Huabeisaurus*. Features shared by these taxa that support a close relationship to Titanosauria comprise: (i) the absence of a hyposphene in anterior caudal vertebrae; (ii) the presence of distinct prespinal and postspinal ridges in anterior caudal neural spines; and, possibly, (iii) the absence of an emarginated ischium. As is the case with *Triunfosaurus*, *Huabeisaurus* also lacks procoelous anterior caudal centra (D'Emic *et al.* 2013). Currently, it is not possible to robustly resolve the position of *Triunfosaurus* within Somphospondyli. As such, we cannot exclude the possibility that *Triunfosaurus* represents a titanosaur and thus would be one of the stratigraphically earliest known members of the clade.

Is *Ninjatitan zapatai* the earliest known titanosaur?

Ninjatitan zapatai was erected based on fragmentary axial and appendicular remains from the upper Berriasian–Valanginian Bajada Colorada Formation of North Patagonia, Argentina (Gallina *et al.* 2021). Although its position and interrelationships were unstable, it was recovered as a titanosaur in the phylogenetic analyses of Gallina *et al.* (2021), which were based on an iteration of the Carballido and Sander (2014) data matrix. Titanosaurian affinities for *Ninjatitan* have been consistently supported in subsequent iterations of this data matrix (Cerda *et al.* 2021, Bellardini *et al.* 2022, Simón and Salgado 2023, Filippi *et al.* 2024, Soto *et al.* 2024, Pérez-Moreno *et al.* 2025). By contrast, in the present study, analysis of its position within an independently developed phylogenetic data matrix consistently recovers it outside of Titanosauria. Whereas our EIW analysis places *Ninjatitan* as the sister-taxon of the late Early Cretaceous Argentinean taxon, *Chubutisaurus* del Corro, 1975, our EQW analysis suggests that it represents a diplodocid.

As discussed by Gallina *et al.* (2021), some features of the anterior caudal vertebra of *Ninjatitan* are not necessarily consistent with a titanosaurian placement for this taxon. Although the presence of a gently convex posterior articular surface of the anterior caudal centrum (i.e. mild procoely) of *Ninjatitan* is also a feature of the 'basal' titanosaur *Andesaurus* (Salgado *et al.* 1997), this morphology also characterizes the non-titanosaurian somphospondylan *Ligabuesaurus* Bonaparte *et al.* 2006 (Bellardini *et al.* 2022), as well as diplodocids and some dicraeosaurids (Upchurch 1998). The anteriormost caudal centra of several somphospondylans are characterized by a sharp-lipped lateral foramen, including *Chubutisaurus*, *Padillasaurus* Carballido *et al.* 2015, and *Savannasaurus* Poropat *et al.* 2016 (Carballido *et al.* 2011, 2015, Poropat *et al.* 2020); however, these are typically much smaller openings than in *Ninjatitan* (Gallina *et al.* 2021), which has an extensive excavation that is most similar to that of diplodocids and some rebbachisaurids (Upchurch 1998, Carballido *et al.* 2012, Mannion *et al.* 2019b). The anterior caudal vertebra of *Ninjatitan* is also characterized by a deep, well-defined prezygapophyseal centrodiapophyseal fossa, excavating the anterior surface of the lower neural arch and proximal portion of the caudal rib. This feature is otherwise known only in diplodocoids, characterizing members of all three diplodocimorph lineages

