

First sauropod dinosaur remains from the Early Cretaceous Shestakovo 3 locality, Western Siberia, Russia

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Abstract

KOKM A, the associated caudal vertebrae of a sauropod from the Lower Cretaceous (Aptian) Ileik Formation at Shestakovo 3 locality in Kemerovo–Kuzbass oblast, Western Siberia, Russia, shows a unique combination of derived caudal vertebrae and plesiomorphic and highly diverse haemal arches (chevrons). The anterior, middle, and posterior caudal vertebrae are deeply procoelous with a ball-like posterior condyle. There are five types of chevrons: closed Y-shaped anterior chevrons with a small haemal canal, closed asymmetric middle chevrons with a small ventral slit, open forked middle chevrons with large ventral slit, separate posterior chevrons with chevron facets, and separate posterior rod-like chevrons without chevron facets. The equal weight and extended implied weighting parsimony analyses place KOKM A within Turiasauria and Titanosauria, respectively. Both these analyses place *Sibirotitan astrosacralis* from the nearby Shestakovo 1 locality of the same stratigraphic unit in Mamenchisauridae. Both equal weight and extended implied weighting analyses combining *S. astrosacralis* and KOKM A in a single terminal taxon place it as a non-lithostrotian titanosaur, in particular, as a sister taxon for *Daxiatitan binglingi* from the Lower Cretaceous of China. *D. binglingi* is similar to *S. astrosacralis* and KOKM A in structure of cervical and caudal vertebrae, respectively. This suggests attribution of KOKM A to *S. astrosacralis*.

Keywords: Dinosauria, Sauropoda, Early Cretaceous, Western Siberia, Russia, Shestakovo 3 locality

Introduction

One of the few dinosaur sites in Russia producing articulated specimens is known from the vicinity of Shestakovo village in Kemerovo–Kuzbass oblast of Russia (Lopatin et al., 2015; Averianov and Lopatin, 2023a). The Shestakovo complex of localities is confined to the Lower Cretaceous (Aptian) Ileik Formation widely distributed in Eastern Siberia (Podlesnov, Morkovin, and Maschenko, 2018). Besides dinosaurs, Shestakovo localities 1 and 3 produce a diverse assemblage of freshwater and terrestrial vertebrates, among which detailed descriptions are published for amphibians (Averianov and Voronkevich, 2002; Skutschas, 2014, 2016), choristoderes (Skutschas and Vitenko, 2015, 2017), pterosaurs (Averianov, Leshchinskiy, Skutschas, and Rezvyi, 2003), non-avian dinosaurs (Averianov et al., 2002, 2018; Averianov, Voronkevich, Leshchinskiy, and Fayngertz, 2006; Skutschas et al., 2017; Podlesnov, 2018a; Averianov and Lopatin, 2022, 2023b), birds (Kurochkin, Averianov, Lesh-

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chinskiy, and Zelenkov, 2011; O'Connor, Averianov, and Zelenkov, 2014), tritylodontids (Tatarinov and Maschenko, 1999), and mammals (Maschenko and Lopatin, 1998; Maschenko, Lopatin, and Voronkevich, 2003; Lopatin et al., 2005; Lopatin, Averianov, Maschenko, and Leshchinskiy, 2009; Lopatin, Averianov, Maschenko, and Leshchinskiy, 2010; Lopatin, Maschenko, and Averianov, 2010). The best known dinosaur from Shestakovo complex is a basal ceratopsian *Psittacosaurus sibiricus* represented by several complete skeletons of various ontogenetic age and numerous skeletal fragments and isolated bones (Voronkevich, 1998; Averianov, Voronkevich, Leshchinskiy, and Fayngertz, 2006; Lopatin et al., 2015; Podlesnov, 2018a; Skutschas et al., 2021). The second dinosaur taxon described from Shestakovo complex is a titanosauriform sauropod *Sibirotitan astrosacralis*, represented by isolated teeth and vertebrae and associated pedal elements from Shestakovo 1 locality (Averianov et al., 2002, 2018; Averianov and Lopatin, 2022). Here we provide a detailed description and discuss the taxonomic attribution of the first sauropod remains from Shestakovo 3 locality. This find is a series of caudal vertebrae and associated haemal arches (chevrons) from a single individual excavated in 2018–2020. The preliminary reports of this discovery, including photographs of bones, were published by Podlesnov (2018b) and Feofanova and Slobodin (2019).

Institutional abbreviations. KOKM, Kuzbass State Museum of Local Lore, Kemerovo, Russia; PIN, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PM TGU, Paleontological Museum, Tomsk State University, Tomsk, Russia.

Geological settings of Shestakovo 3 locality

The Shestakovo localities are situated around Shestakovo village in Chebula rayon of Kemerovo–Kuzbass oblast, Western Siberia, Russia (Fig. 1A). The Shestakovo 1 locality is a high cliff along the right bank of Kiya River 1.5 km downstream of Shestakovo village (GPS coordinates: N 55°54.60', E 87°56.90'). It was discovered in 1953 by geologist A. A. Mosakovsky (Rozhdestvensky, 1955, 1960). Extensive work at this locality began after the discovery of a mammalian jaw in 1995 (Maschenko and Lopatin, 1998). The Shestakovo 3 locality was discovered in 1995 by geologists from Tomsk State University at a road cut south of Shestakovo village (GPS coordinates N 55°52.94, E 87°59.58; Fig. 1A) (Leshchinskiy, Voronkevich, Fayngertz, and Schikhovtzeva, 1997; Saev and Leshchinskiy, 1997; Voronkevich, 1998; Alifanov, Efimov, Novikov, and Morales, 1999).

The fossiliferous beds at Shestakovo 1 and 3 localities belong to the upper part of the Ilek Formation, which is widespread in Chulym–Yenisei Depression. These beds are composed of variegated continental deposits, consisting of a series of sandy-clay bands. The Ilek Formation overlies with erosion the Upper Jurassic Tyazhin Formation and

underlies, also with erosion, the upper Albion Kiya Formation (Golovneva and Nosova, 2012). Cyclical sedimentation is characteristic for the Lower Cretaceous deposits at Shestakovo. The beginning of each cycle is presented in the section in the form of alternating horizons composed of riverine, delta and floodplain facies formed during the regressive phase of sedimentation. These facies, more often with the erosion of the roof of the underlying rocks, are replaced mainly by lake (basin) facies corresponding to the transgressive phase of sedimentation. The full capacity of the Ilek Formation along the sections of drilling wells ranges from several tens to 300–350 meters and increases from the border of the Salair–Caledonian folded structures of the southeastern framing of the West Siberian Platform in the north-westerly direction to the center of the basin, where its greatest observed capacity is 746 m on the Chulym River, near Teguldet village (Lebedev, 1958).

Paleomagnetic studies conducted in the basins of the Kiya, Chulym, and Serta rivers have shown that the Ilek formation, including the Shestakovo strata, has positive magnetization, which excludes the Neocomian age of these deposits (Pospelova and Larionova, 1971). Recent data from spore-pollen spectra indicate the Aptian age of the Ilek formation (Bugdaeva, Markevich, and Volynets, 2017). The composite stratigraphic section along the line Shestakovo 1–4–3 was described previously by Podlesnov, Morkovin, and Maschenko (2018). Below is the description of a stratigraphic section at Shestakovo 3 locality (Fig. 1B).

1) Sand, gray-green, not layered, fine and medium-grained. The exposed thickness is 0.25 m.

2) The sandstone is gray-green, with a finely lenticular structure, there are thin layers of brown mudstone. It contains carbonate nodules and aggregates. The roof of the layer lies with erosion. The exposed thickness is 1.05 m.

3) Mudstones. The layer contains light gray interlayers with traces of wave ripples. Drying cracks filled with sedimentary material from the overlying layer can be traced in the roof of the layer. The exposed thickness is 1.55 m.

4) Sands and sandstones, gray-colored, fine and medium-grained. Closer to the roof of the layer, clay layers with signs of wave ripples are contained. The exposed thickness is 1.55 m.

5) The clays are red and brown-yellow. At the base of the layer an intraformational formation with the psittacosaur skeletons was discovered in 2014. In the middle of the layer, there is an accumulation of both fragments and complete skeletons of crocodylomorphs. The roof of the layer lies with erosion. The exposed thickness is 3.1 m.

6) Sands, fine and medium-grained sandstones. In the middle of the layer, there is a sharp transition from gray sands containing rare layers of red clay to yellowish sands. The roof of the layer is denudated, the exposed thickness is 3 m.

7) Quaternary deposits are up to 1 m thick.

