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Short communication

Caudal vertebrae of titanosaurian sauropod dinosaurs from the Lower Cretaceous Ilek Formation in Western Siberia, Russia

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ABSTRACT

Three sauropod middle caudal vertebrae are described from the three different localities within the Lower Cretaceous (Barremian-Aptian) Ilek Formation in Krasnoyarsk Territory, Western Siberia, Russia. All vertebrae are strongly procoelous and can be referred to Lithostrotia indet. LMCCE 005/40 from Bol'shoi Kemchug 3 locality has a ventral groove on centrum and a very large neural spine that projects posteriorly far beyond the centrum. This specimen also lacks postzygapophyses and bears a heavily sculptured neural spine suggesting high degree of development of the interosseous ligaments. The structure of the neural spine LMCCE 005/40 is similar to that of the saltasaurine *Neuquensaurus* from the Late Cretaceous of South America. However, the Siberian specimen lacks camellate bone texture characteristic for the caudal vertebrae of Saltasaurinae and its similarity with *Neuquensaurus* in development of the neural spine likely was independently acquired. These new findings increase the known diversity of sauropod dinosaurs in the Early Cretaceous of Siberia, which includes three taxa of Lithostrotia indet. described herein, lithostrotian *Tengrisaurus*, and titanosauriform *Sibirotitan*.

1. Introduction

The Lower Cretaceous Ilek Formation widely distributed in Western Siberia (Kemerovo Province and Krasnoyarsk Territory; Fig. 1) produced a variety of freshwater and terrestrial vertebrates, including dinosaurs (see recent reviews in Averianov and Lopatin (2015) and Averianov et al. (2015, 2018)). The dinosaur skeletal remains are found predominantly in two localities in Kemerovo Province: Shestakovo 1 and 3. The most abundant are articulated skeletons and skeletal fragments of the basal ceratopsian *Psittacosaurus sibiricus*, present on both localities but more numerous on Shestakovo 3 (Rozhdestvensky, 1955, 1960; Averianov et al., 2006; Lopatin et al., 2015; Podlesnov, 2018). Skeletal remains of the titanosauriform sauropod *Sibirotitan astrosacralis* have been found only in Shestakovo 1 locality (Averianov et al., 2018). Shestakovo 1 and 3 also produced rare isolated bones of theropod dinosaurs, including birds (Kurochkin et al., 2011; O'Connor et al., 2014). The dinosaur skeletal remains are rare in the eastern group of localities of the Ilek Formation. Majority of vertebrate fossils found there are isolated dinosaur teeth and bones of smaller tetrapods and fishes collected during the screen-washing of the fossiliferous matrix. Among larger dinosaur remains are the three sauropod caudal vertebrae described herein. The sauropod caudals are the most abundant sauropod remains found in fluvial deposits, but surprisingly, no caudal vertebrae are currently known for *Sibirotitan astrosacralis* from Shestakovo 1 locality. The strongly procoelous caudal vertebra from Bol'shoi Kemchug 3 locality (LMCCE 005/40) was collected in 2000 and was mentioned but not described in subsequent publications (Averianov et al., 2002, 2004). Two other specimens were found more recently: LMCCE 005/120 from Bol'shoi Kemchug 5 locality in 2016 and LMMCE 007/25 from Bol'shoi Ilek locality in 2017. Although fragmentary, these specimens provide a new information on the sauropod diversity in the Ilek Formation and contribute to the understanding of distribution of the early lithostrotian titanosaurs.

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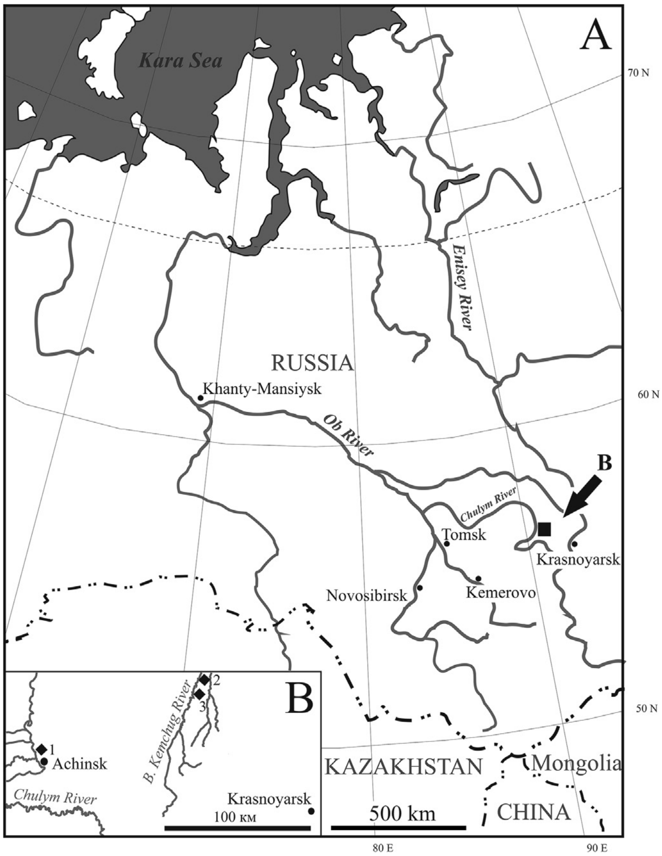

Fig. 1. Map of Western Siberia, Russia (A), and inset B showing position of the sauropod localities: 1, Bol'shoi Ilek; 2, Bol'shoi Kemchug 3; 3, Bol'shoi Kemchug 5.