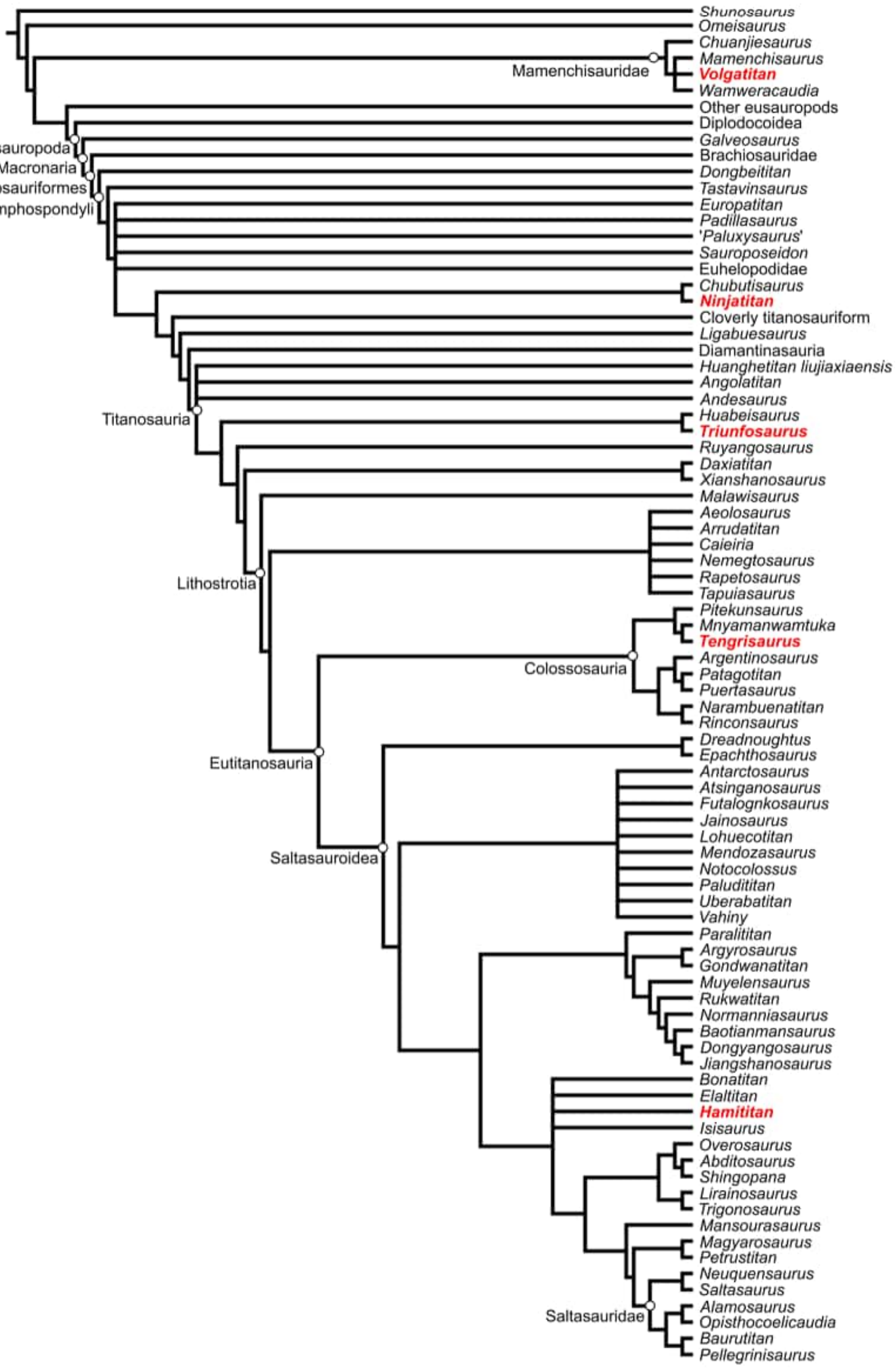

Figure 5. Strict consensus tree resulting from phylogenetic analysis using extended implied weighting (EIW). The five newly incorporated taxa (*Hamititan*, *Ninjatitan*, *Tengrisaurus*, *Triunfosaurus*, and *Volgatitan*) are highlighted in emboldened red font. Some clades are collapsed.

(Mannion *et al.* 2019b, Mannion and Moore 2025). However, other features conflict with a diplodocoid identification. This includes the camellate internal structure of the dorsal vertebra, which is a synapomorphy of Titanosauriformes (Wilson and Sereno 1998), as well as the presence of a well-developed subtriangular process at the posteroventral corner of the scapular acromion. The latter feature is not known in any diplodocoid and is primarily restricted to titanosauriforms, as well as taxa such as *Jobaria* Sereno *et al.* 1999 and *Lourinhasaurus* Lapparent and Zbyszewski, 1957 (Carballido *et al.* 2011, Mannion *et al.* 2013, 2019b, Mocho *et al.* 2014). The locality at which *Ninjatitan* was discovered has also yielded material belonging to a diplodocid, *Leinkupal laticauda* Gallina *et al.* 2014 (Gallina *et al.* 2014), and a dicraeosaurid, *Bajadasaurus pronuspinax* Gallina *et al.* 2019 (Gallina *et al.* 2019). Although the materials assigned to *Ninjatitan* were found associated in a 6 m^2 area from a stratigraphic level four metres below those diplodocoids (Gallina *et al.* 2021), it remains possible that *Ninjatitan* represents a chimera of diplodocoid and titanosauriform specimens.