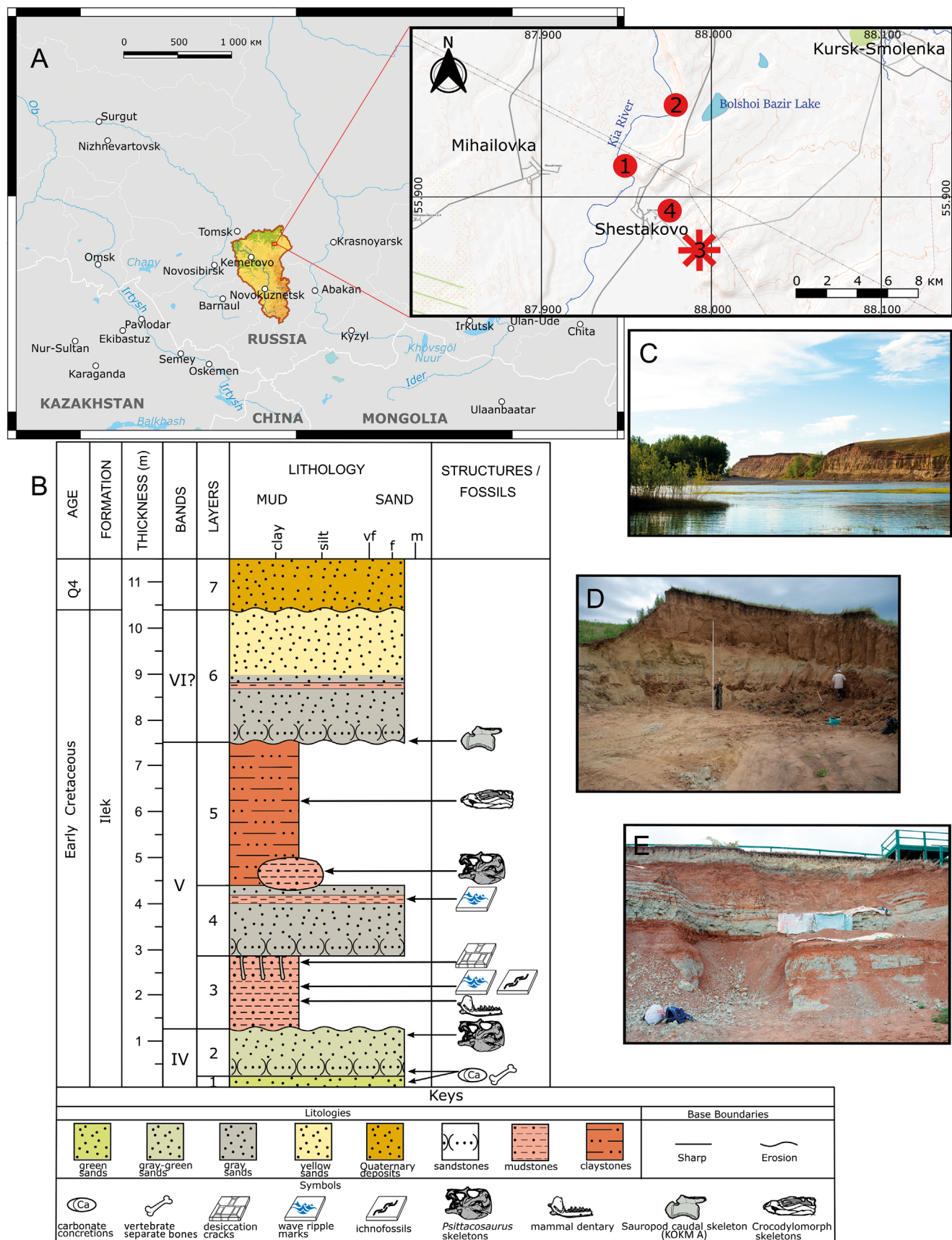


Fig. 1. Geographic and geologic setting of Shestakovo 3 locality. A, Geographical position of Shestakovo and (inset) the localities Shestakovo 1, 2, 3, and 4. B, The lithological section of the Ilek Formation at Shestakovo-3 locality. C-E, photographs of Shestakovo 1 (C), 4 (D), and 3 (E) localities.

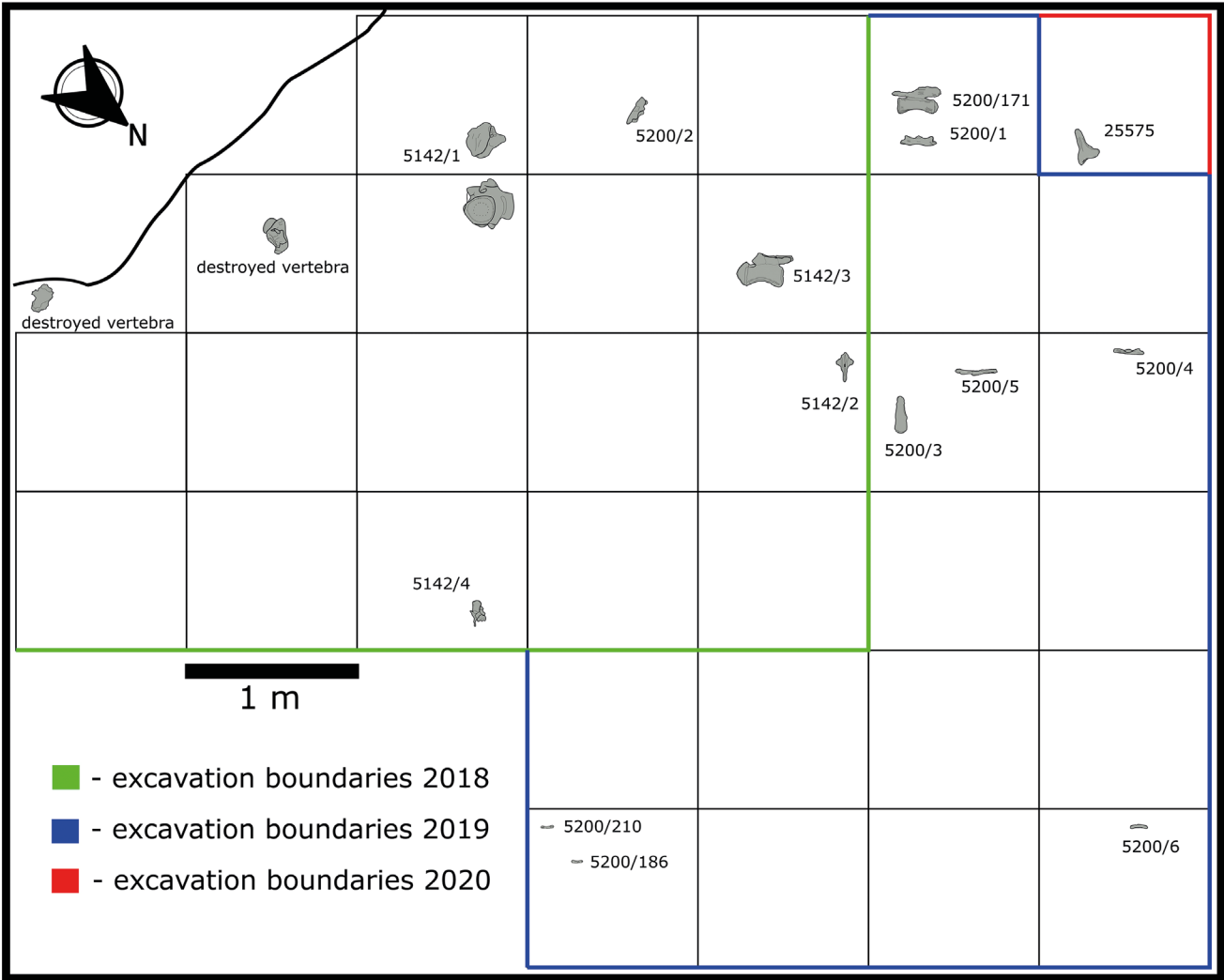


Fig. 2. A quarry map showing the disposition of the skeletal elements of *Sibirotitan astorsacralis* in situ.

Layers 1 and 2 represent the upper part of slice 4 of the geological cross section along the Shestakovo 1 — Shestakovo 4 — Shestakovo 3 line (Podlesnov, Morkovin, and Maschenko, 2018), while layers 3–6 correspond to slice 5 of this section. Layer 6 may be the beginning of a new sedimentation cycle and thus refers to a new slice 6, most of which could have been denudated.

The first fossiliferous level is in the layer 1, which contains complete isolated dinosaur bones. In the gray-green sandstone (layer 2) the psittacosaur skeleton in a partially anatomical articulation was found in 2016. In the mudstones (layer 3) there are both isolated dinosaur bones and disarticulated skeletons (mainly *Psittacosaurus*). In the middle of this layer a fragment of a mammalian skeleton was found in 2016. Numerous finds of various reptiles have been made in red and brown-yellow clays (layer 5). Approximately in the middle of the layer there are numerous finds of crocodylomorphs. In 2014, an intraformational structure containing a large accumulation of *Psittacosaurus* skeletons of different individual age was discovered at the base of the layer (Lopatin et al., 2015). The discov-

ery of a partial sauropod skeleton is confined to the base of a layer of gray-colored sandstones (layer 6). Diagram (Fig. 2) shows that the vertebrae and haemal arches are not anatomically articulated, but are located at some distance from each other. Our data indicates that the studied type of burial is allochthonous. The disintegration of the skeleton and some of its elements into separate parts apparently indicates maceration under subaerial conditions.

Materials and methods

The caudal vertebrae and chevrons were excavated in 2018–2020 at Shestakovo 3 locality in a small area of approximately 9 m². These bones belong to a single specimen, but were catalogued separately according to the Museum rules. The chevron KOKM 25575 is registered for the main collection fund and remaining bones for the temporary storage; their collection numbers can be changed in the future. In this article, we use a conditional number KOKM A for designation of a series of caudal vertebrae and chevrons from one individual from Shestakovo 3.