1.1. Institutional abbreviation

LMCCE – Laboratory of Mesozoic and Cenozoic Continental Ecosystems, Tomsk State University, Tomsk, Russia.

1.2. Vertebral measurements

ACH – anterior height of centrum; ACW – anterior width of centrum; CL – centrum length (on ventral side, without the condyle); PCH – posterior height of centrum; PCW – posterior centrum width.

2. Geological setting

The three sauropod caudal vertebrae described herein come from the three localities in Krasnoyarsk Territory, Western Siberia, Russia (Fig. 1). The brief accounts of these localities are present below. The age of the Ilek Formation is poorly constrained and estimated as Barremian-Aptian (see review in Averianov et al. (2018)). Recently the fossiliferous level at Shestakovo 1 locality has been dated as Aptian by pollen (Bugdaeva et al., 2017).

2.1. Bol'shoi Ilek

The outcrop is 1 km downstream from the city of Achinsk (N 56°19′03.8″, E 90°28′09.1″). This outcrop is the stratotype of Ilek Formation (Ragozin, 1936). In spite of the high total thickness of the Mesozoic deposits up to 80 m, the diversity of facies is low. Most probably, the sedimentation process took place in a large freshwater basin. The lowermost part of the sections is composed of horizontally laminated siltstones and fine-grained sandstones, deposited from the suspended matter, at the foot of the delta front. The middle and upper parts of the section comprise sandstone bodies, formed during the migration of the shoreline. These deposits form steeply inclined beds of fine-grained well-sorted cross-laminated sandstones. The uppermost part of the section comprises the cross-laminated and lenticular medium-grained sandstones with a fossil vertebrate remains, including the caudal vertebra LMCCE 007/25, and silty intraclasts (10–20 cm of thickness) of distributary channels, formed on the erosional surface.

2.2. Bol'shoi Kemchug 3

The section of the outcrop, exposed on the right high bank of the Bol'shoi Kemchug River (N 56°31′38″, E 91°48′49″) of Emelyanovo District, Krasnoyarsk Territory consists of the yellowish and greenish-grey poorly lithified inequigranular polymictic sandstones with inclusions of argillite pebbles. The lower part of the section is relatively massive with rare coalified trunks and branches up to 0.8 m in diameter. The overlaying strata were deposited with discordancy, represented by uneven erosional surface and poorly rounded argillite pebbles up to 0.5 m in diameter, which reflects the sedimentary condition of closeness to the shoreline. The upper part of the section is a series of lenses with a thickness up to 2.0 m with microvertebrate remains and rare macrofossils, including the caudal vertebra LMCCE 005/40, accumulated in the lowermost parts of lenses in yellowish-grey sandstones with small argillite pebbles.

2.3. Bol'shoi Kemchug 5

The site is represented by the 700-m long section on the right bank of Bol'shoi Kemchug River (N 56°40′07″, E 91°55′50″), three kilometers upstream from the mouth of Bol'shoi Terekhtyul River, Emelyanovo District, Krasnoyarsk Territory. With a total height of 22 m, only the lower quarter (around 5.5 m) is composed by the Lower Cretaceous deposits of Ilek Formation, which consist of greenish and yellow-grey inequigranular polymict carbonate sandstones with clayish intraclasts. Sometimes the bedding surfaces are distinguished by the presence of coalified trunks and branches up to 0.4 m in diameter. Cross-bedding, lenticular, and ropy structures of the sediments are typical for alluvial facies. Discovered in 2001, it is still rather preliminary studied. The screen washing and surface prospecting have already revealed remains of fishes, turtles, and dinosaurs. The caudal vertebra (LMCCE 005/120) was found on the on the bank downstream from the outcrop, and most probably originates from the dark greyish-blue inequigranular silty sandstones with a rare coalified wood remains.

3. Description

3.1. LMCCE 005/40

LMCCE 005/40 is the large middle caudal vertebra with the CL more than 220 mm (the anterior margin is not complete; Figs. 2 and 3). The centrum articulation is procoelous, with the convex anterior articular surface and ball-like posterior articular surface. Most of the anterior articulation surface is destroyed, but it is evident that it was distinctly higher than the posterior centrum articulation surface. The posterior condyle is slightly asymmetrical in lateral view, with dorsally displaced the most prominent part of the condyle. There is a distinct pit on this most prominent part of the posterior condyle. There is a strong ridge circumscribing the posterior condyle and the condyle is restricted from the outer margin by a flat area. This flat area is the widest ventrolaterally and narrowest dorsally. The posterior articulation surface was certainly wider than high, but its lateral margin is not complete from the left side (Table 1). The widest part of the posterior articulation surface is closer to the ventral margin so this surface is of somewhat triangular shape in posterior view. The narrow dorsal and much wider ventral margins of the posterior articulation surface are straight.

The centrum is constricted transversely at the middle. The laterally narrowest part of the centrum is 62 mm, which is 1.9 times narrower than the posterior centrum articulation surface width. The lateral centrum surface is deeply concave anteroposteriorly and flat or slightly convex dorsoventrally. The ventral side of the centrum is deeply arched in lateral view. All the ventral side of the centrum is occupied by a groove bordered laterally by shallow ridges which become higher towards the anterior and posterior ends. The posterior end of this groove is about twice wider than the anterior end. There are large but poorly defined chevron facets along the posterior margin of the centrum (the area for chevron facets is destroyed anteriorly).

