The oldest titanosaurian sauropod of the Northern Hemisphere

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Abstract

Volgatitan simbirskiensis, gen. et sp. nov., is described based on a series of anterior and middle caudal vertebrae from a single individual discovered in the Lower Cretaceous (upper Hauterivian, Speetoniceras versicolor ammonite Zone) marine deposits at Slantsevy Rudnik vertebrate locality near Ulyanovsk City, Russia. The new taxon is characterized by strongly procoelous anterior and middle caudal vertebrae, a long centrum of the first caudal vertebra, a strong ventral ridge in the anterior and middle caudal vertebrae, a neural arch positioned at the anterior half of the centrum, hyposphene-hypantrum articulation in the anterior caudal vertebrae, and somphospondylous bone texture. Phylogenetic analysis places the new taxon as a lithostrotian titanosaur, a basal member of the lineage leading to the Lognkosauria. This lineage previously contained only South American taxa with body mass reaching 60–70 tons. *Volgatitan* gen. nov. is the first European and the geologically oldest representative of this lineage. Its body mass is estimated as 17.3 tons. Discovery of *Volgatitan* gen. nov. suggests that the lithostrotian lineage leading to the Lognkosauria had a wider distribution in the Early Cretaceous and became extinct everywhere except South America by the end of the Early Cretaceous.

Keywords: Dinosauria, Sauropoda, Titanosauriformes, Titanosauria, Lithostrotia, Early Cretaceous, Eastern Europe, Russia.

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Introduction

The Cretaceous dinosaurs of European Russia are virtually unknown because most of this territory was covered by epicontinental seas during the whole Cretaceous Period (Moskvin, 1986). The rare dinosaur bones are found in near-shore marine sediments. These findings include an ornithopod tooth and vertebra from the Albian-Cenomanian of Belgorod Province, a poorly preserved theropod tooth and ankylosaur braincase fragment from the Maastrichtian of Volgograd Province, and a partial skeleton of ornithopod *Riabininohadros weberae* from the Maastrichtian of Crimea (Riabinin, 1945; Nesov, 1995; Arkhangelsky and Averianov, 2003; Averianov and Yarkov, 2004).

Another significant discovery of Cretaceous dinosaurs in European Russia was made by one of us (VE) in 1982 during prospecting for vertebrate fossils along the right bank of the Volga River, 0.5 km south of Slantsevy Rudnik settlement, about 5 km north of Ulyanovsk City, Russia. We discovered large bones embedded in two pyritic limestone nodules. In 1984–1987 three more limestone

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modules with bones were found at the same places. The concretions were subsequently washed out from the outcrop by the river. The extraction of the bones from the nodules took several years. Altogether seven fragmentary vertebrae were extracted. The first three recovered vertebrae were referred to as "gigantic vertebrae" of unknown taxonomic attribution (Efimov, 1987). In the early 1990s VE discussed these vertebrae with L. A. Nesov from Saint Petersburg State University, who suggested that they could be anterior caudals of a sauropod dinosaur. Subsequently, five vertebrae were briefly described and one (UPM 976/2) was figured in a short note (Efimov, 1997b). These materials were tentatively attributed to the Brachiosauridae in that publication. Later, the taxonomic attribution of these specimens was changed to the Titanosauridae (Efimov, 2001; Efimov and Efimov, 2015), although they were still referred to the Brachiosauridae in a recent publication (Efimov, 2016). In the later publication a photograph of six vertebrae was published (Efimov, 2016: Fig. 1). Alifanov (2012) noted that these procoelous caudal vertebrae are better referable to the Titanosauridae than to the Brachiosauridae.

The vertebrae represent successive anterior (including the first caudal) and middle caudals undoubtedly belonging to a single individual. The animal was buried in deep water marine deposits together with marine invertebrates and marine reptiles. The only other reliable Early Cretaceous records of dinosaurs in the region are fragmentary sauropod metacarpals found in the upper Hauterivian deposits 0.3 km north of Slantsevy Rudnik settlement (Efimov, 2001, 2016). In this paper we provide a detailed description of the sauropod caudal vertebrae from Slantsevy Rudnik.

The nomenclature of the vertebral fossae and laminae follows Wilson (1999, 2012) and Wilson et al. (2011). The described specimens are housed in Ulyanovsk Paleontological Museum (UPM).

Geological context

The sauropod caudal vertebrae described herein were found along the right bank of the Volga River, 500 m south of Slantsevy Rudnik Village (previously known as Zakharievskii Rudnik) in Ulyanovsk Province, Russia (Fig. 1). The marine Lower Cretaceous section, containing a rich invertebrate fauna, has been described repeatedly in the literature (Pavlow and Lamplugh, 1892; Pavlow, 1901; Chernova, 1951; Sazonova, 1958; Glazunova, 1967, 1973; Myatlyuk, 1984; Baraboshkin et al., 2001; Guzhikov, Baraboshkin, and Birbina, 2003; Blagovetshenskiy and Shumilkin, 2006a, b; Baraboshkin and Blagovetshenskiy, 2010). The section at Slantsevy Rudnik represents the upper part of the Hauterivian with a total thickness of 38.8 m (Baraboshkin and Blagovetshenskiy, 2010). The deposits consist of a monotonous thickness of dark gray, slightly sandy shales, interbedded with siltite beds and containing large carbonate concretions (Fig. 1). These deposits are referred to the ammonite Speetoniceras versicolor Zone, the lower of the three ammonite zones of the upper Hauterivian (Pavlow, 1901; Glazunova, 1967; Baraboshkin and Blagovetshenskiy, 2010). UPM 976 was found in the dark gray shales and siltites of the g-3.1 horizon, in the lower part of the Speetoniceras versicolor Zone (Fig. 1). Besides the abundant invertebrates, the Hauterivian outcrops near Slantsevy Rudnik produced remains of marine reptiles, including the ichthyosaur *Plutoniosaurus bedengensis* and pliosaurids *Makhaira rossica* and *Luskhan itilensis* (Efimov, 1997a; Fischer et al., 2015, 2017).

Systematic paleontology

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Sauropoda Marsh, 1878
Titanosauriformes Salgado et al., 1997
Titanosauria Bonaparte et Coria, 1993
Lithostrotia Upchurch et al., 2004

Volgatitan gen. nov.
urn:lsid:zoobank.org:act:6DF2AAE2-E560-4AA6-B38C-1B2A7314BC85

Etymology — From Volga River and Greek Τιτάν (titan), a member of the second order of divine beings, descended from the primordial deities and preceding the Olympian deities in Greek mythology.

Type species — *Volgatitan simbirskiensis* n. sp.

Differential diagnosis — As for the type and only species.

Distribution — Early Cretaceous, Eastern Europe.

Volgatitan simbirskiensis sp. nov.
urn:lsid:zoobank.org:act:91E2FF16-66DB-4CDD-B8DA-63414DFF30E9
Figs 2–5

Etymology — From Simbirsk, the former name of Ulyanovsk city.

Holotype — UPM 976/1–7, seven caudal vertebrae from a single individual.

Type horizon and locality — Slantsevy Rudnik, near Ulyanovsk city, Ulyanovsk Province, Russia; Lower Cretaceous (upper Hauterivian, Speetoniceras versicolor ammonite Zone).

Diagnosis — Referred to Titanosauriformes based on the neural arch of anterior and middle caudal vertebrae positioned at the anterior half of the centrum. Referred to Titanosauria based on the procoelous anterior and middle caudal vertebrae with strongly convex