The phylogenetic data matrix utilized by Gallina *et al.* (2021) includes approximately 50% of the number of titanosauriform OTUs and ~140 fewer characters as that of the present study. A potentially key difference is the extensive representation of *Diamantinasaurus* and other diamantinasaurians in the data matrix used herein, with nearly all parts of the cranial and postcranial skeleton of this clade captured in character scoring. The Gondwanan clade Diamantinasauria has been consistently recovered as either an early-diverging titanosaurian lineage or as the sister-taxon to Titanosauria in iterations of this data matrix from Poropat *et al.* (2016) onwards, making it a pivotal taxon for polarizing character scores at the base of the titanosaurian radiation (Poropat *et al.* 2021, 2023, Beeston *et al.* 2024). By contrast, iterations of the Gallina *et al.* (2021) matrix include a single diamantinasaurian OTU that is restricted to the holotype of *Diamantinasaurus* described by Hocknull *et al.* (2009) and Poropat *et al.* (2015). Crucially, that OTU lacks cranial remains, as well as parts of the postcranial skeleton such as caudal vertebrae and the pes, for which referred individuals demonstrate plesiomorphic morphologies (Poropat *et al.* 2023, Beeston *et al.* 2024). Along with an overall smaller character-taxon sampling universe, we suggest that the absence of these data in iterations of the Gallina *et al.* (2021) might affect robust recovery of the interrelationships of taxa around the base of Titanosauria.

Evidence for earliest Cretaceous Eurasian titanosaurs

On its initial description, *Tengrisaurus* was incorporated into an earlier iteration of the data matrix used herein (Mannion *et al.* 2013), in which it was recovered as an early-diverging lithostrotian titanosaur under EQW (Averianov and Skutschas 2017). A eutitanosaurian lithostrotian placement was supported in EQW analyses (Averianov and Efimov 2018, Averianov *et al.* 2021, 2026) based on subsequent iterations of this data matrix (González Riga *et al.* 2018, Mannion *et al.* 2019b). A similar position is recovered herein, with a placement as an early-diverging member of Eutitanosauria supported under both EQW and EIW. Anatomical features supporting this position were discussed in detail by Averianov *et al.* (2021, 2026). The phylogenetic affinities of *Tengrisaurus* have yet to be evaluated in an independent data matrix, but its anatomy is consistent with that of a eutitanosaurian titanosaur.

Wang *et al.* (2021) incorporated *Hamititan* into an earlier iteration of the data matrix used herein (Mannion *et al.* 2019a), and its position was also tested in an iteration of the Carballido and Sander (2014) data matrix (Filippi *et al.* 2019). Under both EQW and EIW, Wang *et al.* (2021) consistently recovered *Hamititan* as a titanosaur, although its position was highly labile. Here we recover *Hamititan* either as a turiasaurian eusauropod (i.e. outside of Neosauropoda) or a saltasauroid titanosaur. Part of this increased instability might stem from Wang *et al.* (2021) scoring *Hamititan* for numerous characters (21) pertaining to the anteriormost and middle caudal vertebrae in the Mannion *et al.* (2019a) data matrix, despite these regions of the tail (as defined in the character list) not being preserved: in the present analysis, we are only able to score 17 out of a possible 576 characters. The fragmentary and incomplete nature of the remains, with *Hamititan* known only from seven incomplete caudal vertebrae and chevrons (Wang *et al.* 2021), almost certainly contributes to its unstable phylogenetic position. Unequivocal turiasaurians have yet to be identified in East Asia (Mannion *et al.* 2019b), although the recently described *Yantaloong* Zhang *et al.* 2026 from China might represent a Middle Jurassic member of this clade (Zhang *et al.* 2026); furthermore, their presence in the earliest Cretaceous of Europe (Mannion 2019) and North America (Royo-Torres *et al.* 2017) means that a turiasaurian identification for *Hamititan* would not be that biogeographically surprising. Finally, none of the features proposed by Wang *et al.* (2021) as autapomorphic for *Hamititan* are unique to this taxon and it is likely that the holotypic remains are non-diagnostic at genus-level.