For phylogenetic analysis we used the matrix from Moore et al. (2023), which includes recent scorings of numerous East Asian sauropods and putative mamenchisaurids. For the compositional history and further details of this matrix see that paper. We added to this matrix *Sibirotitan astrosacralis*, described from the nearby Shestakovo 1 locality of the Ileik Formation (Averianov et al., 2018), and KOKM A. With these additions, the matrix consists of 449 characters and 113 taxa. *Sibirotitan* was scored by 64 characters (14.3%) from this matrix: 11(0&1), 17(1), 22(1), 24(0), 105(0), 106(0), 108(0), 109(0), 110(0), 111(0), 112(0), 113(1), 115(2), 117(0), 118(1), 119(1), 120(1), 121(0), 122(2), 123(0), 124(1), 125(0), 129(0), 130(0), 131(0), 141(2), 142(0), 143(1), 144(1), 145(0), 147(2), 148(1), 151(0), 172(1), 173(1), 249(1), 272(1), 278(0), 320(1), 322(0), 323(1), 324(0), 331(1), 333(0), 334(0), 336(1), 338(0), 339(0), 340(0), 346(0), 347(0), 349(0), 395(0), 396(0), 397(1), 402(0), 403(0), 404(0), 405(0), 407(0), 408(0), 429(0), 431(3), and 433(0). KOKM A was scored for 27 characters (6%) from this matrix: 25(1), 26(1), 27(2), 28(1), 29(1), 30(1), 31(1), 35(0), 176(0), 177(2), 178(0), 180(0), 181(1), 182(0), 183(0), 184(1), 185(1), 189(0), 192(0), 193(0), 208(1), 209(0), 210(1), 211(1), 351(0), 356(0), and 357(0).

Characters 11, 14, 15, 27, 40, 51, 104, 122, 147, 148, 195, 205, 259, 297, 430, 432, 438 and 449 were treated as ordered. As in the analysis performed by Moore et al. (2023), five characters (14, 20, 122, 130 and 258) were made inactive prior to analysis and several unstable terminal taxa were excluded from the analysis a priori (*Asiophocaudia*, *Australodocus*, *Brontomerus*, *Fukuititan*, *Fusuisaurus*, *Liubangosaurus*, *Malarguesaurus*, *Monogolosaurus*, and *Tendaguria*).

The parsimony analysis was performed using TNT v. 1.5, with both equal and extended implied weighting of characters (Goloboff, Farris, and Nixon, 2008; Goloboff and Catalano, 2016). The analysis was run with “New Technology Search” algorithm employing sectorial searches, ratchet, drift, and tree fusing with default parameters. These trees were then subjected to traditional TBR branch swapping.

We run analyses for two matrices, one containing *Sibirotitan* and KOKM A as separate terminal taxa (separate analysis), and for another matrix combining scorings for *Sibirotitan* and KOKM A in a single terminal taxon (combined analysis).

The separate analysis with equal weight characters produced 10,000 most parsimonious trees (MPTs) (overflow) of 2097 steps with consistency index=0.22 and retention index=0.56. The separate analysis applying extended implied weighting with a concavity (k) value of 12 produced 180 MPTs with the tree length of 92.95 steps and the same consistency and retention indices. The combined analysis with equal weight charac-

ters produced 10,000 most parsimonious trees (MPTs) (overflow) of 2100 steps with consistency index=0.22 and retention index=0.56. The combined analysis applying extended implied weighting with a concavity (k) value of 12 produced 468 MPTs with the tree length of 93.14 steps and the same consistency and retention indices.

For the sake of brevity, we refer to the monotypic taxa by the generic names only.

Systematic paleontology

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Sauropoda Marsh, 1878

Titanosauriformes Salgado et al., 1997

Titanosauria Bonaparte et Coria, 1993

Sibirotitan astrosacralis Averianov et al., 2018

Figs. 3–12

Titanosauriformes indet.: Averianov et al. (2002: figs. 2–7).

Sibirotitan astrosacralis: Averianov et al. (2018: p. 4, figs. 4–9); Averianov and Lopatin (2022: fig. 1).

Holotype — PM TGU 120/10-Sh1–22, middle dorsal vertebra.

Type horizon and locality — Shestakovo 1, Kemerovo–Kuzbass oblast, Russia; Ileik Formation, Lower Cretaceous (Aptian).

Referred specimens — KOKM 26786, the anterior caudal vertebra, Shestakovo 1 locality, Kemerovo oblast — Kuzbass, Russia; Ileik Formation, Lower Cretaceous (Aptian). For the list of the other referred specimens from Shestakovo 1 locality see Averianov et al. (2018) and Averianov and Lopatin (2022). KOKM A from Shestakovo 3 locality, Kemerovo oblast — Kuzbass, Russia; Ileik Formation, Lower Cretaceous (Aptian). A series of caudal vertebrae and chevrons from a single individual registered under separate museum numbers: KOKM 5142/1, anterior caudal vertebra; 5142/3, 5200/171, middle caudal vertebrae; 5142/4, posterior caudal vertebra; KOKM 5200/3, 25575, 5142/2, 5200/1, 5200/2, 5200/4, 5200/5, 5200/6, 5200/186, 5200/210, chevrons.

Description

KOKM 5142/1 is considered an anterior caudal vertebra because it retains the transverse process. It has a prococious centrum, with a deeply concave anterior articular surface and a ball-like posterior articular surface surrounded by a rim (Fig. 3). The centrum is slightly compressed dorsoventrally, with the centrum articulation surface wider than high (Table 1). The centrum length is similar to the anterior articular surface width. The cen-

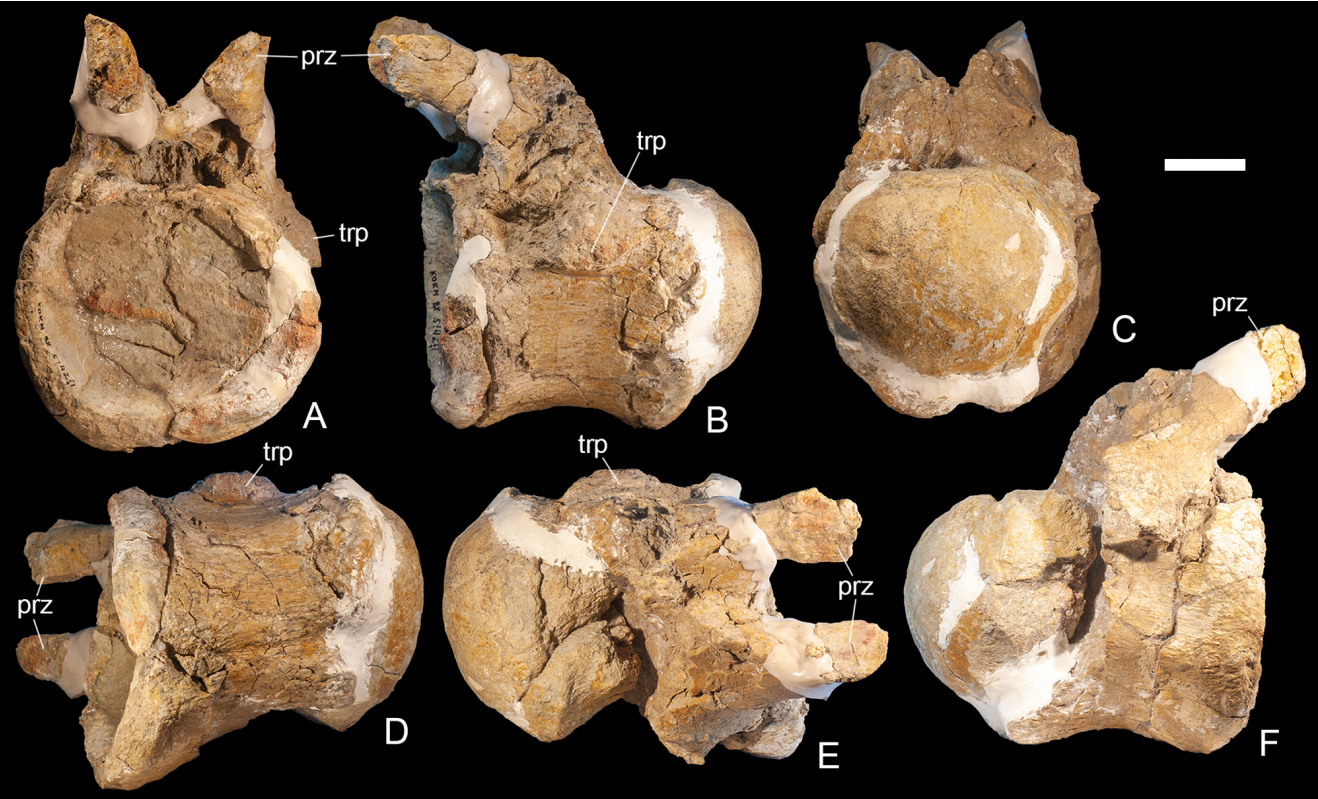


Fig. 3. *Sibirotitan astorsacralis*, KOKM 5142/1, anterior caudal vertebra, in anterior (A), left lateral (B), posterior (B), ventral (D), dorsal (E), and right lateral (F) views. Shestakovo 3, Kemerovo–Kuzbass oblast, Russia; Ilel Formation, Lower Cretaceous (Aptian). Abbreviations: prz, prezygapophysis; trp, transverse process. Scale bar equals 5 cm.