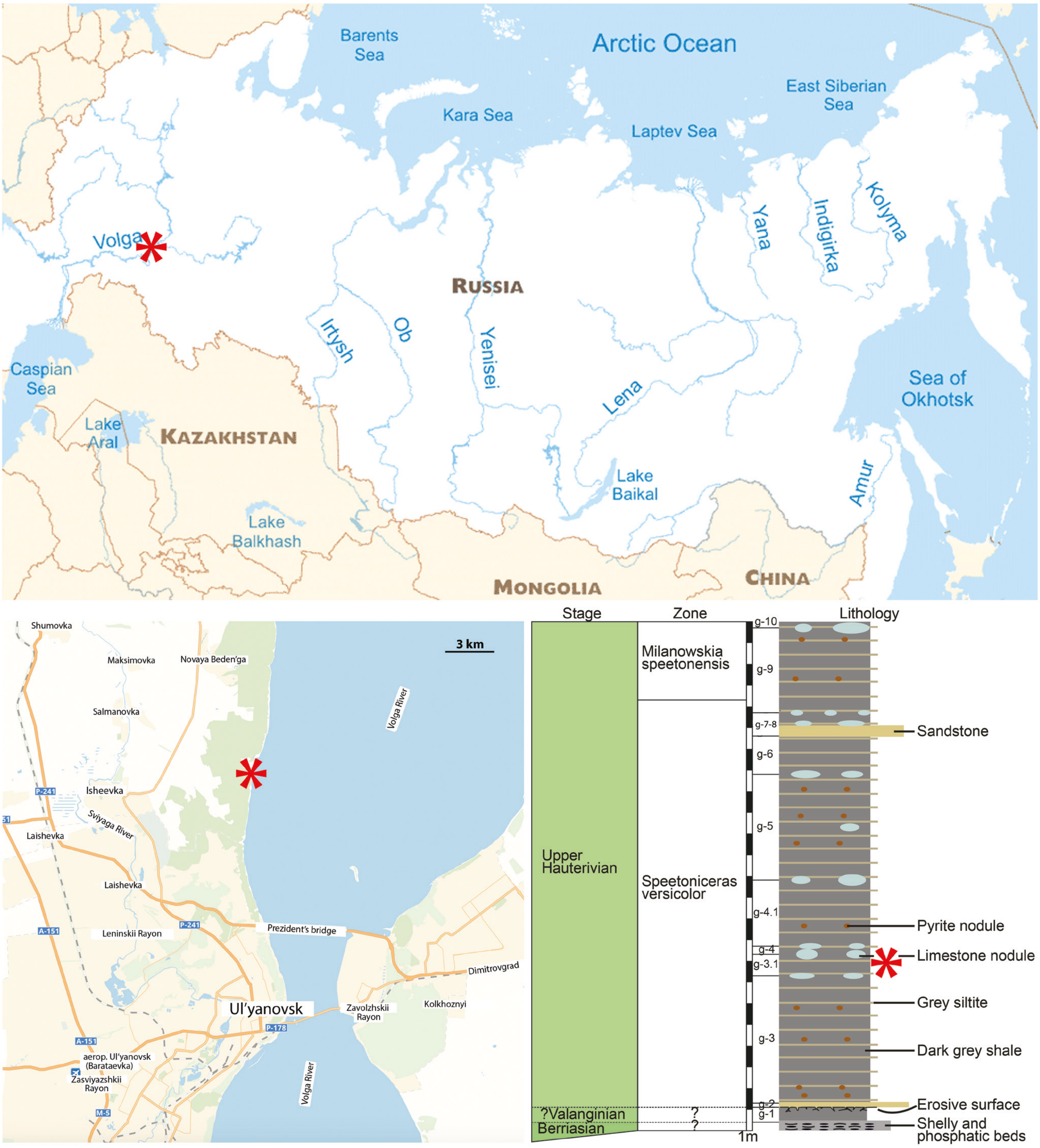

Fig. 1. Geographic position of the Slantsevy Rudnik vertebrate locality (asterisk) on the map of Russia (top) and in the vicinity of Ulyanovsk City (bottom left) and position of UPM 976 in the geological section at the Slantsevy Rudnik vertebrate locality (bottom right; modified from Fischer et al. (2017)).

condyle, somphospondylous (camellate) bone texture of caudal vertebrae, and hyposphenal ridge absent. Referred to the Lithostrotia based on a distinct rim ringing the condyle in middle caudal vertebrae. Among lithostrotians (sensu González Riga et al., 2108) it differs from *Malawisaurus*, *Tengrisaurus*, *Rapetosaurus*, *Aeolosaurus* and Saltasauridae by a ventral ridge instead of a ventral groove in anterior and middle caudal vertebrae, from *Malawisaurus* and Saltasauridae — by the lack of ventrolateral ridges in anterior and middle caudal vertebrae, from *Epachthosaurus* and more derived lithostrotians — by the lack of tubercle on the dorsal surface of the transverse process in the first caudal vertebra. It differs from all sauropods except *Astrophocaudia* and *Epachthosaurus* by hyposphene-hypantrum articulations in anterior caudal vertebrae.

Description

There are seven caudal vertebrae representing anterior and middle caudals. The centrum is procoelous, with concave anterior and deeply convex, ball-like posterior articular surfaces. The posterior articular surface is symmetrical in lateral view, with the apex centered. All vertebrae have a strong ridge on the ventral centrum surface. The neural arch is incompletely preserved or totally missing. None of the preserved vertebrae show distinct chevron facets.

UPM 976/1 (Fig. 2) is the most anterior preserved caudal, most probably the first caudal in the series based on the large and vertically expanded transverse process. The centrum is massive and relatively long, with the centrum length approximately equal to the anterior centrum height (Table 1). The anterior articular surface of the centrum is teardrop-shaped. The posterior articular surface of the centrum is heart-shaped, with a concave dorsal border. In lateral view, the dorsal and ventral centrum surfaces are straight and convex, respectively.

The neural arch is confined to the anterior half of the centrum and vertical. Its anterior border is placed almost on the anterior border of the centrum. The prezygapophyses are directing anterodorsally and project completely beyond the anterior end of the centrum. The prezygapophyseal articular surfaces are slightly convex and face mediodorsally. Ventral to the prezygapophyseal facet, the medial wall of the prezygapophyseal process is distinctly concave. This concavity likely represents the hypantrum receiving a large hyposphene of the last sacral vertebra (Fig. 2E). The posterior opening of the neural canal is egg-shaped, pointed dorsally (the neural canal is obscured by matrix anteriorly). The neural canal is relatively small; its height is about one third of the posterior centrum height. Just dorsal to the neural canal there is a broken posterodorsally directing outgrowth with a wedge-shaped depression on the ventral side (Fig. 2C). This outgrowth is likely a remnant of a large bifid hyposphene. Dorsal to the missing postzygapophyses there is a large and deep postspinal fossa, bounded laterally by the spinopostzygapophyseal laminae (Fig. 2C). The fossa is separated medially by a wide and robust postspinal lamina, which extends ventrally to the bottom of the postspinal fossa.

The transverse process is large, dorsoventrally expanded, and laterally projecting. Its base extends between the levels of the prezygapophysis and the midheight of the centrum. The concave dorsal margin forms a distinct prezygodiapophyseal lamina (PRDL). The ventral margin of the transverse process is slightly concave. The anterior surface of the transverse process is slightly concave. The posterior surface of the transverse process is moderately convex, without a distinct postzygapophyseal centrodiapophyseal fossa (pocdf).

Table 1. Measurements (in mm) of caudal vertebrae of *Volgatitan simbirskiensis* gen. et sp. nov. Slantsevy Rudnik, Ulyanovsk Province, Russia; Lower Cretaceous (Hauterivian). Measurements: ACH, anterior centrum height; ACW, anterior centrum width; CL, centrum length; PCH, posterior centrum height; PCW, posterior centrum width

Specimen	ACH	ACW	CL	PCH	PCW	CL/ACH
UPM 976/1	209	222	205	206	223	0.98
UPM 976/2	204	234	184	191	213	0.90
UPM 976/3	196	230	175	182	184	0.89
UPM 976/4	232	215	218	209	181	0.94
UPM 976/5	188	204	229	185	204	1.22
UPM 976/6	186	188	225	152	182	1.21

In UPM 976/2 (Fig. 3) the centrum length is slightly smaller than the anterior centrum height (Table 1). In contrast with the previous caudal, in UPM 976/2 the anterior centrum articular surface seems to be deeply incised dorsally, although this region is obscured by damage. The posterior centrum articular surface is straight dorsally (convex dorsally in UPM 976/1). The lateral centrum sides are more concave between the anterior and posterior centrum articular surfaces compared with UPM 976/1. The transverse process is more reduced; its ventral side is level with the dorsal third of the centrum. The transverse process projects laterally.

UPM 976/3 (Fig. 4) is similar to UPM 976/2 by dorsal margin of the centrum articular surfaces deeply incised anteriorly and straight posteriorly, and by a relatively shorter centrum, with centrum length to anterior centrum articular surface height ratio of 0.89 (Table 1). The transverse process is a blind outgrowth directed laterally and confined to the dorsal half of the centrum.

The three more posterior caudal vertebrae UPM 976/4–6 have proportionally longer centra, with centrum length to anterior centrum articular surface height ratio of 0.94, 1.22, and 1.21, respectively (Table 1). In UPM 976/4 (Fig. 5A–F) and UPM 976/6 (Fig. 5L–Q), the anterior and posterior centrum articular surfaces are oval, with the long axis vertical. In UPM 976/5 (Fig. 5G–K), the anterior and posterior centrum articular surfaces are nearly circular. In contrast with the other preserved caudal vertebrae, in UPM 976/5 the apex of the posterior articular surface is separated from the rest of the posterior articular surface by a slightly concave dorsal and ventral area. UPM 976/5 and 6 differs from the more anterior caudal vertebrae in having a spool-like centrum, with the ventral and dorsal centrum surfaces concave, not straight or convex (in UPM 976/6 the dorsal centrum surface is obscured by neural arch). The