The phylogenetic affinities of *Volgatitan* have only previously been tested in one study (Averianov and Efimov 2018), in which it was recovered as a lithostrotitan titanosaur under EQW based on its inclusion in an earlier iteration of the data matrix presented herein (González Riga *et al.* 2018). Its recovery as a mamenchisaurid under both EQW and EIW herein is, therefore, perhaps surprising. Mamenchisaurids, or *Mamenchisaurus*-like taxa (see: Moore *et al.* 2020), are primarily a group of Jurassic East Asian non-neosauropod eusauropods (Xing *et al.* 2015, Moore *et al.* 2023). However, there is evidence for mamenchisaurids outside of East Asia (Mannion *et al.* 2019b) and for the group's survival within East Asia into the late Early Cretaceous (Wang *et al.* 2019). As such, the presence of a mamenchisaurid in western Eurasia in the earliest Cretaceous would not be completely unexpected. However, the features present in *Volgatitan* that are recovered as supporting mamenchisaurid affinities are not unique to the group, with the elongate and strongly procoelous anterior caudal centra, as well as the presence of a tubercle on the dorsal surface of anteriormost caudal ribs, all also characteristics of numerous titanosaurs. By contrast, as noted above, nearly all titanosaurs lack a hyposphene in the anterior caudal vertebrae (Upchurch 1998, Mannion *et al.* 2013), with a small number characterized by a ridge-like articulation, including *Tengrisaurus* (Averianov *et al.* 2021). The presence of a prominent, broad hyposphene in *Volgatitan* (Averianov and Efimov 2018) would, therefore, be unusual for a titanosaur, with such a feature otherwise known only in *Epachthosaurus* (Martínez *et al.* 2004). Nevertheless, given the fragmentary and incomplete nature of the known skeletal elements, with only seven partial caudal vertebrae known, the affinities of *Volgatitan* remain uncertain and support for a mamenchisaurid placement requires further testing.

The initial radiation of somphospondylan titanosauriforms

Here, we combine the results of our phylogenetic analyses and our discussion of the affinities of putative early titanosaurs with information on additional early somphospondylans (including putative forms) from the literature. We synthesize these data to present an updated view on the early evolutionary and biogeographic history of Somphospondyli and its subclade Titanosauria (Fig. 6).