The transverse process (preserved on the left side) is very small, ridge-like, directed ventrolaterally and posteriorly. It is placed ventrally to the neurocentral junction but dorsally to the centrum mid-height.

The neural arch is mostly destroyed anteriorly but rather complete posteriorly above the neural canal (Fig. 2A). The neural arch pedicel was close to the anterior margin of the centrum and is separated by about 50 mm from the posterior margin of the centrum (excluding the ball). The anterior opening of the neural canal is small. The partially preserved right prezygapophysis is relatively weak and protruding slightly beyond the centrum articulation surface. The neural arch and neural spine are relatively large compared with the centrum. The most distinctive feature of LMCCE 005/40 is that the neural spine projects posteriorly far beyond the posterior articulation surface (Fig. 2A). The neural spine is anteroposteriorly long and directed posterodorsally. The dorsal lip of the neural spine is separated from the rest of the spine by a deep longitudinal groove. This tip is heavily sculptured laterally and dorsally by longitudinal ridges and grooves. The similar sculpture is present on the prespinal and postspinal laminae (Fig. 3A, C). The prespinal lamina has a concave surface and extends anteriorly to the preserved anterior end of the neural spine without a change in width. The spinoprezygapophyseal laminae are not developed as distinct ridges. The postspinal lamina also has the concave surface. It extends anteriorly along the posteroventral margin of the neural spine and bordered by distinct spinopostzygapophyseal laminae. There are no postzygapophyses and the spinopostzygapophyseal laminae meet ventrally. These laminae border a deep wedge-like depression. The postspinal lamina terminates dorsal to this depression. Some distance ventral to the sculptured lip of the neural spine there is a distinct longitudinal ridge on the lateral surface of neural spine. A smaller but also distinct ridge is present between the former ridge and the sculptured part of the neural spine near the posterior end of the spine. This ridge is oriented anterodorsally-posteroventrally.

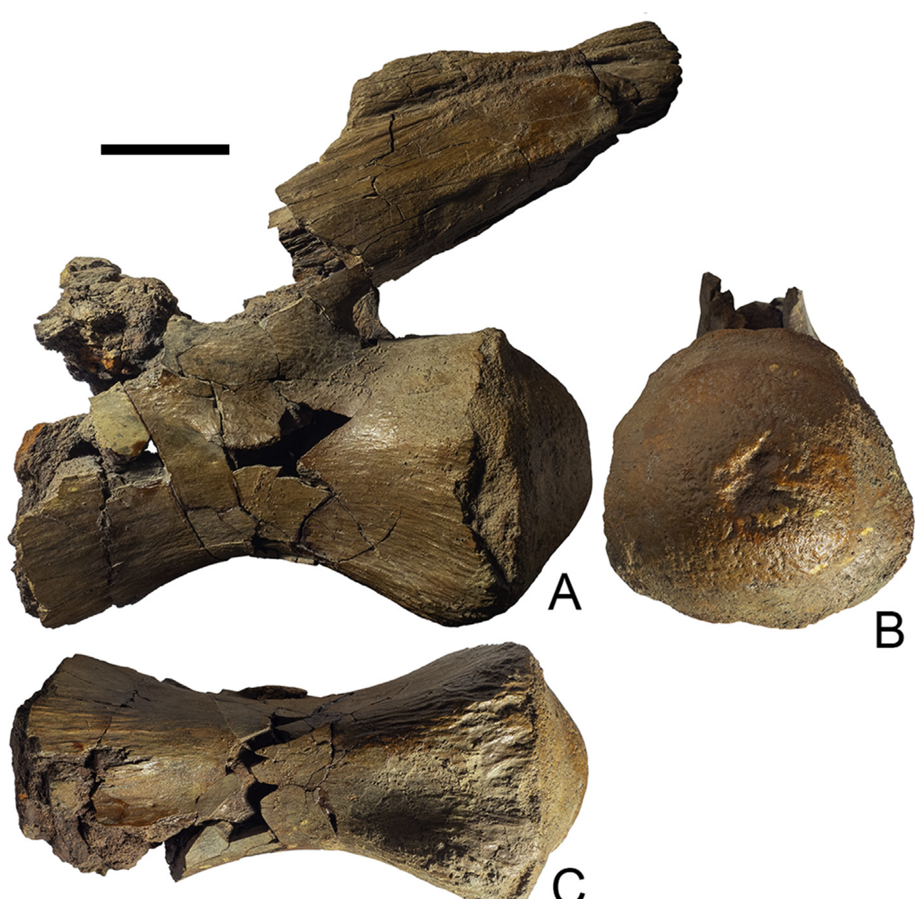

Fig. 2. Lithostrotia indet., LMCCE 005/40 (Bol'shoi Kemchug 3, 2000), middle caudal vertebra, in lateral (A), posterior (B), and ventral (C) views. Ilek Formation, Lower Cretaceous. Scale bar equals 5 cm.