Table 1. Measurements (in mm) of caudal vertebrae. Abbreviations: ACH, anterior centrum height; ACW, anterior centrum width; CL, centrum length; PCH, posterior centrum height; PCW, posterior centrum width					
Specimen KOKM	ACH	ACW	CL*	PCH	PCW
51421/1	162	193	158	160	157
5142/3	103	117	233	115	102
5200/171	62	80	150	54	72
5142/4	36	46	83	27	44

* without the ball.

trum is little constricted between the articular surfaces. In the middle and posterior parts of the centrum ventral side there is a shallow longitudinal groove. A short and bulbous transverse process overhangs the centrum. It is placed close to the centrum — neural arch junction. A horizontal ridge extends anteriorly from the transverse process towards the anterior centrum articular surface.

The anterior opening of the neural canal is dorso-ventrally compressed, with straight dorsal margin. The posterior margin of the neural arch is concave in lateral view and placed some distance anterior to the centrum posterior end. The short prezygapophyses extend anteriorly beyond the centrum. The prezygapophyseal articular surface is oval, higher than wide, and flat to slightly

convex. It is oriented at an angle of 45° to the horizontal. There are pronounced preepipophyseal ridges along the ventrolateral margin of the prezygapophyses. The anterior opening of the neural canal and the floor of the prespinal fossa are separated by a narrow bar of anteriorly facing surface of the neural arch. The spinoprezygapophyseal laminae (sprl) are rounded ridges that extend towards the dorsal margin of the prezygapophyseal articular facets.

Two deeply procoelous caudal vertebrae KOKM 5142/3 and 5200/171 (Figs. 4, 5) are similar in size and morphology and apparently were close in the position. These vertebrae are considered the middle caudals because they lack transverse processes but retain the neural spine and postzygapophyses (Mannion, Upchurch, Barnes and Mateus, 2013).

KOKM 5142/3 (Fig. 4) is larger and more anterior in position than KOKM 5200/171. The anterior articular centrum surface is wider than high, while the posterior articular surface is higher than wide. The posterior ball is separated by a pronounced raised rim which has a broadly concave dorsal margin. There is a small round depression in the middle of the posterior condyle. The ventral centrum side is concave in lateral view. It has shallow grooves anteriorly and posteriorly separated by a raised surface in the middle. The neural arch occupies more than a half of the centrum length and starts close to the centrum anterior end. There is a very small trans-

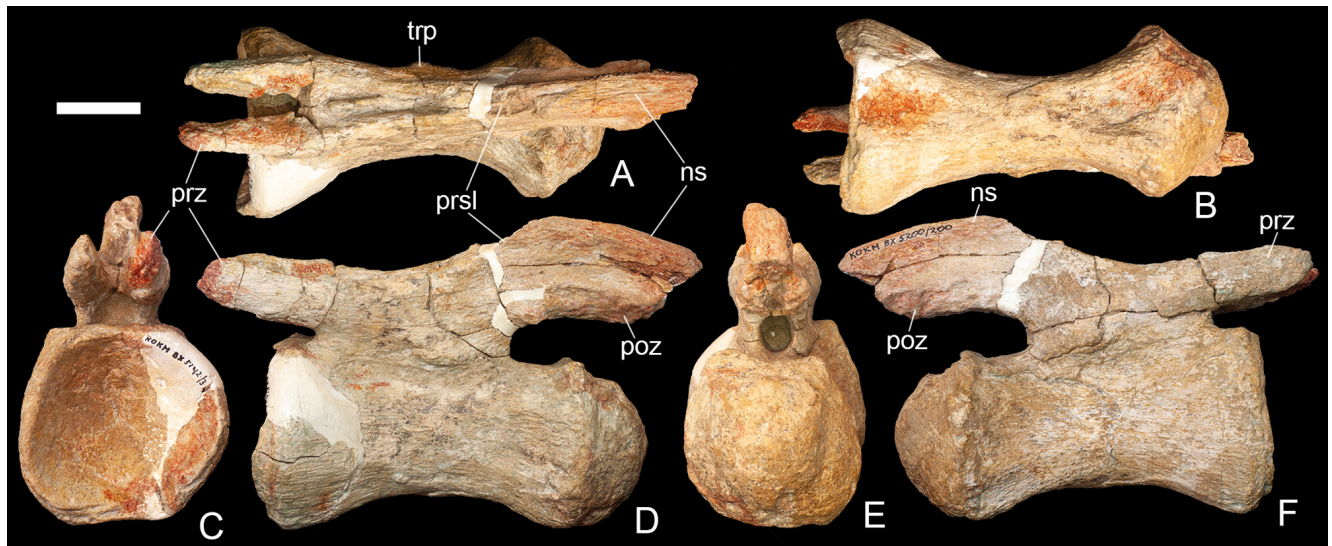


Fig. 4. *Sibirotitan astorsacralis*, KOKM 5142/3, middle caudal vertebra, in dorsal (A), ventral (B), anterior (C), left lateral (D), posterior (E), and right lateral (F) views. Shestakovo 3, Kemerovo-Kuzbass oblast, Russia; Ilel Formation, Lower Cretaceous (Aptian). Abbreviations: ns, neural spine; poz, postzygapophysis; prsl, prespinal lamina; prz, prezygapophysis; trp, transverse process. Scale bar equals 5 cm.

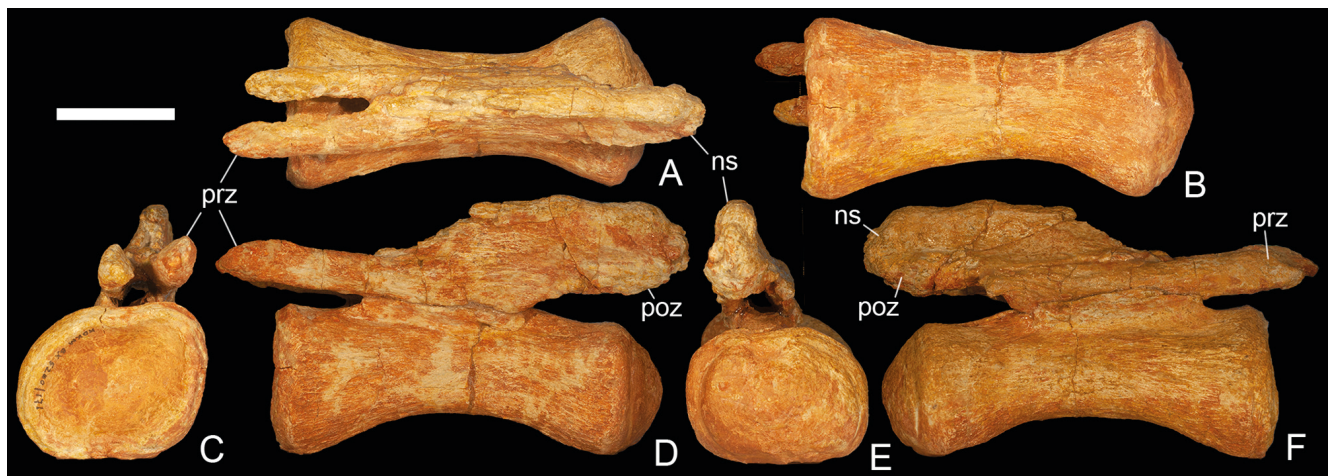


Fig. 5. *Sibirotitan astorsacralis*, KOKM 5200/171, middle caudal vertebra, in dorsal (A), ventral (B), anterior (C), left lateral (D), posterior (E), and right lateral (F) views. Shestakovo 3, Kemerovo-Kuzbass oblast, Russia; Ilel Formation, Lower Cretaceous (Aptian). Abbreviations: ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; trp, transverse process. Scale bar equals 5 cm.

verse process closer to the posterior margin of the neural arch. The prezygapophyses are long and mediolaterally compressed, and extend far beyond the anterior margin of the centrum. There are well-delimited prezygapophyseal articular facets in a form of an elongated oval occupying all of the prezygapophysis beyond the centrum. The articular surface is slightly convex. There is a very deep prespinal fossa bordered by high vertical spino-prezygapophyseal laminae and extending posteriorly towards the middle of the neural arch. There is a short ridge in the anterior part of the prespinal fossa. The prespinal lamina (prsl) is a well-marked rugose area on the anterior slope of the neural spine, between the prespinal fossa and the dorsal margin on the neural spine. The dorsal margin of the low neural spine is convex dorsally. The neural spine extends posteriorly beyond the poste-

rior condyle. The postzygapophyseal articular surfaces are large and demarked by a dorsal ridge. The postzygapophyses are separated by a small but deep postspinal fossa.