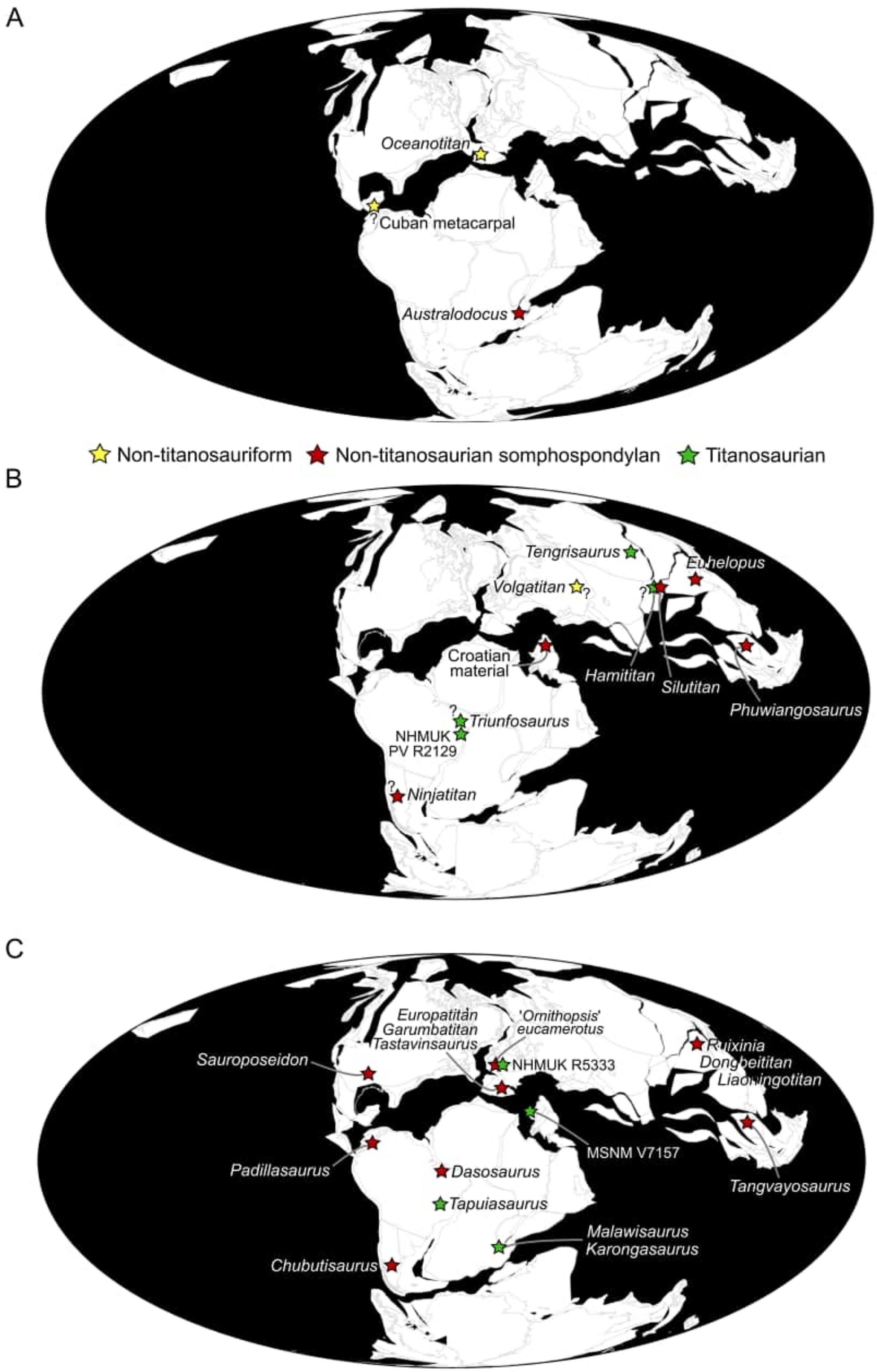

Figure 6. Palaeogeographic distribution of early somphospondylan titanosauriforms, showing occurrences in the: A, Late Jurassic; B, earliest Cretaceous (Berriasian–Hauterivian); and C, late Early Cretaceous (Barremian–Aptian). Red stars denote a non-titanosaurian somphospondylan; green stars denote a titanosaur; and yellow stars denote material previously attributed to Somphospondyli that we regard as a non-titanosauriform eusauropod. A '?' symbol represents where there is uncertainty in this taxonomic assignment. Palaeogeographic reconstructions utilize GPlates and were modified from *The Paleobiology Database's* Navigator (https://paleobiodb.org/navigator/). The palaeogeographic reconstructions represent the Tithonian (A), Valanginian (B), and Barremian (C) stages.

Footprints from the Bathonian (late Middle Jurassic) of the UK were originally interpreted as the traces of titanosaurs (Day *et al.* 2002). This identification was based on the wide gauge of the trackways and the lack of manual phalangeal impressions, which are both consistent with the anatomy of titanosaurs (Wilson and Carrano 1999). These footprints and others like them have been the subject of extensive debate (e.g. Wilson 2005; see: Mannion *et al.* in press). A wide gauge has since been attributed to a broader array of eusauropods, with body mass and substrate potentially key additional factors in determining gauge (Farlow *et al.* 1989, Henderson 2006); furthermore, there is evidence that sauropods could switch between narrow and wide gauges within an individual trackway (e.g. Marty *et al.* 2010). Finally, at least some narrow-gauge sauropod trackways preserve footprints that lack manual phalangeal impressions (Heredia *et al.* 2019). As such, whilst these Bathonian UK footprints could represent the stratigraphically earliest known titanosaurs, at present it is not possible to assign them beyond Eusauropoda.