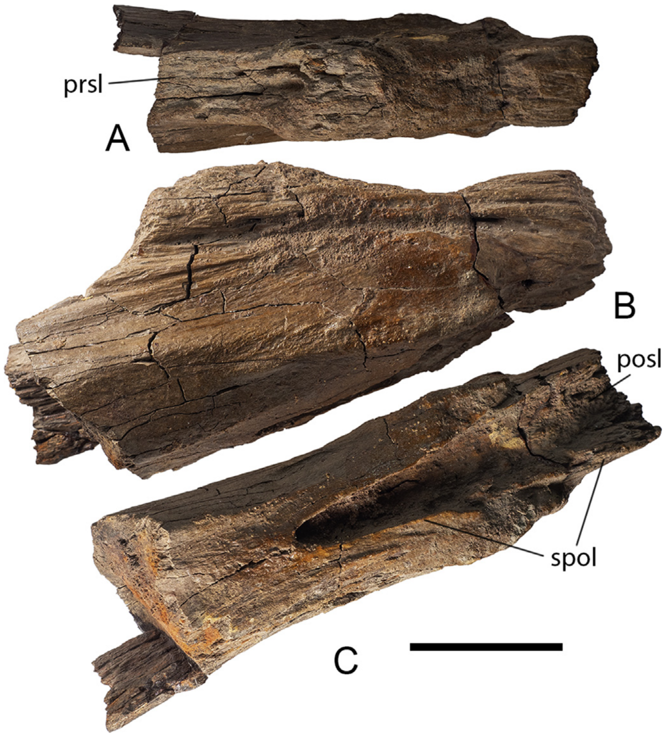

Fig. 3. Lithostrotia indet., LMCCE 005/40 (Bol'shoi Kemchug 3, 2000), neural spine of the middle caudal vertebra, in dorsal (A), lateral (B), and ventral (C) views. Ilek Formation, Lower Cretaceous. Abbreviations: prsl, prespinal lamina; posl, postspinal lamina; spol, spinopostzygapophyseal lamina. Scale bar equals 5 cm.

3.2. LMCCE 005/120

LMCCE 005/120 is a distinctly smaller middle caudal vertebra with more complete centrum but neural arch badly preserved anteriorly and posteriorly (Fig. 4). The centrum articulation is procoelous, with deeply convex anterior articulation surface and ball-like posterior articulation surface. The anterior articulation surface is higher than wide (Table 1), of hexagonal shape. The narrow dorsal margin of the anterior centrum articulation surface is straight. The lateral margin is divided into larger dorsal and smaller ventral parts. The anterior centrum articulation surface is higher and wider than the posterior surface (Table 1). The posterior centrum articulation surface is cone-like in lateral view, with the most prominent point placed in the middle. The posterior centrum articulation surface is also hexagonal in posterior view, but the dorsal arm of the lateral margin is much higher compared with the ventral arm. The dorsal and ventral margins of the posterior centrum articulation surfaces are straight. The lateral sides of the centrum at the junction with the posterior condyle are excavated by large and deep depression.

The centrum is constricted at the middle, with the narrowest point being 54 mm which is 72% from the anterior centrum articulation surface width. The lateral surface of the centrum is concave anteroposteriorly and convex dorsoventrally. The ventral margin of the centrum is gently concave in lateral view. On the ventral centrum surface, there is a shallow depression anteriorly and elevated area in the middle. There are no longitudinal grooves or lateral ridges. There are poorly defined chevron facets along the anterior and posterior margins of the centrum. The anterior facets are smaller.

There is no transverse process, but in this place, there is a prominent elevated area accentuated by a semilunar groove ventrally, anteriorly, and posteriorly.

The pedicel of the neural arch is separated by 15 mm from the centrum anterior margin and by 32 mm from the centrum posterior margin (excluding the ball), so the neural arch is anteriorly placed in the centrum. The neural canal is relatively large and round anteriorly and smaller, egg-shaped (pointed dorsally) posteriorly. The prezygapophyses are broken but apparently were robust, rod-like, and extending anteriorly beyond the anterior margin of the centrum. The postzygapophyses and most of the neural spine are missing. The prespinal lamina is about twice narrower than the neural arch in the middle. Between the anterior end of the prespinal lamina and anterior margin of the neural arch the prezygapophyses are separated by a very shallow depression. It is bordered by low spinoprezygapophyseal laminae that terminates anteriorly before the anterior margin of neural arch between the prezygapophyses. The angle of the neural spine to the neural arch is about 30°.

Table 1
Measurements (in mm) of the sauropod caudal vertebrae from the Lower Cretaceous Ilek Formation in Western Siberia, Russia. Measurements: ACH, anterior height of centrum; ACW, anterior width of centrum; CL, centrum length (on ventral side, without the condyle); PCH, posterior height of centrum; PCW, posterior centrum width; EI, elongation index (CL/ACH).

Specimen	ACH	ACW	CL	PCH	PCW	EI
LMCCE 005/40	–	–	220[a]	114	116[a]	–
LMCCE 005/120	78.5	74.5[b]	171	68	67[b]	2.18
LMCCE 007/25	126	136.5	190	99[a]	99.5[a]	1.51

[a] Incomplete.
[b] Estimate.