In KOKM 5200/171 the centrum is dorsoventrally compressed (Fig. 5). The dorsal margins of the anterior and posterior articular centrum surfaces are slightly concave. There is no rim surrounding the posterior condyle, in contrast with KOKM 5142/3, while their ventral margins are straight. The centrum ventral margin is concave in lateral view. There is a wide shallow groove along the entire ventral centrum surface. The zygapophyses extends anteriorly and posteriorly beyond the centrum. The base of the neural arch occupies about a half of the centrum length and is placed somewhat closer to the anterior centrum end. The anterior end of

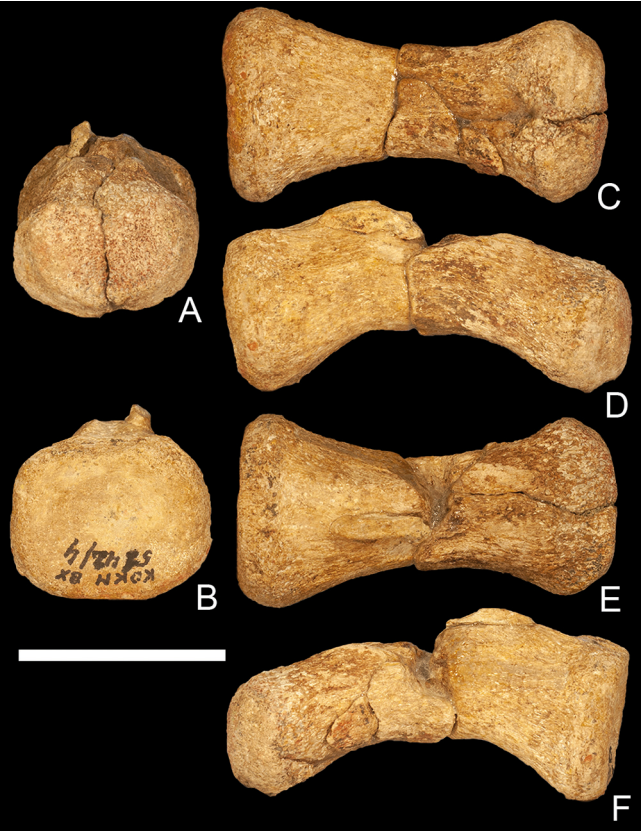


Fig. 6. *Sibirotitan astorsacralis*, KOKM 5142/4, posterior caudal vertebra, in anterior (A), posterior (B), ventral (C), left lateral (D), dorsal (E), and right lateral (F) views. Shestakovo 3, Kemerovo-Kuzbass oblast, Russia; Ilel Formation, Lower Cretaceous (Aptian). Scale bar equals 5 cm.

the neural arch in KOKM 5200/171 is placed far more posteriorly to the centrum anterior end compared with KOKM 5142/3. The prezygapophyses are rod-like, with clear elongate prezygapophyseal facets. The neural spine starts at the anterior end of the neural arch between the prezygapophyses. There is a deep prespinal fossa on the anterior slope of the neural spine. In contrast with KOKM 5142/3, in KOKM 5200/171 there are no transverse processes and prespinal lamina. The neural spine is low and convex dorsally posterior to the prespinal fossa. The prezygapophyseal facets are recognizable and placed near the posterior end of the neural arch. The neural canal is small. Anteriorly, the ventral floor of the neural canal is grooved into the centrum. Posteriorly, it is elevated above the remaining dorsal centrum surface.

The small posterior caudal vertebra KOKM 5142/4 (Fig. 6) is represented by the procoelous centrum which is strongly bent in dorsoventral plane and compressed dorsoventrally. The anterior centrum articular surface is rectangular, with slightly concave dorsal margin. The ventral centrum surface is wide and flat. Only a small piece of the neural arch is preserved closer to the anterior centrum end.

There are five type of chevrons, described according to their position in the caudal section (Table 2). The first

Table 2. Measurements (in mm) of chevrons.
Abbreviations: L — length; W — width

KOKM	L	W
5200/3	85	118
25575	194	94
5142/2	63	110*
5200/2	—	79
52001/1	174	73
5200/5	179	—
5200/4	161	—
5200/6	99	—
5200/210	89	—
5200/186	78	—

* estimate.

and most anterior type is represented by KOKM 5200/3 (Fig. 7) which apparently belongs to the anterior caudal section. It is V-shaped in anterior or posterior view, with diverging proximal processes connected proximally by a transverse bridge, and mediolaterally compressed chevron blade directed ventrally. The proximal processes account for less than a half of the chevron height. The anterior and posterior margins of the proximal processes and the chevron blade are sharp. The haemal canal is oval in section and confined to the dorsal part of the space between the proximal processes. The bulbous ar-

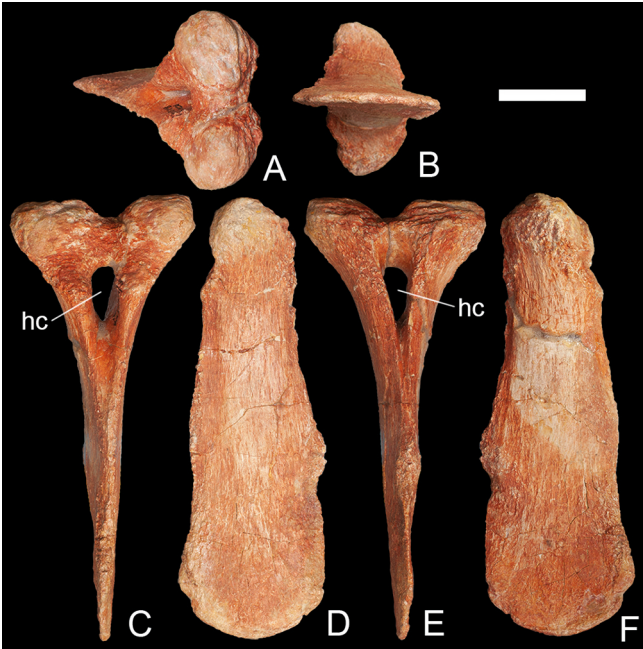


Fig. 7. *Sibirotitan astorsacralis*, KOKM 5200/3, anterior chevron, in dorsal (A), ventral (B), anterior (C), left lateral (D), posterior (E), and right lateral (F) views. Shestakovo 3, Kemerovo-Kuzbass oblast, Russia; Ilel Formation, Lower Cretaceous (Aptian). Abbreviation: hc, haemal canal. Scale bar equals 5 cm.



Fig. 8. *Sibirotitan astorsacralis*, KOKM 25575, middle chevron, in dorsal (A), right lateral (B), left lateral (C), anterior (D), posterior (E), and ventral (F) views. Shestakovo 3, Kemerovo–Kuzbass oblast, Russia; Ileik Formation, Lower Cretaceous (Aptian). Abbreviations: hc, haemal canal; vs, ventral slit. Scale bar equals 5 cm.

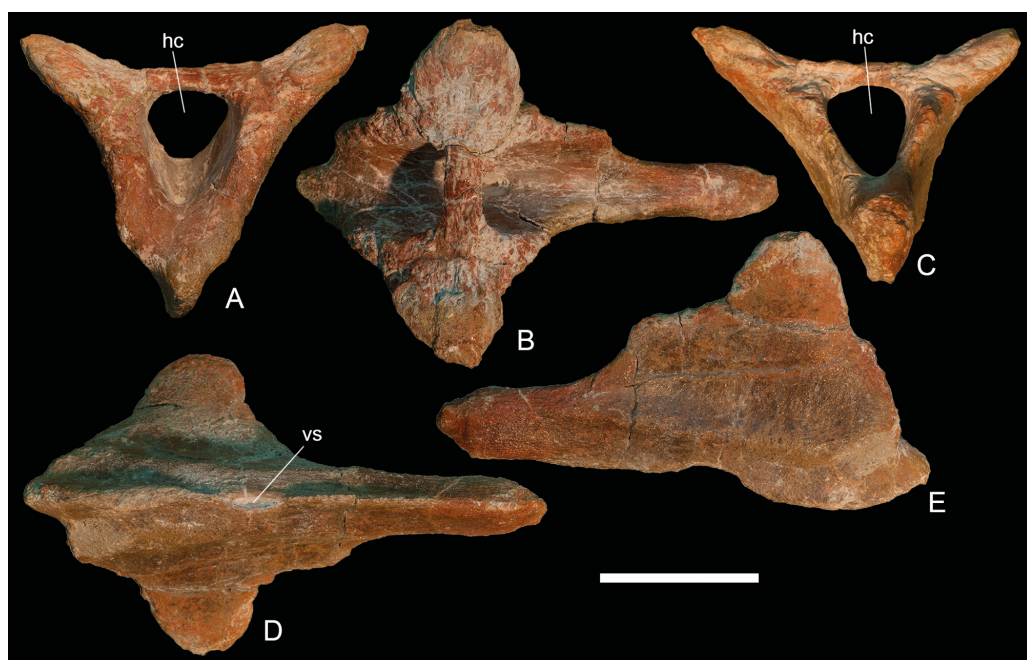


Fig. 9. *Sibirotitan astorsacralis*, KOKM 5142/2, middle chevron, in anterior (A), dorsal (B), posterior (C), ventral (D), and right lateral (E) views. Shestakovo 3, Kemerovo–Kuzbass oblast, Russia; Ileik Formation, Lower Cretaceous (Aptian). Abbreviations: hc, haemal canal; vs, ventral slit. Scale bar equals 5 cm.



Fig. 10. *Sibirotitan astorsacralis*, KOKM 5200/1, middle chevron, in dorsal (A), right lateral (B), left lateral (C), anterior (D), posterior (E), and ventral (F) views. Shestakovo 3, Kemerovo–Kuzbass oblast, Russia; Ilel Formation, Lower Cretaceous (Aptian). Abbreviation: vs, ventral slit. Scale bar equals 5 cm.