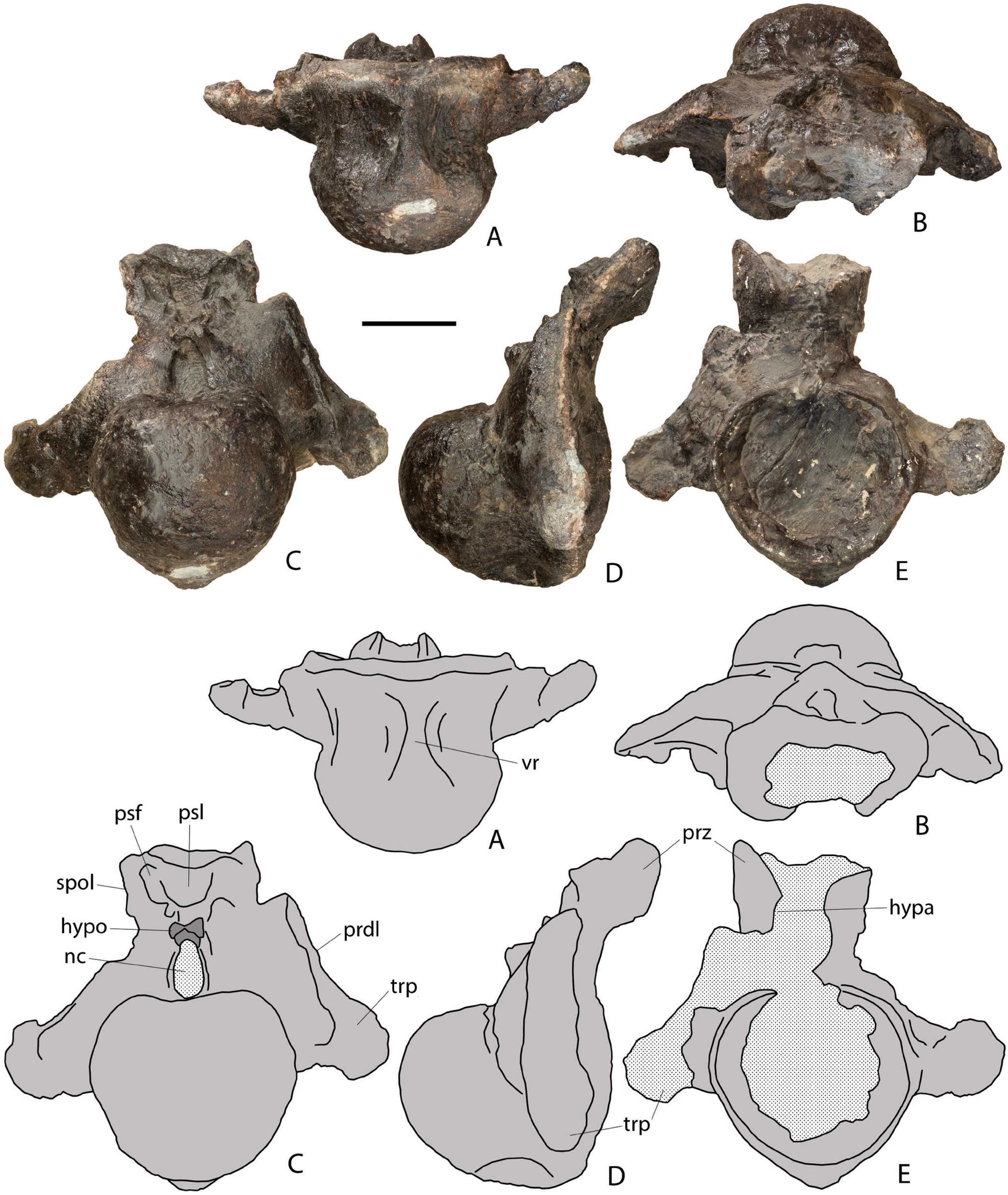

Fig. 2. *Volgatitan simbirskiensis* gen. et sp. nov., UPM 976/1, first caudal vertebra (holotype), in ventral (A), dorsal (B), posterior (C), lateral (D), and anterior (E) views; photographs (top) and explanatory drawings (bottom). Slantsevy Rudnik, Ulyanovsk Province, Russia; Lower Cretaceous (upper Hauterivian). Abbreviations: hypa, hypantrum; hypo, hyposphene; nc, neural canal; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; psf, postspinal fossa; psl, postspinal lamina; spol, spinopostzygapophyseal lamina; trp, transverse process; vr, ventral ridge. Scale bars equals 10 cm.

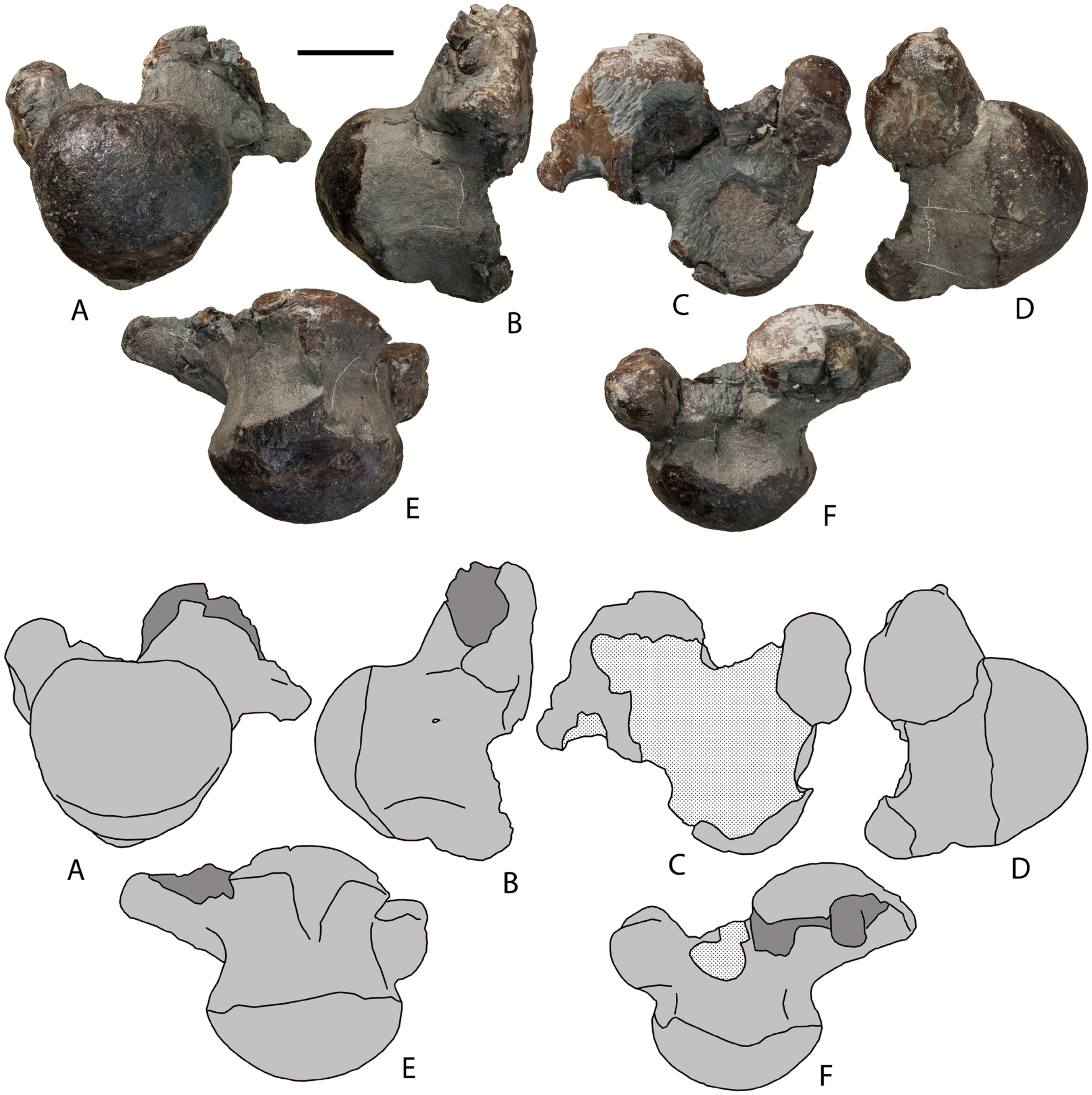

Fig. 3. *Volgatitan simbirskiensis* gen. et sp. nov., UPM 976/2, anterior caudal vertebra (holotype), in posterior (A), right lateral (B), anterior (C), left lateral (D), ventral (E), and dorsal (F) views; photographs (top) and explanatory drawings (bottom). Slantsevy Rudnik, Ulyanovsk Province, Russia; Lower Cretaceous (upper Hauterivian). Scale bar equals 10 cm.

centrum is also more constricted laterally between the articular surfaces compared with the other caudal vertebrae. In UPM 976/5 and 6 the posterior centrum articular surface is circumscribed by a strong rim, separating the condyle from the lateral surface of the main body of the centrum, in contrast with the more anterior caudal vertebrae, which have a smooth transition between the centrum and its posterior articular surface. The neural arch occupies the anterior half of the centrum length in UPM 976/5 and likely in UPM 976/6 (the posterior margin of the neural arch is obscured by the matrix). In UPM 976/5 a small dorsoventrally compressed transverse process is directed more posteriorly than laterally. In UPM 976/6 the transverse process is about two times smaller compared with the previous caudal vertebra and directed posteroventrally. The transverse process is confined to the neural arch and placed dorsal to the centrum in both vertebrae.

UPM 976/7 is a poorly preserved caudal centrum with teardrop-shaped anterior and posterior centrum articular surfaces.