3.3. LMCCE 007/25

LMCCE 007/25 is poorly preserved relatively short procoelous middle caudal vertebra (Fig. 5). The anterior articulation surface is subcircular, slightly wider than high, with almost flat dorsal and round lateral surfaces. The posterior articulation surface is mostly damaged but likely was cone-like, wider than high. Its narrow dorsal margin is deeply concave. The anterior centrum articulation surface is distinctly wider than the posterior one. The centrum is constricted at the middle, with the narrowest point about twice narrower than the anterior centrum articulation surface width. This constricted part is closer to the posterior centrum margin. The lateral centrum surface is concave anteroposteriorly and convex dorsoventrally. There is a small longitudinal through channel on the left lateral side of the centrum. Dorsoventral diameters of its openings are 8.5 mm. The distance between the openings is 26 mm. The ventral centrum surface is not well preserved posteriorly. Anteriorly it is flat to slightly convex, with a shallow longitudinal groove. There are no chevron facets along the anterior centrum margin.

There is no transverse process. The neural arch is placed much closer to the anterior centrum margin than to the posterior. The cleft-like neural canal is unusual. It is wide but very shallow anteriorly and high and very narrow posteriorly. The prezygapophyses (anteriorly incomplete) are robust, rod-like and projects anteriorly beyond the anterior margin of the centrum. The prezygapohyses are widely separated by a depression and bear prominent spinoprezygapophyseal laminae dorsally. Between these laminae, there is a relatively narrow prespinal lamina which terminates anteriorly well before the anterior margin of the neural arch between the prezygapophyses. The neural spine and postzygapophyseal area are missing.

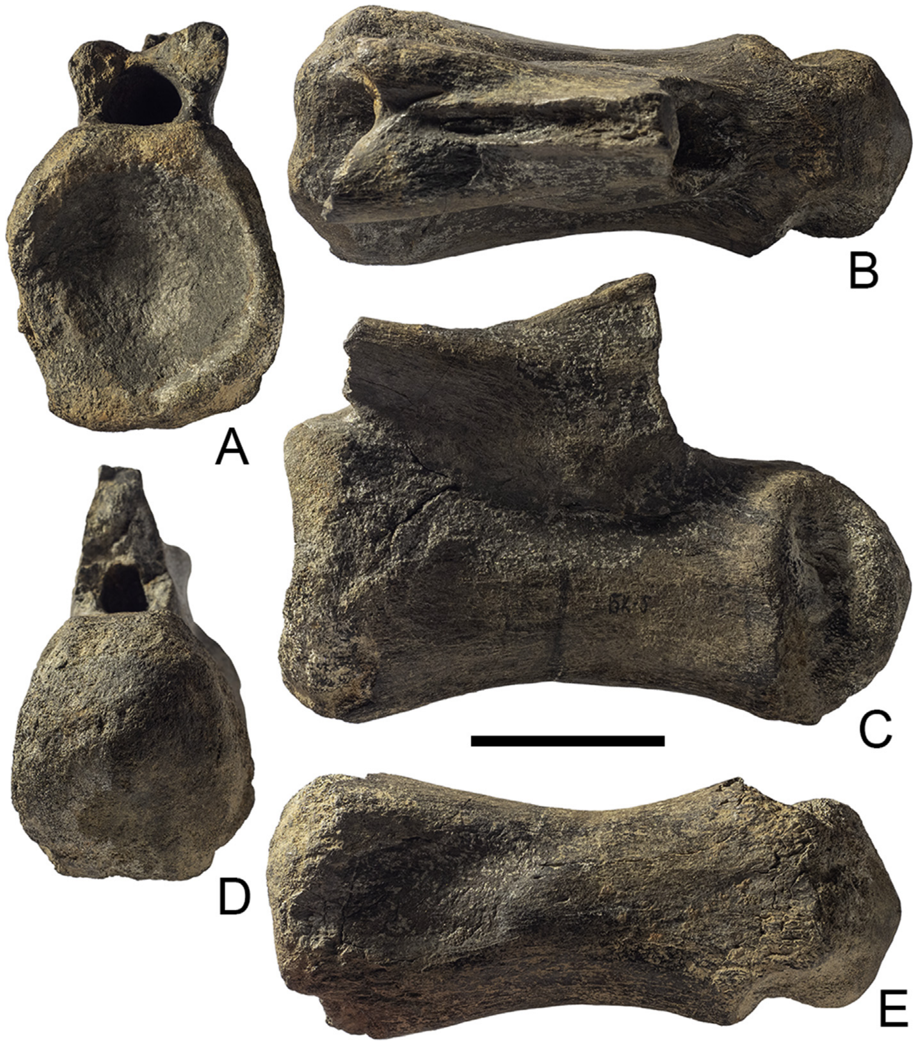

Fig. 4. Lithostrotia indet., LMCCE 005/120 (Bol'shoi Kemchug 5, 2016), middle caudal vertebra, in anterior (A), dorsal (B), lateral (C), posterior (D), and ventral (E) views. Ilek Formation, Lower Cretaceous. Scale bar equals 5 cm.

4. Comparison

By comparison with the caudal series of *Alamosaurus* (Gilmore, 1946) the estimated position of LMCCE 005/40 is caudal 13–14, LMCCE 005/120 – caudal 20–21, and LMCCE 007/25 – caudal 16–17. LMCCE 005/40 is clearly different from LMCCE 005/120 by a ventral groove on the centrum and very large neural spine. LMCCE 005/40 differs from LMCCE 007/25 by more pronounced ventral groove with lateral ridges. LMCCE 005/120 differs from LMCCE 007/25 by laterally constricted centrum, with the centrum articulation surfaces slightly higher than wide. This suggests that all three specimens belong to three different sauropod taxa.