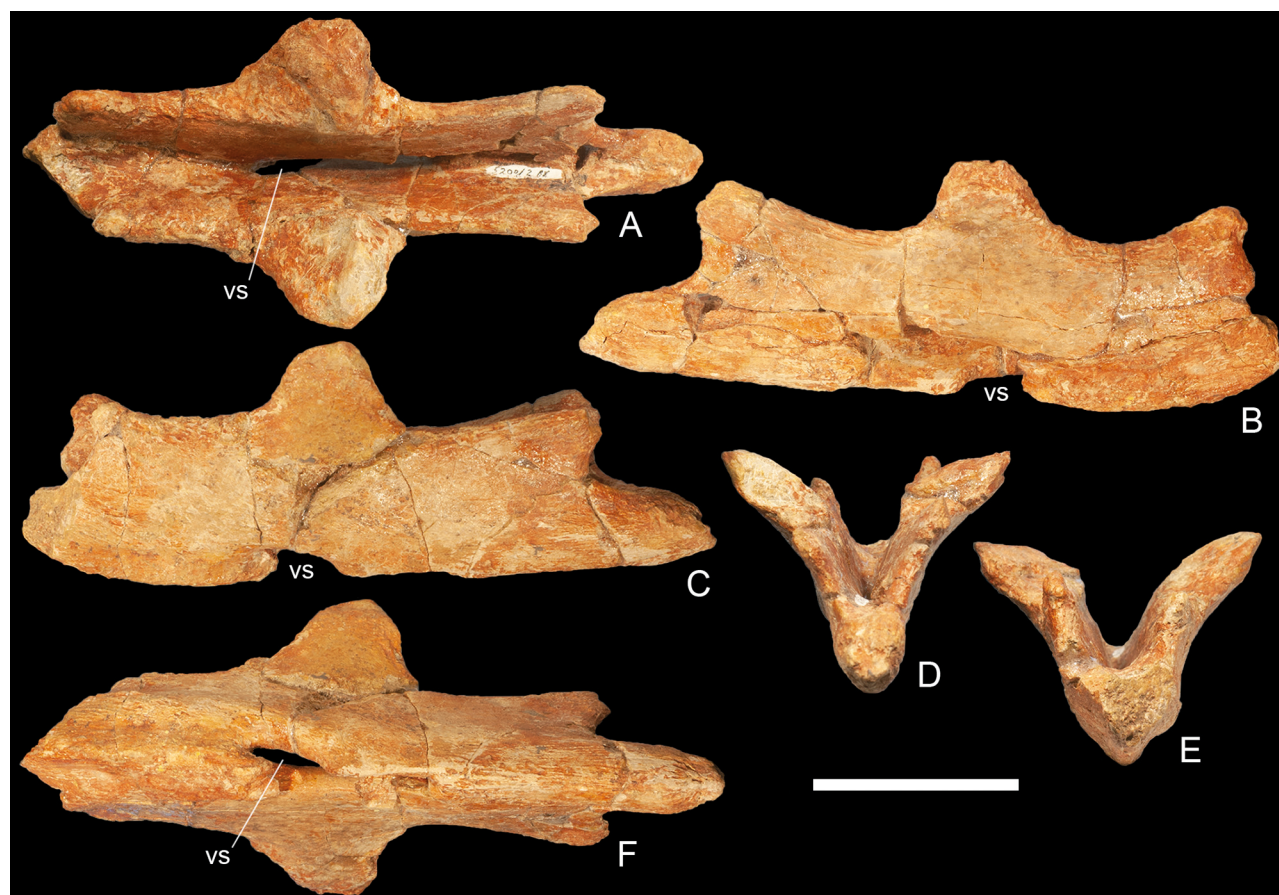


Fig. 11. *Sibirotitan astorsacralis*, KOKM 5200/2, middle chevron, in dorsal (A), right lateral (B), left lateral (C), anterior (D), posterior (E), and ventral (F) views. Shestakovo 3, Kemerovo–Kuzbass oblast, Russia; Ilel Formation, Lower Cretaceous (Aptian). Abbreviation: vs, ventral slit. Scale bar equals 5 cm.



Fig. 12. *Sibirotitan astorsacralis*, posterior chevrons. Shestakovo 3, Kemerovo–Kuzbass oblast, Russia; Ilel Formation, Lower Cretaceous (Ap-tian). A–D, KOKM 5200/5, in dorsal (A), lateral (B), ventral (C), and medial (V) views. E–H, KOKM 5200/4, in dorsal (E), lateral (F), ventral (G), and medial (H) views. I–L, KOKM 5200/6, in lateral (I), medial (K), in dorsal (K), and ventral (L) views. M–O, KOKM 5200/210, in lateral (M), medial (N), and dorsal (O) views. P–R, KOKM 5200/186, lateral (P), dorsal (Q), and ventral (R) views. Scale bar equals 5 cm.

ticular surfaces of the transverse ridge are separated by a depression on the dorsal side of the transverse ridge. The poorly defined articular surfaces face anterodorsally and extend on the anterior side of the proximal processes. The chevron blade slightly flares distally in lateral view and has a round distal margin.

There are two chevrons of the second type, KOKM 25575 and 5142/2 (Figs. 8, 9). These chevrons are asymmetric according to the classification of Otero, Gallina,

Canale, et al. (2012). They are trilobate in lateral view, with the chevron blade divided into in a short anterior process directed anteroventrally and a longer posterior process directed posteroventrally. The ventral margin of the chevron blade is concave in the middle between the anterior and posterior processes. The third lobe is made by the diverging proximal processes connected proximally by the transverse bridge. These processes are triangular in lateral view, wide distally and tapering

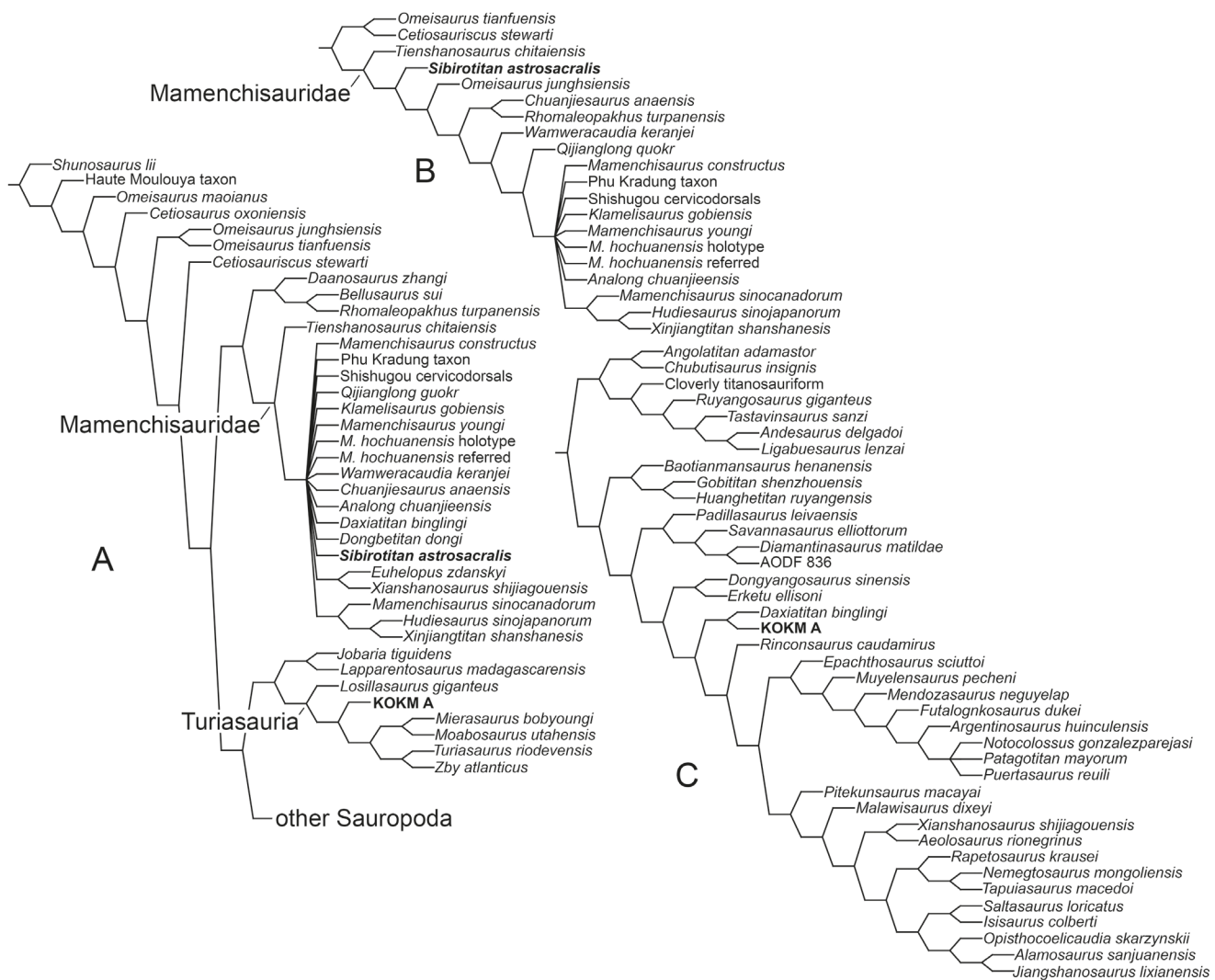


Fig. 13. Fragments of the strict consensus trees of the separate analyses using *Sibirotitan astrosacralis* and KOKM A as separate terminal taxa with characters of equal weight (A) and implied weighting (K=12; B, C). (A) Base of cladogram with Mamenchisauridae and Turiasauria. (B) Mamenchisauridae. (C) Titanosauria.

proximally. The proximal facets face anterodorsally. The haemal canal is large, higher anteriorly than posteriorly. The haemal canal extends into a depression between the anterior and posterior processes of the chevron blade which opens by a slit-like foramen on the left lateral side in KOKM 25575 (Fig. 8C, F) and on the midline of the chevron blade in KOKM 5142/2 (Fig. 9D).