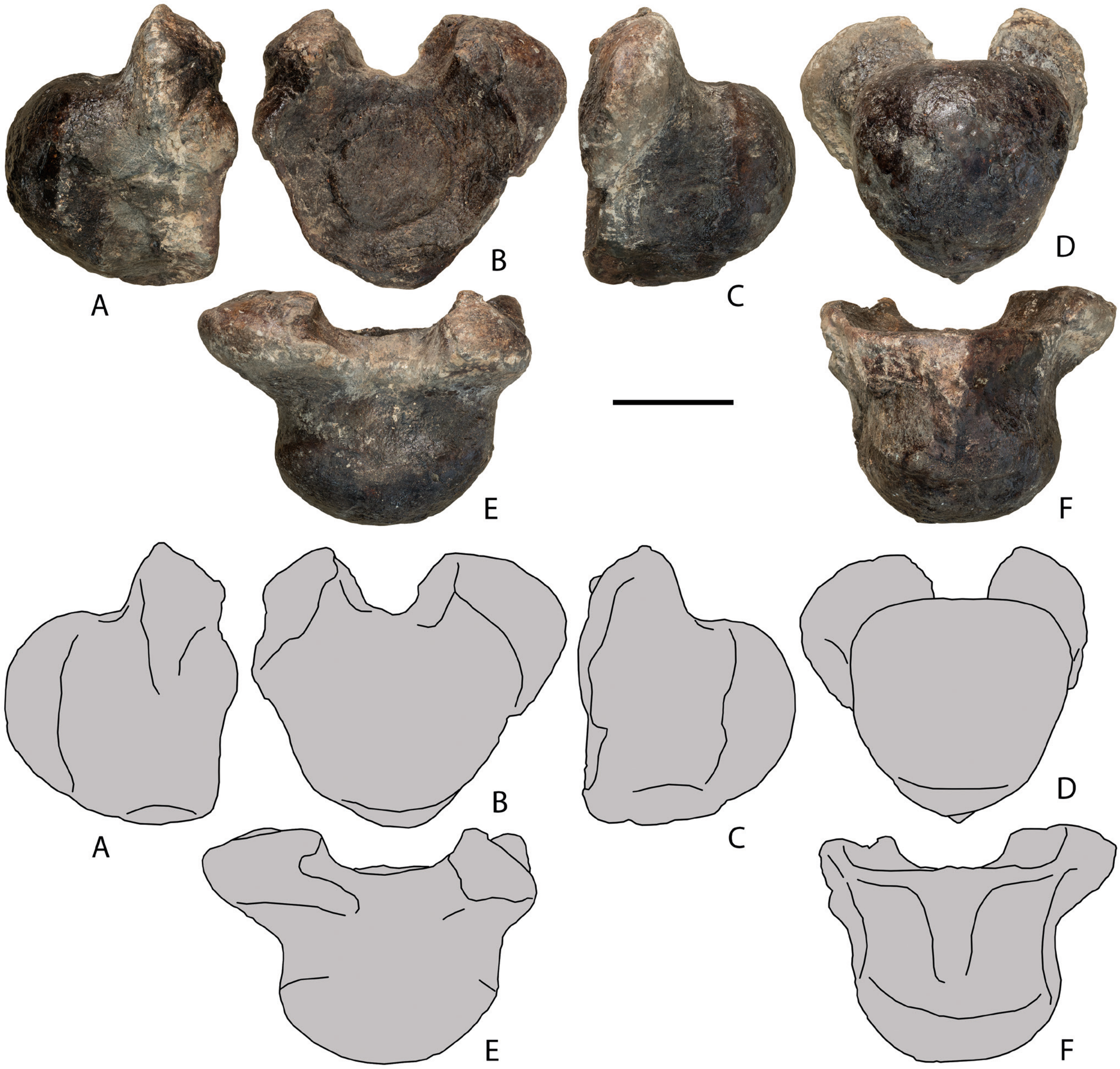

Fig. 4. *Volgatitan simbirskiensis* gen. et sp. nov., UPM 976/3, anterior caudal vertebra (holotype), in right lateral (A), anterior (B), left lateral (C), posterior (D), dorsal (E), and ventral (F) views; photographs (top) and explanatory drawings (bottom). Slantsevy Rudnik, Ulyanovsk Province, Russia; Lower Cretaceous (upper Hauterivian). Scale bar equals 10 cm.

The internal camellate bone structure is revealed by the breakage in UPM 976/4 (Fig. 5B, D). It is composed of cells varying in size from 1–2 to several centimeters.

Measurements — see Table 1.

Phylogenetic position of *Volgatitan*

For the phylogenetic analysis we used a recent matrix of sauropods, focused on Titanosauriformes, presented by González Riga et al. (2018). We added to this matrix also the lithostrotian titanosaur *Tengrisaurus* recently described from the Early Cretaceous of Transbaikalia, Russia (Averianov and Skutschas, 2017). The matrix included 86 taxa and 423 characters (one character uninformative). The multistate characters 11, 14, 15, 27, 40, 51, 104, 122, 147, 148, 177, 195, 205 and 259 are ordered. *Volgatitan* gen. nov. and *Tengrisaurus* can be scored for 31 (7.3 %) and 37 (8.8 %) characters, respectively. The scored characters for both taxa can be found in Appendix 1. In the data matrix considered, many taxa were coded as having block-like hyposphene in ante-

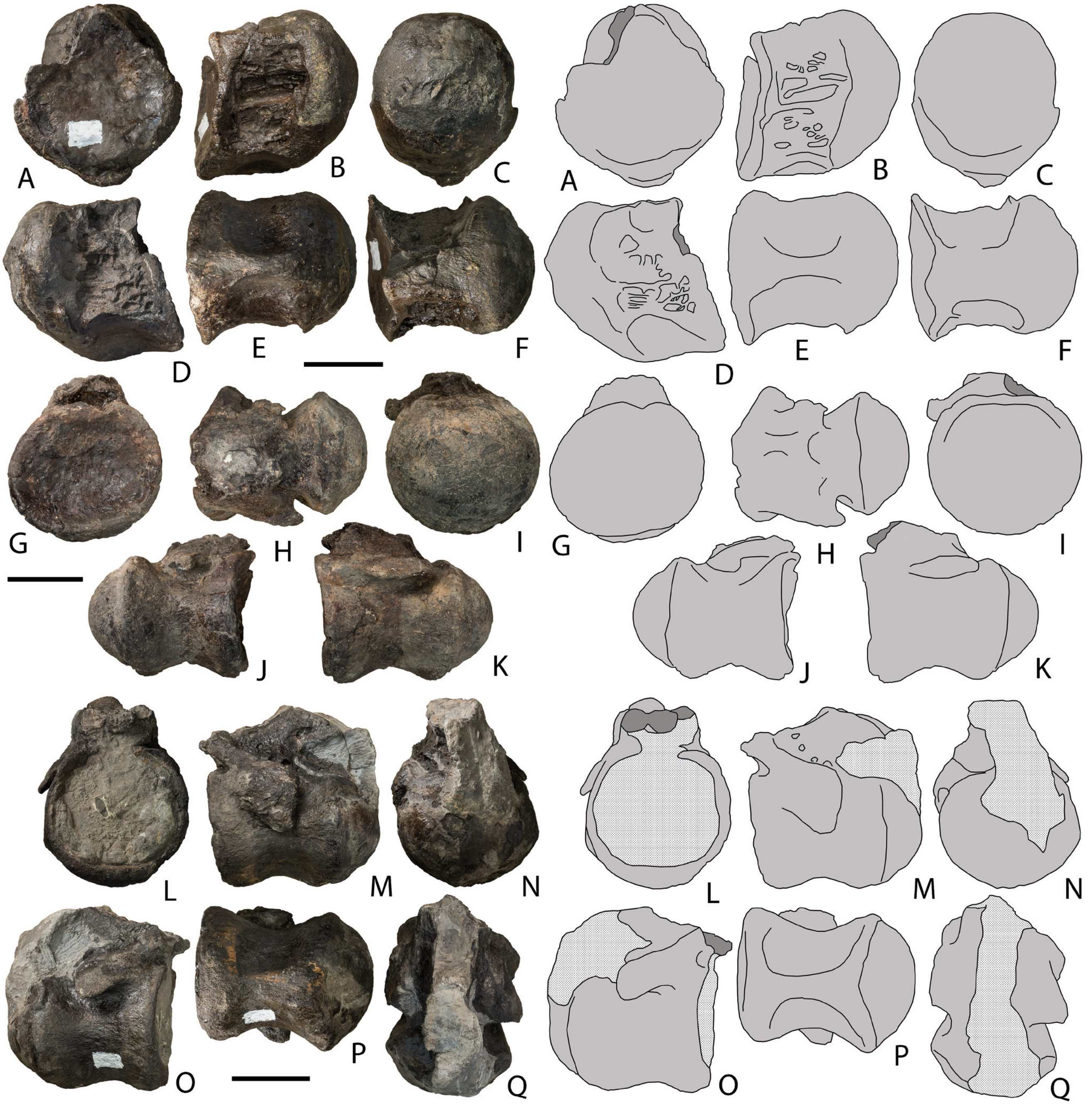

Fig. 5. *Volgatitan simbirskiensis* gen. et sp. nov., UPM 976/4-6, middle caudal vertebrae (holotype). A-F, UPM 976/4, in anterior (A), right lateral (B), posterior (C), left lateral (D), ventral (E), and dorsal (F) views. G-K, UPM 976/5, in anterior (G), dorsal (H), posterior (I), right lateral (J), and left lateral (K) views. L-Q, UPM 976/6, in anterior (L), left lateral (M), posterior (N), right lateral (O), ventral (P), and dorsal (Q) views. Photographs (left) and explanatory drawings (right). Slantsevy Rudnik, Ulyanovsk Province, Russia; Lower Cretaceous (upper Hauterivian). Scale bars equal 10 cm.

rior caudal neural arches (character 188(1)). Actually, this character is present only in *Astrophocaudia*, *Epachthosaurus*, and *Volgatitan* gen. nov. (see discussion in the next section). For all other taxa the scoring of this character was changed from one to zero. The analytical protocol of the phylogenetic analyses follows that of González Riga et al. (2018). Eight incomplete and unstable taxa were excluded from the matrix prior to the analysis (*Astrophocaudia*, *Australodocus*, *Brontomerus*, *Fukuititan*, *Fusuisaurus*, *Liubangosaurus*, *Mongolosaurus*, and *Tendaguria*). The pruned data matrix was analyzed using the 'Stabilize Consensus' option in the 'New Technology Search' in TNT vs. 1.1 (Goloboff, Farris, and Nixon, 2008). The memory for maximum trees was changed from default 100 to 10,000 trees. Searches were carried out using sectorial searches, drift and tree fusing, with the consensus stabilized five times, prior to using the resultant trees as the starting trees for a 'Tradi-