A partial metacarpal from the Oxfordian of Cuba was referred to Somphospondyli by Apesteguía *et al.* (2021), primarily on the basis of its shared curvature with the first and second metacarpals of some members of that clade (Apesteguía 2005). However, the element is too fragmentary and incomplete to confidently reconstruct its morphology, precluding a confident taxonomic identification (Mannion *et al.* in press). As such, we regard it as an indeterminate eusauropod of uncertain affinities. Despite initially being considered as a possible somphospondylan, *Oceanotitan dantasi*, from the upper Kimmeridgian Praia de Amoreira–Porto Novo Formation of Portugal (Mocho *et al.* 2019b), is now regarded as a non-titanosauriform macronarian (Mocho *et al.* 2024a). Therefore, *Australodocus bohetii*, from the Tithonian section of the Tendaguru Formation, Tanzania (Remes 2007), is currently the only pre-Cretaceous evidence of a somphospondylan titanosauriform (Mannion *et al.* 2019b). Known from just two cervical vertebrae, *Australodocus* can only be regarded as a probable member of this lineage, although this identification is supported by the presence of a camellate internal structure throughout the centrum and neural arch (Mannion *et al.* 2019b), which is otherwise known only in Somphospondyli (Wilson and Sereno 1998).

By the earliest Cretaceous, somphospondylans that appear to lie outside of the titanosaur radiation are rare, but seemingly widespread, comprising: (probably) *Ninjatitan* (upper Berriasian–Valanginian) and (possibly) *Triunfosaurus* (Berriasian–lower Hauterivian) from South America; *Euhelopus* (Berriasian–Valanginian), *Silutitan* Wang *et al.* 2021 (Valanginian), and *Phuwiangosaurus* (upper Valanginian–lower Hauterivian) from East Asia (D'Emic 2012, Wang *et al.* 2021); and generically indeterminate remains from the upper Hauterivian (or lower Barremian) of Croatia, which at the time was part of the Afro-Arabian plate (Dalla Vecchia 2005). By the Barremian, this distribution had expanded into western Europe, with *Europatitan* Torcida Fernández-Baldor *et al.* 2017, *Garumbatitan*, and *Tastavinsaurus* from Spain (Canudo *et al.* 2008, Torcida Fernández-Baldor *et al.* 2017, Mocho *et al.* 2024a), as well as fragmentary remains from the UK (Upchurch *et al.* 2011, Higgins *et al.* 2024), in addition to *Padillasaurus* from northern South America [Mannion *et al.* 2017; though see Carballido *et al.* (2015) regarding brachiosaurid affinities].

Globally, the stratigraphically earliest known species for which our analyses are consistent with regard to a titanosaurian placement is *Tengrisaurus* from the Valanginian of eastern Eurasia (Averianov and Skutschas 2017, Averianov *et al.* 2026). It remains possible that *Hamititan*, from the Valanginian of East Asia, also represents a titanosaur (Wang *et al.* 2021), but the results of our analyses do not consistently support this interpretation. Other Laurasian pre-Albian remains that appear to represent Titanosauria are restricted to a fragmentary partial caudal vertebral series (NHMUK R5333) from the Barremian of the UK (Upchurch *et al.* 2011, D'Emic 2012, Mannion *et al.* 2013). The stratigraphically earliest remains from Gondwana that can unequivocally be attributed to Titanosauria are dated to the Aptian, represented by *Malawisaurus* and *Karongasaurus* Gomani, 2005 from Malawi (East Africa) and *Tapuiasaurus* from south-eastern Brazil (Jacobs *et al.* 1993, Gomani 2005, Zaher *et al.* 2011). An isolated caudal vertebra from the Aptian–Albian of present-day Italy (MSNM V7159), which at the time would have been part of the Afro-Arabian plate (Randazzo *et al.* 2021), also appears to represent a titanosaur (Dal Sasso *et al.* 2016, Mocho *et al.* 2019a). However, another caudal vertebra (NHMUK PV R2129), that probably emanates from the upper Hauterivian–Barremian Pojuca Formation of north-east Brazil, seems to represent a stratigraphically earlier Gondwanan occurrence (Bandeira *et al.* 2025). If the results from our EIW analysis are correct, then *Triunfosaurus* would predate these remains as the earliest known titanosaur from Gondwana and possibly globally, although limited constraint on its stratigraphic age (i.e. Berriasian–lower Hauterivian) precludes an exact assessment of the latter.