In the chevrons of the third type (KOKM 5200/1 and 5200/2; Figs. 10, 11) the chevron blade is extremely reduced and represented by the posterior prong adjacent to the anteroposteriorly long and dorsoventrally low transverse processes. There is no transverse bridge. The chevron facets face anterodorsally. The proximal processes are separated distally by a large slit-like foramen, which is irregular in shape in KOKM 5200/2. The ventral margin of the chevron is convex in lateral view at the distal foramen in KOKM 5200/1.

In the chevrons of the fourth type (KOKM 5200/4 and 5200/5; Fig. 12A–H), the chevron blade is absent

and the proximal processes (= chevron rami) are completely separate. The chevron facets are large and face anterodorsally. The chevrons of the fifth type are represented by small separated chevron rami which are mediolaterally compressed and sigmoidally curved (Fig. 12I–R). The chevron facets are absent.

Phylogenetic analysis

In the separate analysis with equal weight characters, *Sibirotitan* falls into a polytomy with mamenchisaurids and *Euhelopus*, and KOKM A is a member of Turiasauria (Fig. 13A). KOKM A possesses two of three unambiguous synapomorphies uniting Turiasauria in this analysis, both related to the dorsoventral compression of the anterior caudal centrum (characters 27[2] and 28[1]). The clade uniting KOKM A and all turiasaurs except *Losillasaurus* is supported by a single unambiguous synapomorphy, the presence of a longitudinal hollow on

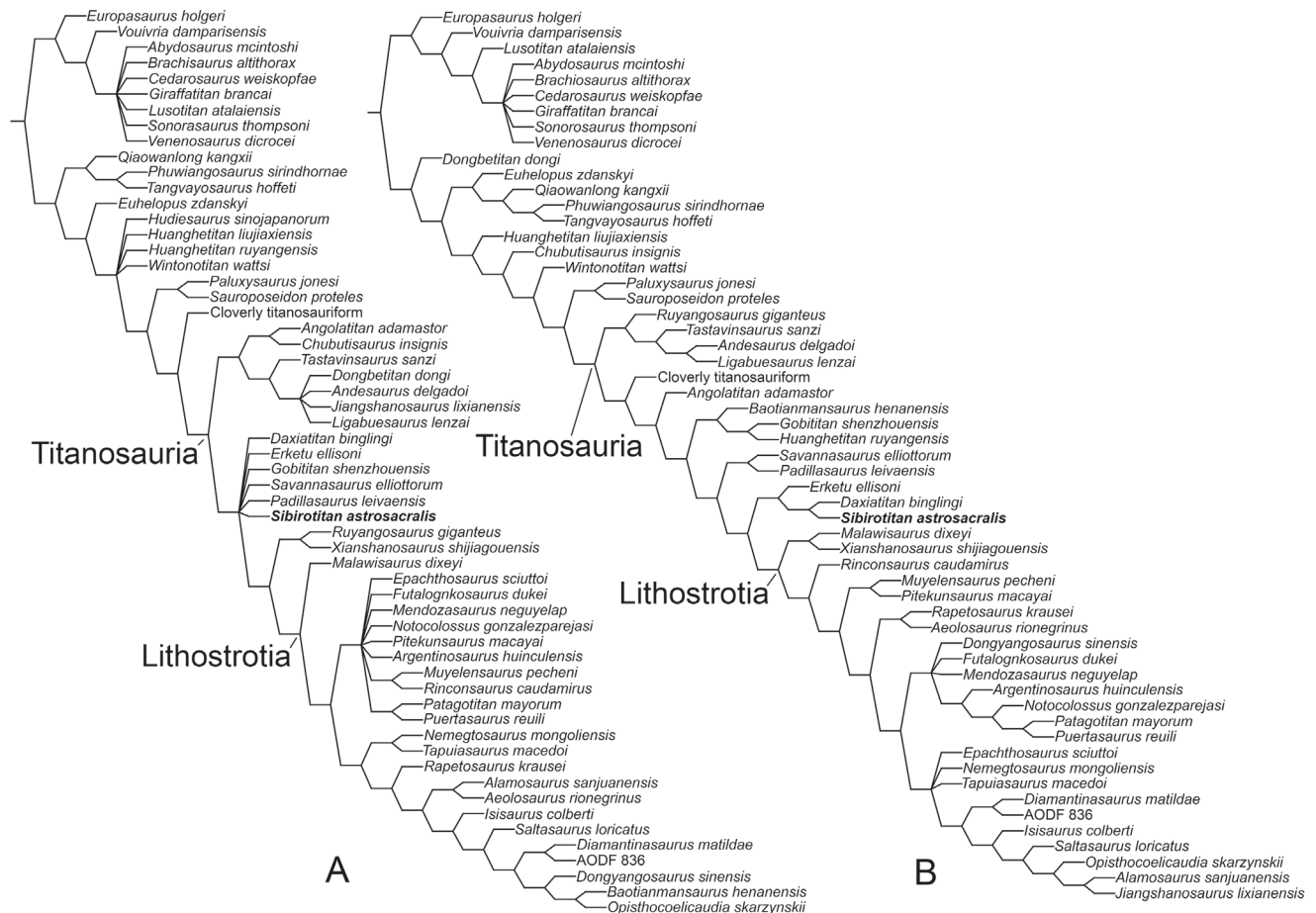


Fig. 14. Fragments of the strict consensus trees of the analyses combining *Sibirotitan astrosacralis* and KOKM A into a single terminal taxon showing interrelationships within Titanosauriformes. (A) Equal weight analysis. (B) Implied weighting analysis (K=12).

the ventral centrum side of anterior and middle caudal vertebrae (character 181[1]). In the separate analysis with implied weighting (K=12) *Sibirotitan* is the sister taxon to the clade uniting *Omeisaurus* and more derived mamenchisaurids (Fig. 13B), and KOKM A is the sister taxon for *Daxiatitan* within Titanosauria (Fig. 13C). KOKM A and *Daxiatitan* are united by two unambiguous synapomorphies, ventral centrum side in anterior-middle caudal vertebrae with longitudinal hollow (character 181[1]) and anterior chevrons bridged dorsally by a bar of bone (character 208[1]).

In the combined analysis with equal weight, *Sibirotitan* is recovered as a non-lithostrotian titanosaur in a polytomy with several taxa, including *Daxiatitan*, *Erketu*, and *Gobititan* (Fig. 14A). In the combined analysis with implied weighting (K=12) *Sibirotitan* is a non-lithostrotian titanosaur within the clade *Erketu* + (*Sibirotitan* + *Daxiatitan*) (Fig. 14B). The latter clade is supported by two unambiguous synapomorphies, both present in *Sibirotitan*: dorsoventral compression of the middle-posterior caudal centra (character 17[1]) and ventral displacement of cervical ribs on middle-posterior cervical vertebrae (character 124[1]).

Discussion

Placement of *Sibirotitan* in Mamenchisauridae in the separate phylogenetic analysis (Fig. 13) is supported by a single unambiguous synapomorphy: restricted size of the lateral pleurocoel in postaxial cervical vertebrae (character 323[1]). Placed within Mamenchisauridae, *Sibirotitan* has a reversal of 13 characters uniting this clade. *Sibirotitan* is similar to Mamenchisauridae by retention of five sacral vertebrae (character 24[0]), while in *Euhelopus* and most Titanosauriformes there are six or more. The camellate internal tissue structure of the cervical and dorsal vertebrae (character 115[2]), found in *Sibirotitan*, was developed in parallel in Mamenchisauridae and Titanosauriformes. In *Sibirotitan* at least some anterior caudal vertebrae were procoelous, judging from the procoelous posterior sacral vertebrae (Averianov et al., 2018). A recently discovered deeply procoelous anterior caudal vertebra from Shestakovo 1 locality is likely belonging to *Sibirotitan* (Fig. 15). It is very similar to the anterior caudal KOKM 5142/1 (Fig. 3). The procoelous anterior caudal vertebrae were developed in parallel in Mamenchisauridae and Titano-