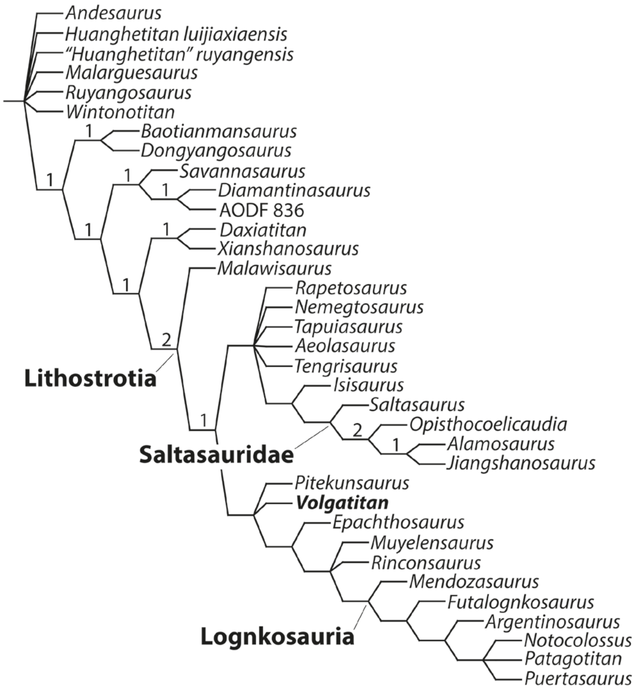

Fig. 6. Part of the strict consensus tree of 192 most parsimonious trees produced by TNT analysis, showing the interrelationships of Titanosauria including *Volgatitan* gen. nov. The figures at nodes are Bremer support values calculate in TNT.

tional Search' using Tree Bisection-Reconstruction. The search produced 192 most parsimonious trees with tree length of 1771 steps, consistency index of 0.25, and retention index of 0.56. The strict consensus tree shows a good resolution within Titanosauria (Fig. 6). As in the previous analysis (González Riga et al., 2018), the Lithostrotia is divided into two main branches: one leading to the Saltasauridae and another to the Lognkosauria. *Volgatitan* gen. nov. is recovered as a basal member of the second lineage. *Tengrisaurus* is a non-saltasaurid lithostrotian (Fig. 6), which is consistent with the previous phylogenetic analysis based on a different data matrix (Averianov and Skutschas, 2017).

Volgatitan gen. nov. has the following synapomorphies for the clade ((*Daxiatitan* + *Xianshanosaurus*) + Lithostrotia) (Fig. 6): 27(2), anterior caudal centra posterior articular surface of centrum strongly convex; 176(1), anteriormost caudal vertebrae, camellate internal tissue structure present; 177(2), anterior caudal centra, posterior articular surface convex throughout all anterior caudal vertebrae with ribs. The synapomorphies of *Volgatitan* gen. nov. for the clade uniting the lineages leading to the Saltasauridae and Lognkosauria are: 184(1), middle–posterior caudal centra (at least some), posterior articular surface convex; 185(1), middle–posterior caudal centra with convex posterior articular surface: distinct rim rings the condyle, separating it from the lateral surface of the main body of the centrum.

Diagnostic characters of *Volgatitan*

Procoelous anterior caudal centra — In *Volgatitan* the anterior caudals are deeply procoelous, with a distinctly concave anterior articular surface (cotyle) and a strongly convex, ball-like posterior articular surface (condyle). The procoelous anterior caudal centra are found in the Mamenchisauridae, Flagellicaudata, and Titanosauriformes (Upchurch, 1998; Wilson, 2002; Upchurch, Barrett, and Dodson, 2004a; Curry Rogers, 2005; Sekiya, 2011; Whitlock, D'Emic, and Wilson, 2011; D'Emic, 2012; Xing et al., 2015). However, in the Flagellicaudata (Dicraeosauridae + Diplodocidae) the anterior caudals are weakly procoelous, with a moderately convex posterior articular surface (Whitlock, D'Emic, and Wilson, 2011). In basal titanosauriforms the anterior caudals can be amphicoelous, platycoelous, or procoelous-opisthoplatyan (Mo et al., 2006; You, Li, Zhou, and Ji, 2006; Lü et al., 2007; González Riga, Previtera, and Pirrone, 2009; D'Emic, 2013). The ball-like posterior articulation surface of the anterior caudals, seen in *Volgatitan*, is more reminiscent of strongly procoelous anterior caudal vertebrae in Mamenchisauridae and Titanosauria more derived than *Andesaurus*.

Procoelous middle caudal centra — In *Volgatitan* the middle caudal centra have the same degree of procoelity as the anterior caudal centra. This contrasts the condition of Mamenchisauridae and Flagellicaudata, where the middle caudal centra are amphicoelous or amphyplatyan (Sekiya, 2011; Xing et al., 2015). In the basal titanosaurs *Andesaurus* and *Malawisaurus* the procoelous anterior caudal vertebrae are associated with amphicoelous or platycoelous middle caudal vertebrae (González Riga, Previtera, and Pirrone, 2009). The combination of procoelous anterior and middle caudal vertebrae is found only in advanced lithostrotians (Upchurch, Barrett, and Dodson, 2004a).

Length of anterior caudal centra — Most sauropods have anteroposteriorly short anterior caudal centra, with the centrum length to anterior centrum height ratio around 0.5-0.6 (Upchurch, 1998; Upchurch, Barrett, and Dodson, 2004a; Upchurch and Mannion, 2009). This ratio is close to 1.0 in basal sauropodomorphs and some advanced titanosaurs. In *Volgatitan* this ratio is 0.98 in the first caudal vertebra (Table 1). Among titanosaurs the long centrum of anterior caudal vertebrae is present in *Mendozasaurus*, *Aeolasaurus*, and *Pellegrinisaurus* (González Riga, Previtera, and Pirrone, 2009, Fig. 10).

Ventral ridge on anterior and middle caudal centra — In *Volgatitan* there is a prominent ventral ridge on the anterior and middle caudal centra. In advanced diplodocids and lithostrotians there is a wide and deep ventral fossa on the anterior caudal centra (Upchurch, 1998; Wilson, 2002; Upchurch, Barrett, and Dodson, 2004a; Curry Rogers, 2005; D'Emic, 2012). In saltasaurid titanosaurs this ventral fossa is present on anterior and middle caudal centra, where it is bounded by marked ventrolateral ridges (D'Emic and Wilson, 2011). In non-lithostrotian titanosaurs *Andesaurus*, *Xianshanosaurus*, and *Dreadnoughtus* at least one of the anterior caudals has a ventral ridge while in more posterior anterior caudals there is a longitudinal ventral groove bounded by ventrolateral ridges (Lü et al., 2009; Mannion and Calvo, 2011; Lacovara et al., 2014).

Position of the neural arch on the centrum — In *Volgatitan* the neural arch is confined to the anterior half of the centrum in the anterior and middle caudals. This is a derived condition within the Titanosauriformes (Upchurch, Barrett, and Dodson, 2004a; Curry Rogers, 2005; D'Emic, 2012). In a euhelopodid *Huabeisaurus* and in a basal titanosauriform *Sauroposeidon* the neural arch occupies most of the length of the centrum in the anteriormost caudal vertebrae, while it is positioned in the anterior part of the centrum in the middle caudal vertebrae (D'Emic and Foreman, 2012; D'Emic et al., 2013). This is apparently related to the anteroposteriorly short centra of anterior caudal vertebrae in these taxa.

Hyposphene-hypantrum complex — Hyposphene-hypantrum articulation is present in the middle and posterior dorsal vertebrae of most sauropods, except Lithostrotia (Upchurch, Barrett, and Dodson, 2004a; Apesteguía, 2005). However, in most sauropods the hyposphene-hypantrum articulation is not developed in the caudal series, where the hyposphene is replaced by the hyposphenal ridge. The only previously known sauropods which the hyposphene-hypantrum articulation extended to the caudal series are a basal titanosauriform *Astrophocaudia* and a basal titanosaur *Epachthosaurus* (Martínez et al., 2004; D'Emic, 2013). In both taxa these additional articulations are present in anterior and middle caudal vertebrae (in caudals 1-14 of *Epachthosaurus*). Also a small hyposphene was reported for the anterior caudal vertebrae of rebbachisaurid *Demandasaurus* (Torcida Fernández-Baldor et al., 2011). In *Volgatitan* gen. nov. the hyposphene-hypantrum articulations is present at least on the anterior caudal vertebrae. The bifid hyposphene of *Volgatitan* is more similar with that of *Epachthosaurus*.

Hyposphenal ridge — In many sauropods the postzygapophyseal facets of anterior caudal vertebrae meet ventrally and merge into a hyposphenal ridge that extends ventrally to the top of the neural canal opening (Upchurch, 1998; Upchurch, Barrett, and Dodson, 2004a). This ridge is lacking in *Volgatitan* and in a non neosauropod *Cetiosaurus*, in some rebacchisaurids and titanosauriforms, particularly in all known European titanosaurs (Upchurch and Martin, 2003; Díez Díaz, Pereda Suberbiola, and Sanz, 2013; Mannion, Upchurch, Barnes, and Mateus, 2013). The absence of the hyposphenal ridge in *Volgatitan* is apparently correlated with development of a hyposphene on anterior caudal vertebrae.