All the middle caudals from the Ilek Formation are deeply procoelous. In the basal titanosaurs *Andesaurus* and *Malawisaurus* the procoelous anterior caudal vertebrae are associated with amphicoelous or platycoelous middle caudal vertebrae (González Riga et al., 2009). The procoelous middle caudal vertebrae is a synapomorphy of Lithostrotia (Wilson, 2002; Upchurch et al., 2004; D'Emic, 2012; Averianov and Skutschas, 2017). By this character, all the three caudal vertebrae from the Ilek Formation can be referred to Lithostrotia. LMCCE 005/40 differs from the middle caudal of *Tengrisaurus*, a lithostrotian titanosaur from the Early Cretaceous of Transbaikalia, Russia (Averianov and Skutschas, 2017), by much higher neural spine and lack of postzygapophyses. LMCCE 005/120 is narrower transversely than the middle caudal of *Tengrisaurus*. LMCCE 007/25 is similar in proportions with the middle caudal of *Tengrisaurus*, which also has a more horizontal posterior opening of the neural canal, but differs in having narrower, clef-like anterior and posterior openings of the neural canal.

In LMCCE 005/40 there is a longitudinal ventral groove flanked by low ridges, while in two other specimens this groove is absent and ventral centrum side is flat or convex. The presence of a ventral groove on anterior and middle caudals was considered a synapomorphy for the Titanosauria (Wilson, 2002; D'Emic, 2012) or a more inclusive clade within Titanosauria (Curry Rogers, 2005; Averianov and Skutschas, 2017). The ventrolateral ridges are often but not always present together with the ventral groove. Both characters are found, for example, in *Isisaurus*, *Alamosaurus*, *Neuquensaurus*, and *Saltasaurus* (Gilmore, 1946; Powell, 1992; Jain and Bandyopadhyay, 1997; D'Emic and Wilson, 2011). The ventral groove LMCCE 005/40 is not as deep as in Saltasaurinae. In the saltasaurines *Saltasaurus* and *Rocasaurus*, and in an undetermined saltasaurine from the Campanian Angostura Colorada Formation in Argentina, on the ventral side of the centrum in middle caudals there is a very large longitudinal depression subdivided by a

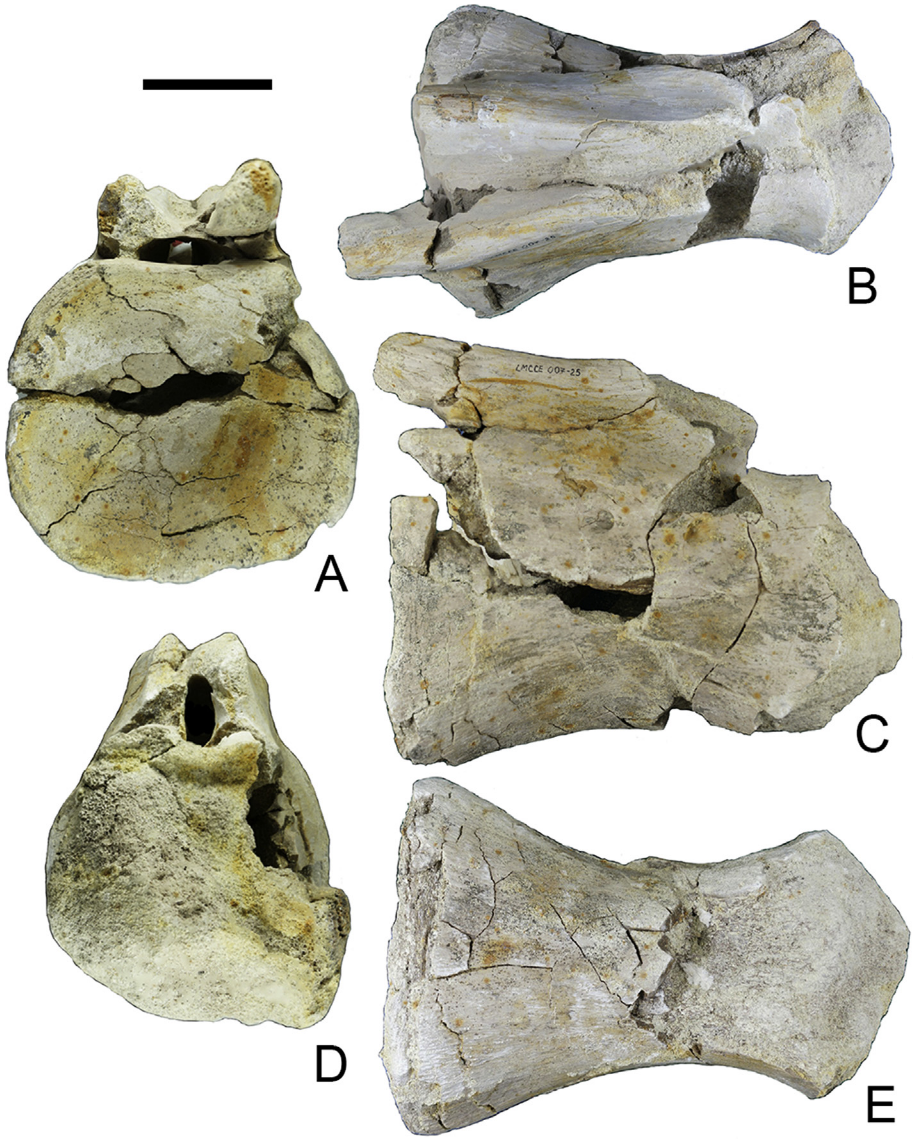

Fig. 5. Lithostrotia indet., LMCCE 007/25 (Bol'shoi Ilek, 2017), middle caudal vertebra, in anterior (A), dorsal (B), lateral (C), posterior (D), and ventral (E) views. Ilek Formation, Lower Cretaceous. Scale bar equals 5 cm.

median ridge (Salgado and Azpilicueta, 2000; Zurriaguz et al., 2017: fig. 3).