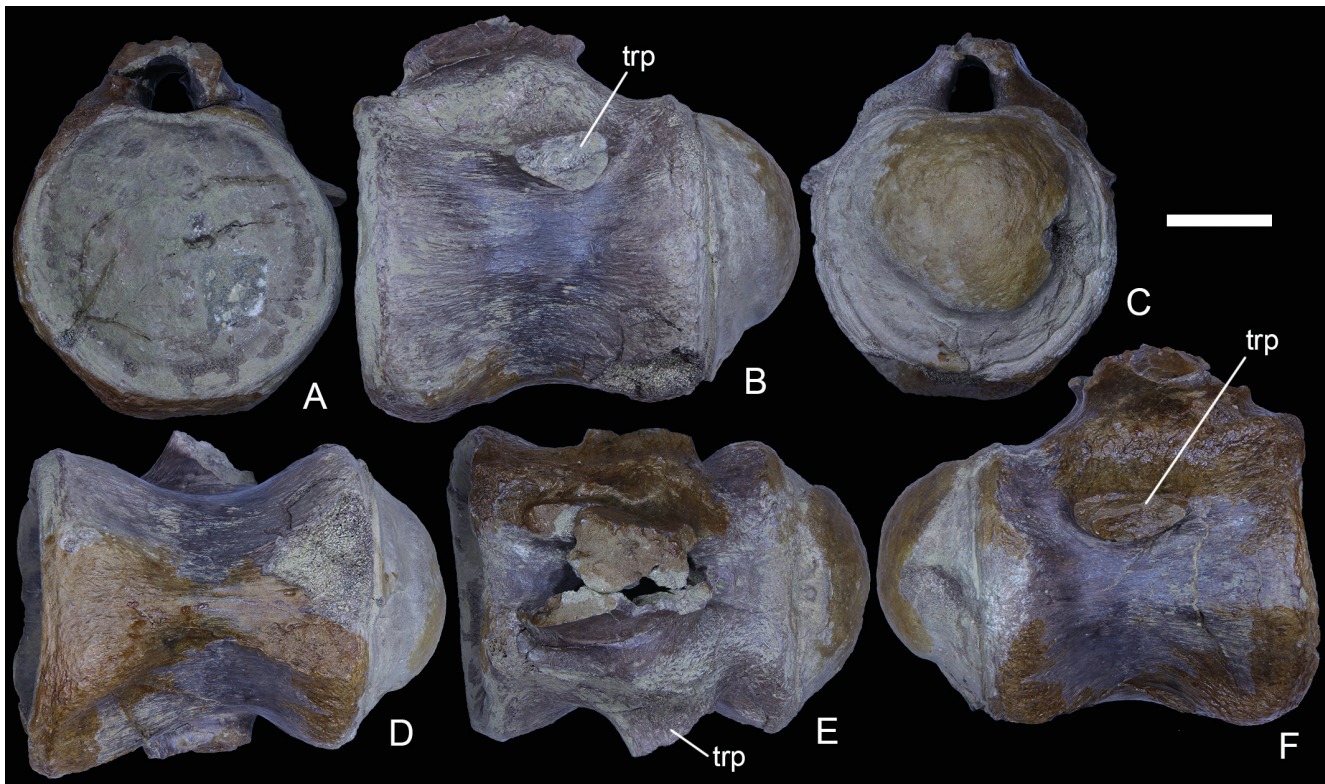


Fig. 15. *Sibirotitan astorsacralis*, KOKM 26786, anterior caudal vertebra, in anterior (A), left lateral (B), posterior (C), ventral (D), dorsal (E), and right lateral (F) views. Shestakovo 1, Kemerovo–Kuzbass oblast, Russia; Ilek Formation, Lower Cretaceous (Aptian). Abbreviation: trp, transverse process. Scale bar equals 5 cm.

sauria (Upchurch, Barrett, and Dodson, 2004). Among Euhelopodidae, the caudal vertebrae are amphicoelous to platycoelous in *Phuwiangosaurus*, *Tangvasaurus*, and *Gobititan* and unknown in other taxa (Wang et al., 2021). *Sibirotitan* shares with *Euhelopus* a unique construction of the sacrum with the sacral ribs converging to the center (Averianov et al., 2018). The position of *Euhelopus* is unstable: different analyses of the same matrix place this taxon either in Mamenchisauridae, or in Somphospondyli (Moore et al., 2020, 2023). Although the known sample of the isolated teeth from Shestakovo 1 is small, all these teeth lack marginal denticles, in contrast with mamenchisaurids. This supports the referral of *Sibirotitan* to Neosauropoda. Currently, attribution of *Sibirotitan* to Mamenchisauridae seems unlikely.

KOKM A from Shestakovo 3 locality is unusual in combining derived morphology of caudal vertebrae and plesiomorphic construction of their haemal arches (chevrons). The procoelous middle and posterior caudal vertebrae (character 184[1]), found in KOKM A, sporadically occur in sauropods, including some turiasaurs, but it is more characteristic for titanosaurs. Upchurch, Barrett, and Dodson (2004) diagnosed *Lithostrotia* as having strong procoely in all caudal vertebrae except the most anterior ones. This diagnosis contradicts the use of *Malawisaurus* as a clade specifier for *Lithostrotia* by these authors, because in this taxon the middle and

posterior caudals are not procoelous (Gomani, 2005; see comment on the status of *Malawisaurus* and *Lithostrotia* in Carballido et al., 2022: p. 288).

In KOKM A, at least some chevrons of the middle and posterior vertebrae have a transverse bony ridge closing the haemal canal proximally (character 208[1]). This is a plesiomorphic condition found in non-macronarian sauropods and other archosaurs (Wilson and Sereno, 1998). In Macronaria, and some non-macronarian taxa (*Shunosaurus*, *Haplocanthosaurus*, *Limaysaurus*) this bridge is absent and the haemal canal is roofed by the vertebrae (Upchurch, 1995; Wilson and Sereno, 1998; Wilson, 2002). Among macronarian sauropods, the proximally bridged chevron is known in the non-titanosaurian titanosauriform *Dongbeititan* (Wang et al., 2007: fig. 1e), in the putative euhelopodid *Daxiatitan* (P. Mannion, comment in review), and the lithostrotian titanosaur *Xianshanosaurus* (Lü et al., 2009: fig. 8B).

In KOKM A, the proximal bony bridge is present in the anterior “forked” chevrons (chevrons of the second type), but absent in more posterior “forked” chevrons. In the eusauropod *Barapasaurus*, mamenchisaurid *Omeisaurus*, and diplodocoids *Diplodocus* and *Dicraeosaurus* the anterior chevrons have completely enclosed haemal canals, while the posterior “forked” chevrons are open proximally (Osborn, 1899: fig. 12; Janensch, 1929: fig. 53; He, Li, and Cai, 1988: fig. 40; Bandyopadhyay, Gillette,

Ray, and Sengupta, 2010: fig. 7D). The posterior “forked” chevrons are bridged proximally in a vulcanodontid *Tazoudasaurus* (Allain and Aquesbi, 2008: fig. 19C, D).

In KOKM A, the haemal canal of the anterior caudal chevron is dorsoventrally low, less than half of the space between the proximal processes (Fig. 7C, E). A haemal canal height that is 50 % or greater of the total chevron height is considered a synapomorphy of Titanosauriformes (Mannion et al., 2013) or Titanosauria (Wilson, 2002).

In non-sauropod sauropodomorphs all chevrons are simple strut-shaped bones. In many eusauropods except titanosaurs the posterior chevrons are “forked”, have distinct anterior and posterior prongs which extend away from the base of the chevron (Upchurch, 1995; Wilson and Sereno, 1998; Otero, Gallina, and Canale, 2012). The presence of “forked” chevrons is considered a synapomorphy of Eusauropoda reversed in Titanosauria (Wilson and Sereno, 1998). The condition of this character is not known for *Brachiosaurus* and *Euhelopus*.

In KOKM A there is a ventral foramen in the middle chevrons that increases in size to ventral slit in more posterior chevrons, and the posteriormost chevrons are completely separated into left and right rami. In Dicraosauridae and Diplodocidae the posterior “forked” chevrons possess a midline ventral slit, and more posterior rod-like chevrons are completely separate (Osborn, 1899: fig. 13; Upchurch, 1995: fig. 15). The posterior chevrons with completely separate chevron rami are present also in the vulcanodontid *Tazoudasaurus* (Allain and Aquesbi, 2008: fig. 19C, D) and the titanosaur *Alamosaurus* (Gilmore, 1946: fig. 4).

Concluding, the procoelous middle and posterior caudal vertebrae of KOKM A suggest affinities with Titanosauria or even Lithostrotia, while proximally bridged chevrons, small haemal canal of anterior chevrons, and “forked” posterior chevrons are more characteristic for non-titanosaurian or even non-macronarian sauropods.

There are several lines of evidence, which suggest the attribution of the caudal skeleton KOKM A from Shestakovo 3 locality to *Sibirotitan* known previously from the nearby Shestakovo 1 locality. First, the procoelous anterior, middle, and posterior caudal vertebrae of KOKM A are consistent with the procoelous anteriormost caudal vertebrae of *Sibirotitan*. Second, the similarity of *Sibirotitan* and *Euhelopus* in unique construction of sacrum with converging sacral ribs. Third, clustering of KOKM A in the separate phylogenetic analysis with the putative euhelopodid *Daxiatitan* (Fig. 13C) from the Lower Cretaceous of Gansu Province, China, which has a very similar anterior caudal vertebra (You, Li, Zhou, and Ji, 2008: fig. 1f). Fourth, *Daxiatitan* has the cervical vertebra very similar to that of *Sibirotitan* (compare You, Li, Zhou, and Ji (2008: fig. 1a) and Averianov et al. (2018:

fig. 5)). *Daxiatitan* is different from *Sibirotitan* by having opisthocoelous anterior caudal vertebrae (Averianov and Sues, 2021). In the combined phylogenetic analysis *Sibirotitan* is clustered with *Daxiatitan* and close to some other putative euhelopodids (Fig. 14B), including *Erketu* from the Late Cretaceous of Mongolia (Ksepka and Norell, 2006, 2010) and *Gobititan* from the Lower Cretaceous of Gansu Province, China (You, Tang, and Luo, 2003). Thus, the most reasonable current interpretation of sauropod specimens from the Shestakovo 1 and 3 localities is that KOKM A belongs to *Sibirotitan*, and *Sibirotitan* is a non-titanosaurian titanosaur (Fig. 14), or titanosauriform, if it is closely related to *Euhelopus*.

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