Postspinal fossa — The postspinal fossa is located at the base of neural spine, between the postzygapophyses, in anterior caudal vertebrae (Wilson, 2002; Upchurch, Barrett, and Dodson, 2004a). In *Volgatitan* the postspinal fossa is extremely large. The presence of a postspinal fossa on anterior caudal vertebrae has been considered a synapomorphy for a clade including *Malawisaurus* and some advanced titanosaurs (Curry Rogers, 2005).

Dorsoventrally expanded transverse process of anterior caudal vertebrae — In *Volgatitan* the transverse process of the first caudal is dorsoventrally expanded and extends between the level of the prezygapophyses and the midheight of the centrum. A transversely wide fan-like transverse process of anterior caudals is considered a synapomorphy for the Diplodocoidea (Upchurch, 1998; Upchurch and Mannion, 2009; Whitlock, D'Emic, and Wilson, 2011). It is present in the Flagellicaudata and variably occurs in the Rebbachisauridae. In *Volgatitan* the transverse process of the first caudal is not as wide transversely as in the diplodocoids and more similar with the condition present in the titanosaurs *Mendozasaurus*, *Futalognkosaurus*, *Patagotitan* and *Lohuecotitan* (Whitlock, D'Emic, and Wilson, 2011: Fig. 3; Díez Díaz et al., 2016; Carballido et al., 2017).

Transverse process in middle caudal vertebrae — In sauropods the transverse process is present in the first 14–16 caudal vertebrae (Upchurch, Barrett, and Dodson, 2004a). In some titanosaurs (*Opisthocoelicaudia*, *Alamosaurus*) the transverse process disappeared by caudal 10 (Wilson, 2002; Curry Rogers, 2005). However, in a titanosaur *Trigonosaurus* the transverse process is present up to the 20th caudal vertebra (Campos, Kellner, Bertini, and Santucci, 2005). In *Volgatitan* the transverse process may have persisted longer in the caudal series compared with the most other sauropods, at it is present in the middle caudal vertebrae. The transverse process is not reduced in the middle caudals also in *Saltasaurus* (Powell, 1992: Fig. 23).

Internal bone structure — In *Volgatitan* the bone structure is evident in one middle caudal vertebra (UPM 976/4; Fig. 5B, D). It is composed of cells varying in size from 1-2 to several centimeters. Wedel, Cifelli, and Sanders (2000) proposed classification of sauropod vertebrae based on pneumatic characters. According to these authors, both camellate and somphospondylous vertebrae have internal bone structure composed entirely of camellae, but the neural arch laminae are not reduced in the former and reduced in the later. The presence of neural arch laminae is not a pneumatic character and the use of this character for classification of internal bone structure is not helpful. Other authors consider the terms somphospondylous and camellate as synonyms (Whitlock, D'Emic, and Wilson, 2011). The internal structure of UPM 976/4 lacks large camerae and can be classified as som-

Table 2. Measurements of the first caudal centrum and body mass estimate for Eusauropoda. Groups: NNEUS, non neusauropod Eusauropoda; DIPLO, Diplodocoidea; NTMAC, non titanosaurian Macronaria; TITAN, Titanosauria. Measurements (in mm): ACH, anterior centrum height; ACW, anterior centrum width; CL, centrum length; PCH, posterior centrum height; PCW, posterior centrum width

Taxon	Group	Specimen	Body mass, kg	CL	ACH	ACW	PCH	PCW	Reference
Ferganasaurus verzilini	NNEUS	PIN 3042/1	8805	130	171*	195	206*	190	Alifanov and Averianov, 2003
Mamenchisaurus youngi	NNEUS	ZDM 0083	6240	145	156*	112*	130*	72*	Ouyang and Ye, 2002
Apatosaurus ajax	DIPLO	NSMT-PV 20375		150	245	245	224*	232*	Upchurch, Tomida, and Barrett, 2004
Apatosaurus louisae	DIPLO	CM 3018	41269	240	404*	326*	383*	300	Gilmore, 1936
Barosaurus lentus	DIPLO	AMNH 6341	13164	153	283	300	295	265	McIntosh, 2005
Comahuesaurus windhauseni	DIPLO	MOZ-PV 06741	12332	185	150*	162*	190	220	Carballido et al., 2012
Demandasaurus darwini	DIPLO	MDS-RVII 605		145	160	135	170	159*	Fernández-Baldor et al., 2011
Dicraeosaurus hansemanni	DIPLO	HMN		130	201	200	208	190	Janensch, 1929
Dicraeosaurus sattleri	DIPLO	HMN	10163	136	152	177	146	155	Janensch, 1929
Diplodocus carnegii	DIPLO	CM 84	13801	188	325*	362*	331*	348*	Hatcher, 1901
Haplocanthosaurus delfsi	DIPLO	CMNH 10380		176	370	270	370	270	McIntosh and Williams, 1988
Camarasaurus lewisi	NTMAC	BYU 9047		149	233	280	224	277	McIntosh, Miles, Cloward, and Parker, 1996
Europatitan eastwoodi	NTMAC	MDS-OTII 2		145	310	260	320	290	Fernández-Baldor et al., 2017
Giraffatitan brancai	NTMAC	HNM SII	34003	145	230	223	239	234	Janensch, 1950
Huabeisaurus allocotus	NTMAC	HBV 20001		126	250	232	253	268	D'Emic et al., 2013
"Huanghetitan" ruyangensis	NTMAC	41HIII 0001		182	269	320	284*	365*	Lü et al., 2007
Vouivria damparisensis	NTMAC	DAM 10	14627	88	193	197	182	196	Mannion, Allain, and Moine, 2017
Baurutitan britoi	TITAN	MCT 1490-R		175	119	131	113*	154*	Kellner, Campos, and Trotta, 2005
Bonitasaura salgadoi	TITAN	MPCA 460		120	130*	197*	152*	188*	Gallina and Apesteguía, 2015
Dreadnoughtus schrani	TITAN	MPM-PV 1156	59290	304*	250	320	310	310	Lacovara et al., 2014
Narambuenatitan palomoi	TITAN	MAU-Pv 425/01		90	105*	110*	103*	115*	Filippi, García, and Garrido, 2011
Opisthocoelicaudia skarzynskii	TITAN	ZPAL MgD-I/48	25418	230	217*	219*	219*	234*	Borsuk-Bialynicka, 1977
Patagotitan mayorum	TITAN	MPEF-PV 3400	69092	340	405*	425*	400	413*	Carballido et al., 2017
Rapetosaurus krausei	TITAN	FMNH PR 2209	1646	69	65	63	70	73	Curry Rogers, 2009
Volgatitan simbirskiensis	TITAN	UPM 976		205	209	222	206	223	This study

*Calculated from the figure.

phospondylous (= camellate). The presence of somphospondylous bone texture in anterior caudal vertebrae has been considered a synapomorphy of Saltasaurinae (Whitlock, D'Emic, and Wilson, 2011). Anterior caudal vertebrae are somphospondylous also in a basal titanosauriform *Jiutaisaurus* (Whitlock, D'Emic, and Wilson, 2011).

Proportions of the first caudal centrum in Eusauropoda

As was noted in the previous section, *Volgatitan* gen. nov. has an unusually long centrum of the first caudal vertebrae. To further explore the significance of this character, we collected all available in the literature measurements