In LMCCE 005/40 the apex of the posterior centrum condyle is somewhat dorsally displaced. This is a common feature of Lithostrotia, except *Aeolosaurus* which have the apex close to the centrum midline (Santucci and De Arruda-Campos, 2011).

The neural arch of all three caudal vertebrae is confined to the anterior half of the centrum. This is synapomorphy of the Titanosauriformes (Curry Rogers, 2005; D'Emic, 2012).

LMCCE 005/40 with the estimated position in the series as caudal 13–14 preserves rudimentary but distinct transverse process. In most eusauropods the caudal transverse processes disappeared by caudal 15, but in some titanosaurs, like *Alamosaurus* or *Opisthocoelicaudia*, it disappeared by caudal 10 (Gilmore, 1946; Borsuk-Bialynicka, 1977; Wilson, 2002; Upchurch et al., 2004; Curry Rogers, 2005). In other titanosaurs (*Volgatitan*, *Trigonosaurus*, and *Saltasaurus*), in contrast, the transverse process is present in the middle caudals (Powell, 1992; Campos et al., 2005; Averianov and Efimov, 2018).

The most striking feature of LMCCE 005/40 is its very large and posteriorly directed neural spine, which extends posteriorly far beyond the centrum. The strongly posteriorly directed neural spine of anterior and middle caudal vertebrae is a characteristic feature of the Saltasaurinae (e.g., *Neuquensaurus*) (Salgado et al., 2005). In other titanosaurs, the neural spine of anterior and middle caudal vertebrae is vertical, or even anteriorly inclined. In *Neuquensaurus* in the middle caudals 9–14 the neural spine extends posteriorly beyond the centrum (Salgado et al., 2005: fig. 6D), as in LMCCE 005/40, but these caudals preserve well developed functional postzygapophyses, while in the Siberian specimen the postzygapophyses are already totally absent. In *Isisaurus*, *Alamosaurus* and *Trigonosaurus* in the middle caudals there are well developed functional postzygapophyses (Gilmore, 1946; Jain and Bandyopadhyay, 1997; Campos et al., 2005). In *Saltasaurus* in the middle caudal the neural spine is directing posterodorsally, as in LMCCE 005/40, but does not project posteriorly beyond the centrum and has a functional postzygapophysis (Powell, 1992: fig. 23).

In LMCCE 005/120 and LMCCE 007/25 the neural arch is relatively low and occupies more than half of the centrum length. This contrast the condition of derived Gondwanan titanosaurs, where the middle caudals often have tall neural arch occupying half or less of the centrum length (Calvo et al., 2007; Curry Rogers, 2009; Carballido et al., 2011; Filippi et al., 2011).

The middle caudal LMCCE 005/120 is similar to that of *Isisaurus*, *Ampelosaurus*, and *Alamosaurus* in having gently sloping anterior margin of the neural spine (Gilmore, 1946; Jain and Bandyopadhyay, 1997; Le Loeuff, 2005). In other titanosaurs, the neural spine of middle caudals has vertical or even anteriorly protruding anterior margin (Gomani, 2005; González Riga et al., 2018; Gorscak and O'Connor, 2019).

The middle caudal LMCCE 007/25 is unique in the shape of the anterior and posterior openings of the neural canal. Both openings are narrow, cleft-like, the anterior opening is oriented horizontally while the posterior opening is oriented vertically.

5. Discussion

All three described middle caudal vertebrae from the Ilek Formation belong to lithostrotian taxa based on strongly procoelous centra. The taxonomic attribution of LMCCE 005/120 and LMCCE 007/25 cannot be determined beyond this level (Lithostrotia indet.). LMCCE 005/40 possess, however, the derived characters that link it with the Saltasaurinae (*Saltasaurus*, *Neuquensaurus*, and *Rocasaurus* from the Campanian-Maastrichtian of Argentina) (Powell, 1992; Salgado et al., 2005): the ventral groove on centrum flanked by low lateral ridges and the neural spine, which is very large, posteriorly directed, and protruding posteriorly beyond the centrum. While the ventral groove is not as deep as in the South American Saltasaurinae, the derived condition of the neural spine in this specimen is not paralleled by any Asiatic taxon and found only in the South American Campanian *Neuquensaurus* (Salgado et al., 2005). In the Campanian-Maastrichtian *Lirainosaurus* from Spain, which is considered a derived lithostrotian close to the Saltasaurinae (Sanz et al., 1999; Díez Díaz et al., 2013), the neural spine of middle caudals is much smaller than in LMCCE 005/40.