Taken at face value, the fossil record might imply that Somphospondyli originated in south-eastern Africa in the latest Jurassic, spreading westwards and northwards, including into Eurasia, in the earliest Cretaceous. However, fossil occurrences of the sister-taxon to Somphospondyli, i.e. Brachiosauridae, date back to the Oxfordian (Mannion *et al.* 2017). Furthermore, brachiosaurids had a widespread Late Jurassic distribution that included Laurasia and Gondwana, and their centre of origin is unknown (e.g. D'Emic 2012, Mannion *et al.* 2013). As such, somphospondylans must also have been present back in the Oxfordian and it is, therefore, not possible to deduce their biogeographic origin. The results of our phylogenetic analyses, coupled with a literal reading of the fossil record, might point to two possible scenarios for the biogeographic origin of Titanosauria. With *Triunfosaurus* as the earliest known titanosaur, Titanosauria potentially originated in east-central South America in the earliest Cretaceous, spreading southwards and to the north-east, including into Eurasia. If *Triunfosaurus* is not a titanosaur, then we might envisage that the clade originated in eastern Eurasia (e.g. see: Averianov *et al.* 2026), spreading westward and into western Gondwana during the middle Early Cretaceous, and diversifying in the mid-Cretaceous. However, we consider arguments supporting either scenario as premature given spatiotemporal sampling failure that clouds our understanding of much of the Mesozoic dinosaur record, especially that of the earliest Cretaceous (Mannion 2024). This is further reinforced in that the taxa often recovered as stratigraphically early titanosaurs do not typically belong to the earliest diverging titanosaurian lineages (see also: Mannion *et al.* 2019a, Mocho *et al.* 2019a, Averianov *et al.* 2021, 2026). With the possible exception of *Triunfosaurus*, taxa recovered as early-diverging titanosaurs or their closest relatives are all from the mid-Cretaceous. Furthermore, these earliest diverging titanosaurs and their closest relatives (e.g. *Andesaurus*, Diamantinasauria, and *Huabeisaurus*) are widely distributed, coming from both Gondwana (Argentina, Australia, and Brazil) and Laurasia (China). Based on the anatomy of taxa such as *Andesaurus* and Diamantinasauria, we would expect the earliest diverging titanosaurs to be morphologically closest to them, rather than sharing 'typical' titanosaurian features (e.g. strongly procoelous anterior caudal vertebrae) with taxa such as *Tengrisaurus*. As such, even if *Tengrisaurus* is the stratigraphically earliest known member of Titanosauria, we do not regard this as support for an Eurasian origin of this clade (*contra* Averianov *et al.* 2026). Collectively, this implies that we are yet to sample representatives of the initial titanosaur radiation, meaning that any assessment of the group's biogeographic origin is potentially problematic, especially if this does not factor in spatiotemporal heterogeneity in our sampling of their fossil record.

CONCLUSION

Re-evaluation of the earliest Cretaceous Brazilian sauropod dinosaur *Triunfosaurus leonardii* shows that it represents a valid species of somphospondylan titanosauriform, but phylogenetic analyses utilizing different character-weighting strategies yield conflicting results as to whether or not it is a member of Titanosauria. A contemporaneous species from Argentina, *Ninjatitan zapatai*, previously proposed as the earliest known member of Titanosauria, is consistently recovered outside of this clade. Our analyses provide renewed support for eutitanosaurian affinities for the earliest Cretaceous Eurasian species *Tengrisaurus starkovi*. Although this might be interpreted to indicate a notably different biogeographic origin for the group than typically proposed, we argue that sampling failure masks our understanding of both the timing and place of origin for both Somphospondyli and Titanosauria.

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SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

All data are available in the publication and in the Supporting Information.

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APPENDIX

The following character scores were revised for existing OTUs in the Díez Díaz *et al.* (2025) data matrix (with the first number denoting the character and the number/symbol in parentheses indicating the new score):

Alamosaurus: 176 (0)

Bonatitan: 176 (0)

Diamantinasaurus (AODF 0603): 394 (1)

Lusotitan: 48 (0&1); 162 (?); 206 (0&1); 210 (1); 211 (1); 334 (?); 419 (?); 481 (?); 483 (?); 500 (?); 524 (1); 525 (0)

Malawisaurus: 176 (0)

Pellegrinisaurus: 176 (?)

Savannasaurus: 176 (0)

Tastavinsaurus: 162 (1); 163 (0); 175 (?); 256 (1)

Wintonotitan: 45 (?); 46 (?); 192 (0&1); 206 (?); 217 (1); 228 (?); 236 (?); 239 (?); 249 (?); 252 (?); 282 (?); 284 (1); 358 (?); 376 (?); 513 (1)