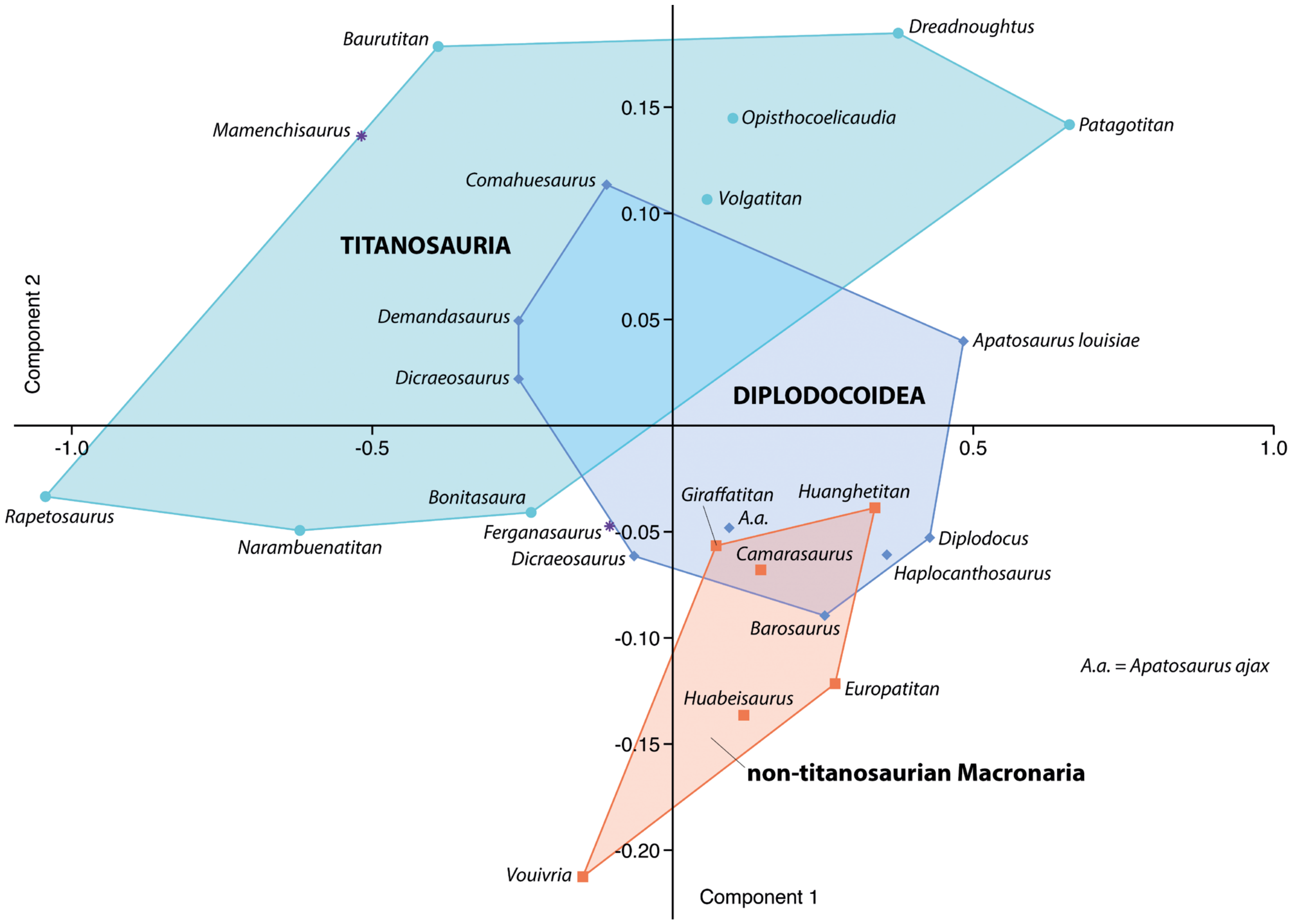

Fig. 7. Principal components analysis, components 1 and 2 of the of firs caudal measurements in Eusauropoda.

of the first caudal centrum in eusauropod taxa. Altogether, we managed to find data on 25 taxa summarized in Table 2. We examined these data using the principal components analysis (PCA) available in the PAST3 software (Hammer, Harper, and Ryan, 2001). All measurements were $\log_{10}$ transformed to account for differences in size. The first and second components (PC1 and PC2) explain 95.19 % of the variance (88.48 % and 6.71 %, respectively; Table 3). In the PC1 and PC2 scatterplot the morphospaces of Titanosauria and non-titanosaurian Macronaria are fully separated (Fig. 7). The morphospace of Diplodocoidea is partially overlapping with the two latter groups. The centrum length (CL) has the greatest loading on the PC2 while other measurements have slightly greater loading on the PC1 (Table 3). *Volgatitan* gen. nov. is placed within the morphospace of Titanosauria, close to the derived lithostrotians *Opisthocoelicaudia*, *Dreadnoughtus*, and *Patagotitan*, which is consistent with its phylogenetic position recovered by the phylogenetic analysis.

Table 3. Component loadings and eigenvalue data for PCA of the measurements of the first caudal centrum in Eusauropoda

	PC1	PC2	PC3	PC4
CL	0.309	0.951	–0.000	0.014
ACH	0.475	–0.171	–0.601	–0.043
ACW	0.477	–0.137	0.228	–0.803
PCH	0.481	–0.144	–0.315	0.424
PCW	0.469	–0.167	0.698	0.416
Eigenvalue	0.149	0.11	0.06	0.01
% of total variance	88.48	6.71	3.62	0.88

Body size of *Volgatitan*

There are two principal methods of body mass estimate in sauropods: long bone circumference and volumetric reconstruction (Bates et al., 2015; Carballido et al., 2017). Both these methods are not applicable for the body mass estimate in *Volgatitan* gen. nov. because of its incompleteness. To estimate the body mass in *Volgatitan* gen. nov. we use the measurements of the first caudal centrum and body mass estimates for the same specimens obtained by

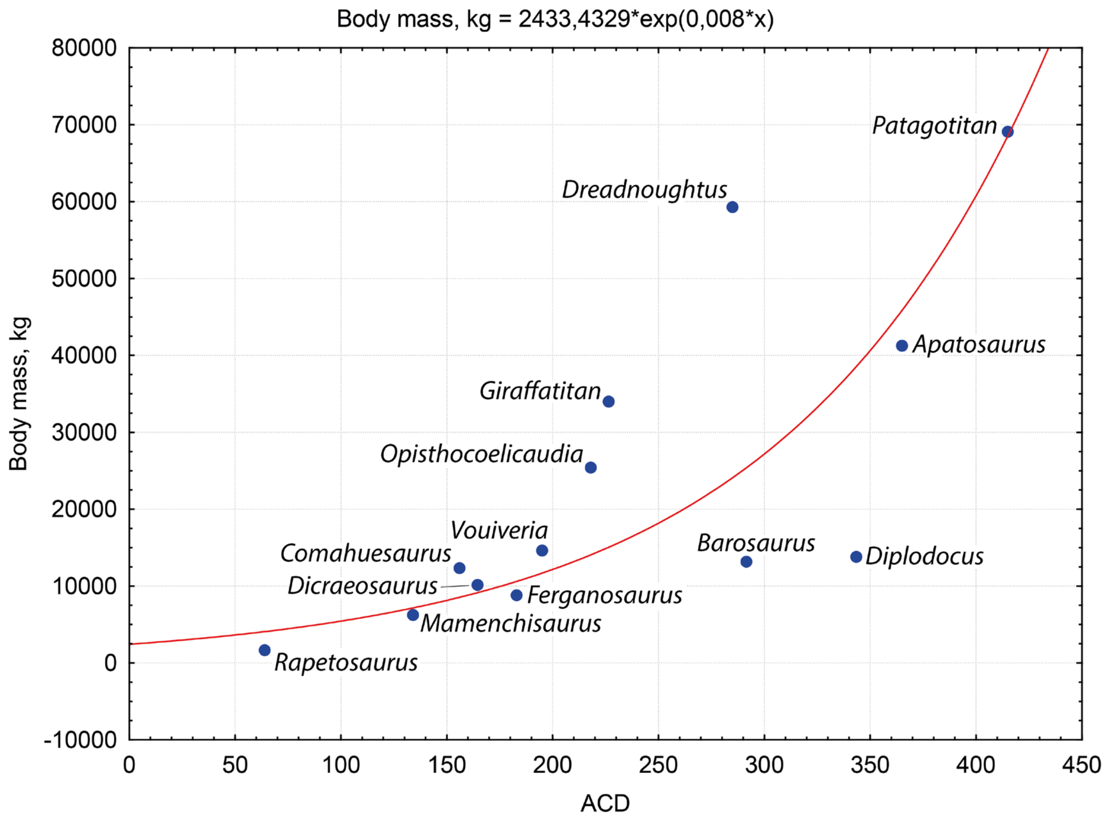

Fig. 8. Plot of body mass (kg) and first caudal diameter of the anterior centrum articular surface (ACD, mm) in Eusauropoda.

long bones scaling (Table 2). The values of body mass for *Dreadnoughtus* and *Patagotitan* are taken from Lacovara et al. (2014) and Carballido et al. (2017), respectively; for other taxa — from Benson et al. (2014). We use diameter of the anterior articular surface of the centrum (ACD) as a proxy of the first caudal centrum size. The ACD = (ACH + ACW) / 2, where ACH is the anterior centrum height and ACW is the anterior centrum width. The exponential fit of ACD to body mass produced the equation expressed in Fig. 8. Substitution of ACD value for *Volgatitan* gen. nov. (215.5 mm) in this equation gives the body mass of 13644 kg for this taxon. The linear fit of these data produced a much larger estimate of the body mass for *Volgatitan* gen. nov.: 20971 kg (the equation is Body mass = −12526.6831+155.4413×ACD). The average of these values is 17308 kg. This figure can be considered as a conservative body mass estimate for *Volgatitan* gen. nov. The *Volgatitan* gen. nov. is placed phylogenetically at the base of the lineage containing the largest titanosauriform sauropods with body mass of 60-70 tons: *Argentinosaurus*, *Dreadnoughtus*, *Notocolossus*, *Patagotitan*, and *Puertasaurus* (Bonaparte and Coria, 1993; Novas, Salgado, Calvo, and Agnolin, 2005; Lacovara et al., 2014; González Riga et al., 2016; Carballido et al., 2017). These taxa obtained gigantic size early in the history of the lineage, at the end of the Early Cretaceous, and maintained it through the whole Late Cretaceous: Albian (*Patagotitan*), Cenomanian (*Argentinosaurus*), Coniacian-Santonian (*Notocolossus*), Campanian-Maastrichtian (*Dreadnoughtus*), and Maastrichtian (*Puertasaurus*).

Evolutionary History of Titanosauria

In the Early Cretaceous the three main groups of titanosauriforms dominated in geographically different areas: brachiosaurids in North America, euhelopids in Eastern Asia, and titanosaurs in Gondwana (Mannion and Calvo, 2011; D'Emic, 2012). The lithostrotian titanosaurs split into two main groups, one which is nearly globally widespread (the clade including Saltasauridae) and another known previously to be distributed strictly in South America (the clade including Lognkosauria) (González Riga et al., 2018). *Volgatitan* gen. nov. is the first European and geologically oldest (Hauterivian) representative of the latter group. Its geological age and basal position within the group suggest that this lineage may have had initially a wider geographic distribution and it vanished everywhere except South America by the Late Cretaceous. The secondary dispersal of *Volgatitan* gen. nov. from South America to Europe seems less plausible because in South America there are no titanosaurs of this lineage older than Albian. The discovery of *Volgatitan* gen. nov. implies that Titanosauria may have had a long virtually unknown early evolutionary history in Laurasia.