LMMCE 005/40 is very unusual in having a very large neural spine together with the total lack of the postzygapophyses. The lack of zygapophyseal articulation in this region may be explained by the development of the strong interosseous ligament between the neural spines of adjacent caudals, which is marked by the pronounced sculpturing of the dorsal part of the neural spine. The lack of postzygapophysis prevents checking the position of the anterior margin of the neural spine relative to the postzygapophysis. Posterior position of this margin to the anterior end of the postzygapophysis in the middle caudal vertebrae was once considered a synapomorphy for the Saltasaurinae (Salgado et al., 1997), but actually found also in *Bonatitan*, a sister taxon to the Saltasauridae (Salgado et al., 2015). However, if the dorsal end of the prespinal lamina is considered as the anterior margin of the neural spine, it is located posterior to the posterior incision between the neural spine and the centrum, i.e. it is posterior to the postzygapophysis if it would be present.

LMMCE 005/40 lacks an important character considered a synapomorphy for Saltasaurinae: camellate bone texture (with large internal cells) of middle to posterior caudal vertebrae (Powell, 1992; Wilson, 2002; Wedel, 2003; Whitlock et al., 2011; Cerda et al., 2012; Zurriaguz et al., 2017). LMCCE 005/40, as well as the two other caudal vertebrae from the Ilek Formation, has solid bone internal texture. In Saltasaurinae the middle caudal vertebrae also have the centrum which is wider than tall (Powell, 1992; Salgado et al., 2005), which contrasts the middle caudal vertebrae from the Ilek Formation, which have centra taller than wide.

Two interpretations of LMCCE 005/40 are possible. First, that it belongs to a basal member of the Saltasaurinae which retains plesiomorphic bone texture and centrum proportions of the middle caudal vertebrae. Second, that this taxon acquires large posteriorly projecting neural spine and ventral groove of centrum on middle caudal vertebrae independently from the Saltasaurinae. The second interpretation seems more plausible taking into account a large temporal and geographic gap between the Early Cretaceous Siberian taxon and the Late Cretaceous South American Saltasaurinae. The Saltasaurinae includes *Saltasaurus*, *Neuquensaurus*, and *Rocasaurus* (Salgado et al., 1997; Curry Rogers, 2005; Bonaparte et al., 2006; Calvo et al., 2007; Bandeira et al., 2016) and only one taxon (*Neuquensaurus*) approaches the condition of the neural spine of middle caudal vertebrae seen in LMCCE 005/40.

The specimens described herein document presence of at least three lithostrotian taxa in the Lower Cretaceous Ilek Formation of Western Siberia. This complements the sauropod dinosaur *Sibirotitan* described previously from the Shestakovo 1 locality within this formation (Averianov et al., 2018). The phylogenetic analysis recovered *Sibirotitan* as non-titanosaurian titanosauriform. However, the caudal vertebrae are not known for this taxon. Discovery of procoelous caudal vertebrae from Shestakovo 1, which may be attributed to *Sibirotitan*, may change the phylogenetic position of this taxon. Another sauropod known from the Early Cretaceous of Siberia is a derived lithostrotian *Tengrisaurus* from the Murtoi Formation (Barremian-Aptian) of Transbaikalia (Averianov and Skutschas, 2017). This limited data at hands suggest that derived lithostrotian dinosaurs were widely distributed and diverse in the Lower Cretaceous of Siberia. This contrasts the dinosaurian faunas in Central Asia and China where lithostrotian titanosaurs were not present until the Late Cretaceous (Averianov and Sues, 2017).

6. Conclusions

There are two sauropod dinosaurs already described from the Early Cretaceous of Siberia, a non-titanosaurian somphospondylan *Sibirotitan* from the Ilek Formation (Aptian) at the Shestakovo 1 locality in Kemerovo Province, Western Siberia, and a lithostrotian titanosaur *Tengrisaurus* from the Murtoi Formation (Barremian?-Aptian) at the Mogoito locality in Buryatia, Transbaikalia. The three strongly procoelous caudal vertebrae described here document presence of three different taxa of lithostrotian titanosaurs in the Ilek Formation of Western Siberia. They come from three different localities in Krasnoyarsk Territory: Bol'shoi Kemchug 3 (LMCCE 005/40), Bol'shoi Kemchug 5 (LMCCE 005/120), and Bol'shoi Ilek (LMCCE 007/25). In LMCCE 005/40 from Bol'shoi Kemchug 3 locality there is a ventral groove on centrum and a very large neural spine that projects posteriorly far beyond the centrum. This specimen also lacks postzygapophyses and bears a heavily sculptured neural spine suggesting high degree of development of the interosseous ligaments. The structure of the neural spine LMCCE 005/40 is similar to that of the saltasaurine *Neuquensaurus* from the Late Cretaceous of South America. However, the Siberian specimen lacks camellate bone texture characteristic for the caudal vertebrae of Saltasaurinae and its similarity with *Neuquensaurus* in development of the neural spine likely was independently acquired. In LMCCE 005/120 and LMCCE 007/25 the neural arch is relatively low and occupies more than half of the centrum length. In derived Gondwanan titanosaurs the middle caudals usually have tall neural arch occupying half or less of the centrum length. In LMCCE 007/25 both anterior and posterior openings of the neural canal are narrow, cleft-like. The anterior opening is oriented horizontally while the posterior opening is oriented vertically. These characters are not found in other titanosaurs.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2019.104309.