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Appendix 1. Characters scored in the matrix published by González Riga et al. (2018) for the phylogenetic analysis

VOLGATITAN SIMBIRSKIENSIS GEN. ET SP. NOV.

25(1): Anterior caudal centra, mediolateral width to dorsoventral height (excluding chevron facets) of anterior surface ratio: 1.0 or greater [1.06].

26(1): Anterior caudal centra, lowest average Elongation Index (aEI; centrum anteroposterior length [excluding articular ball] divided by the mean average value of the anterior surface mediolateral width and dorsoventral height) value of: 0.6 or greater [0.79].

27(2): Anterior caudal centra, anteroposterior length of posterior condylar ball to mean average radius ([mediolateral width + dorsoventral height] divided by 4) of anterior articular surface of centrum ratio: greater than 0.3 (posterior articular surface of centrum is strongly convex) [0.63].

28(1): Middle caudal centra, mediolateral width to dorsoventral height (excluding chevron facets) of anterior surface ratio: 1.0 or greater [1.09].

29(0): Middle caudal centra, average Elongation Index (aEI; centrum anteroposterior length [excluding articular ball] divided by the mean average value of the anterior surface mediolateral width and dorsoventral height [excluding chevron facets]) value: less than 1.4 [0.94].

176(1): Anteriormost caudal vertebrae, camellate internal tissue structure: present.

177(2): Anterior caudal centra, posterior articular surface: convex throughout all anterior caudal vertebrae with ribs.

178(0): Anterior caudal centra, lateral pneumatic fossae or foramina: absent.

180(0): Anterior–middle caudal centra, small, shallow vascular foramina pierce the lateral and/or ventral surfaces: absent.

181(0): Anterior–middle caudal centra (excluding the anteriormost caudal vertebrae), ventral longitudinal hollow: absent.

182(0): Anterior–middle caudal centra (excluding the anteriormost caudal vertebrae), distinct ventrolateral ridges, extending the full length of the centrum: absent.

183(0): Middle caudal centra, anteroposteriorly elongate ridge situated at approximately two-thirds of the way up the lateral surface: absent.

184(1): Middle–posterior caudal centra (at least some), posterior articular surface: convex.

185(1): Middle–posterior caudal centra with convex posterior articular surface: distinct rim rings the condyle, separating it from the lateral surface of the main body of the centrum.

187(1): Anterior caudal neural arches, hyposphenal ridge: absent.

188(1): Anterior caudal neural arches, hyposphenal ridge shape: block-like hyposphene.

189(1): Anterior caudal neural arches, distinct prezygodiapophyseal lamina (PRDL): present.

190(0): Anterior caudal neural arches, sharp lipped lateral coel (postzygapophyseal centrodiapophyseal fossa [POCDF]) bounded by posterior centrodiapophyseal lamina (PCDL [or caudal rib itself]), centropostzygapophyseal lamina (CPOL) and postzygodiapophyseal lamina (PODL): absent.

192(1): Middle caudal neural arches: located on the anterior half of the centrum.

202(0): First caudal rib (transverse process), with prominent ventral bulge: absent.

203(0): First caudal rib, expands anteroposteriorly towards its distal end, forming an 'anchor' shape in dorsal view: absent.

204(1): Anterior caudal ribs, shape in anterior view: wing-like, with a dorsolaterally oriented dorsal margin.

205(0): Anterior caudal ribs: curve strongly anterolaterally.

206(0): Anterior caudal ribs: do not extend beyond posterior end of centrum (excluding posterior ball).

349(0): First caudal centrum, anterior articular face shape: flat or concave.

350(0): Anterior–middle caudal centra (excluding Cd1), comparison of anterior and posterior articular faces: anterior face more concave than posterior one, or these two faces are equally concave.

351(0): Middle caudal centra with convex posterior articular surface, condyle dorsally displaced: absent.

352(0): Anteriormost caudal neural arches, prezygapophyses curve downwards ('droop') at their distal ends: absent.

354(0): First caudal rib, subtriangular process projects posteriorly at approximately midlength: absent.

355(0): Anteriormost caudal ribs, tubercle on dorsal surface at approximately midlength: absent.

409(0): Anteriormost caudal centra, ACDL: absent, or represented by no more than a faint ridge.

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25(1): Anterior caudal centra, mediolateral width to dorsoventral height (excluding chevron facets) of anterior surface ratio: 1.0 or greater [1.01].

27(2): Anterior caudal centra, anteroposterior length of posterior condylar ball to mean average radius ([mediolateral width + dorsoventral height] divided by 4) of anterior articular surface of centrum ratio: greater than 0.3 (posterior articular surface of centrum is strongly convex) [0.72].

28(1): Middle caudal centra, mediolateral width to dorsoventral height (excluding chevron facets) of anterior surface ratio: 1.0 or greater [1.13].

29(1): Middle caudal centra, average Elongation Index (aEI; centrum anteroposterior length [excluding articular ball] divided by the mean average value of the anterior surface mediolateral width and dorsoventral height [excluding chevron facets]) value: 1.4 or higher [1.43].

33(1): Anterior caudal neural spines, maximum mediolateral width to anteroposterior length ratio: 1.0 or greater [1.93].

34(1): Anterior caudal neural spines, maximum mediolateral width to minimum mediolateral width ratio: 2.0 or greater (spines expand dorsally, forming 'club'- or 'mace'-shaped spinous processes) [2.28]

176(0): Anteriormost caudal vertebrae, camellate internal tissue structure: absent.

177(2): Anterior caudal centra, posterior articular surface: convex throughout all anterior caudal vertebrae with ribs.

178(0): Anterior caudal centra, lateral pneumatic fossae or foramina: absent.

180(0): Anterior–middle caudal centra, small, shallow vascular foramina pierce the lateral and/or ventral surfaces: absent.

181(1): Anterior–middle caudal centra (excluding the anteriormost caudal vertebrae), ventral longitudinal hollow: present.

182(0): Anterior–middle caudal centra (excluding the anteriormost caudal vertebrae), distinct ventrolateral ridges, extending the full length of the centrum: absent.

183(0): Middle caudal centra, anteroposteriorly elongate ridge situated at approximately two-thirds of the way up the lateral surface: absent.

184(1): Middle–posterior caudal centra (at least some), posterior articular surface: convex.

185(1): Middle–posterior caudal centra with convex posterior articular surface: distinct rim rings the condyle, separating it from the lateral surface of the main body of the centrum.

187(0): Anterior caudal neural arches, hyposphenal ridge: present.

188(0): Anterior caudal neural arches, hyposphenal ridge shape: slender ridge.

189(0): Anterior caudal neural arches, distinct prezygodiapophyseal lamina (PRDL): absent.

190(0): Anterior caudal neural arches, sharp lipped lateral coel (postzygapophyseal centrodiapophyseal fossa [POCDF]) bounded by posterior centrodiapophyseal lamina (PCDL [or caudal rib itself]), centropostzygapophyseal lamina (CPOL) and postzygodiapophyseal lamina (PODL): absent.

192(1): Middle caudal neural arches: located on the anterior half of the centrum.

193(1): Middle–posterior caudal neural arches, distance that prezygapophyses extend beyond the anterior margin of the centrum: 20 % or greater of centrum length (excluding ball), elongate prezygapophyses [41 %].

194(0): Anteriormost caudal neural spines, sharp lipped lateral coel (spinodiapophyseal fossa [SDF]) bounded by spinoprezygapophyseal lamina (SPRL), spinopostzygapophyseal lamina (SPOL) and postzygodiapophyseal lamina (PODL): absent.

195(0): Anterior caudal neural spines, project: posterodorsally.

196(0): Anterior caudal neural spines, anterodorsal margin of neural spine: level with or posterior to posterior margin of postzygapophyses.

197(1): Anterior caudal neural spines, prespinal and postspinal laminae: form distinct mediolaterally narrow ridges or laminae along the midline of the prespinal and postspinal fossae.

198(0): Anterior caudal neural spines, spinoprezygapophyseal lamina (SPRL)–spinopostzygapophyseal lamina (SPOL) contact: absent.

199(0): Middle caudal neural spines, in lateral view, widen anteroposteriorly (approximately doubling) from their base to their summit: absent.

200(0): Middle caudal neural spines, extend posteriorly to the mid-point (or beyond) of the proceeding caudal centrum: present (0); absent (usually do not extend beyond the posterior margin of the centrum).

204(0): Anterior caudal ribs, shape in anterior view: triangular, tapering distally.

350(0): Anterior–middle caudal centra (excluding Cd1), comparison of anterior and posterior articular faces: anterior face more concave than posterior one, or these two faces are equally concave.

351(0): Middle caudal centra with convex posterior articular surface, condyle dorsally displaced: absent.

352(0): Anteriormost caudal neural arches, prezygapophyses curve downwards ('droop') at their distal ends: absent.

353(0): Anterior caudal neural spines, anterior expansion of lower portion of spinoprezygapophyseal lamina (SPRL): absent.

409(0): Anteriormost caudal centra, ACDL: absent, or represented by no more than a faint ridge.

410(0): Anterior–middle caudal neural arches: spinopostzygapophyseal lamina (SPOL) shape: SPOL grades smoothly toward postzygapophyses.

411(0): Anterior–middle caudal neural arches, anteroposteriorly oriented ridge and fossa ('shoulder') between prezygapophyses and postzygapophyses: absent.

419(0): Anteriormost caudal neural spines, medial spinoprezygapophyseal laminae (mSPRLs) merge into the prespinal lamina (PRSL) close to the base of the spine: absent.