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STEGOSAUR REMAINS FROM THE MIDDLE JURASSIC OF WEST SIBERIA

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ABSTRACT

The Middle Jurassic (Bathonian) Itat Formation at Berezovsk Quarry, Krasnoyarsk Territory (West Siberia, Russia) has produced abundant remains of stegosaurs. Numerous isolated teeth are found at various microvertebrate sites, and associated skeletal remains, mostly vertebrae, ribs, and ilio-sacral block fragments were excavated at the Stegosaur Quarry. These remains likely belong to one taxon which is characterized by numerous secondary ridges on one crown side in cheek dentition, six vertebrae in the synsacrum, four sacral and one dorsosacral ribs, lack of dorsal process on the transverse process in anterior caudals, moderately expanded tops of the neural spines in anterior caudals, and large triangular transversely thin dorsal dermal plates. The combination of these and other features is not characteristic for any other known stegosaur taxon and the Berezovsk stegosaur likely represents a new taxon. Among known stegosaurs it is most similar with *Stegosaurus* from the Late Jurassic and Early Cretaceous of North America and Asia by having numerous secondary ridges on teeth, a right angle between the supraacetabular flange and the anterior iliac process of ilium and in the structure of the dorsal dermal plates. It differs from *Stegosaurus* by plesiomorphically unexpanded tops of the neural spines and lack of dorsal process on the transverse processes in the anterior caudal vertebrae. The Berezovsk stegosaur is among the oldest stegosaurs in the fossil record.

Key words: Dinosauria, Middle Jurassic, Russia, Stegosauria, West Siberia

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ОСТАТКИ СТЕГОЗАВРОВ ИЗ СРЕДНЕЙ ЮРЫ ЗАПАДНОЙ СИБИРИ

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РЕЗЮМЕ

Многочисленные остатки стегозавров обнаружены в отложениях среднеюрской (бат) итатской свиты, вскрытой в Березовском карьере Красноярского Края (Западная Сибирь, Россия). Многочисленные изолированные зубы происходят из различных местонахождений микропозвоночных в карьере. Ассоциированные скелетные остатки (в основном позвонки, ребра и фрагменты подвздошно-крестцового блока) найдены в “стегозавровом раскопе”. Эти остатки, вероятно, принадлежат особям одного таксона, который характеризу-

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ется многочисленными вторичными гребнями на одной стороне коронки щечных зубов, шестью позвонками в сложном крестце, четырьмя крестцовыми и одним спино-крестцовым ребрами, отсутствием дорсального отростка на поперечных отростках передних хвостовых позвонков, умеренно расширенными вершинами остистых отростков передних хвостовых позвонков и большими треугольными поперечно тонкими спинными костными пластинками. Комбинация этих и других признаков не характерна для какого-нибудь известного таксона стегозавров, и, поэтому, Березовский стегозавр, вероятно, принадлежит к новому таксону. Среди известных стегозавров он наиболее сходен с *Stegosaurus* из поздней юры и раннего мела Северной Америки и Азии по наличию многочисленных вторичных гребней на зубах, по прямому углу между надвертлужным флангом и передним отростком подвздошной кости и по строению спинных костных пластинок. Березовский стегозавр отличается от *Stegosaurus* такими примитивными чертами, как слабо поперечно расширенные вершины остистых отростков и отсутствие дорсального отростка на поперечных отростках передних хвостовых позвонков. Березовский стегозавр является одним из наиболее древних стегозавров известных в геологической летописи.

Ключевые слова: Dinosauria, средняя юра, Россия, Stegosauria, Западная Сибирь

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INTRODUCTION

The Middle Jurassic (Bathonian) beds of the Itat Formation, revealed in the Berezovsk Quarry on the south of Krasnoyarsk Territory, West Siberia (Fig. 1) has produced a diverse fauna of vertebrates, including fishes, salamanders, turtles, choristoderes, lizards, crocodiles, pterosaurs, dinosaurs, tritylodontids, and diverse mammals (see Averianov et al. 2005 for details). This fauna is known mostly from small sized disarticulated specimens obtained during underwater screen-washing at various fossiliferous strata within the Itat Formation, but in one place, called the Stegosaur Quarry (Fig. 2), associated but usually not articulated larger dinosaur bones were excavated by S.A. Krasnolutskii and his assistants during three field seasons (2005–2007). Majority of dinosaur bones from this quarry belong to stegosaurs, and at least two individuals are present. The bones are irregularly scattered along the surface indicating a long period of sub-aerial exposure. The burial was biased to mostly vertebrae, ribs, and ilio-sacral blocks. The limb bones and dermal plates are known from single specimens and the cranial bones are lacking altogether. The purpose of this paper is to give a detailed morphological description to the stegosaur remains from this quarry and the microvertebrate sites. In the taxonomy of Stegosauria we follow the recent revision by Maidment et al. (2008).

Tooth measurements. BCW, basal crown width; FABL, fore-aft-basal length; TCH, tooth crown height. All linear measurements are in mm.

Institutional abbreviations. SHRM, Sharypovo Regional Museum, Krasnoyarsk Territory, Russia.

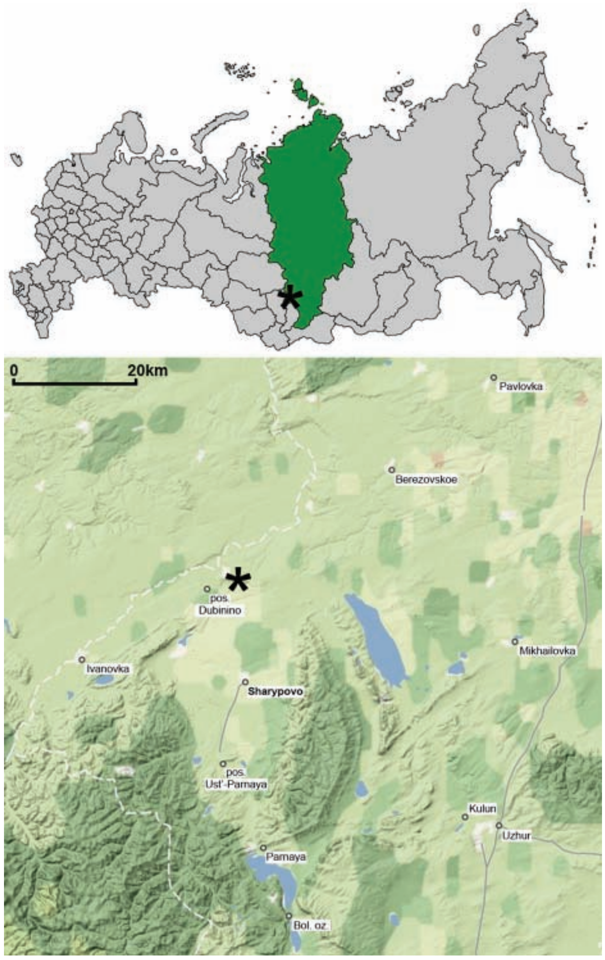

Fig. 1. Geographic position of Berezovsk Quarry (asterisk) on the map of Russia (top, Krasnoyarsk Territory is in green) and in the vicinity of Sharypovo city (bottom; the map is modified from http://maps.google.ru/maps).

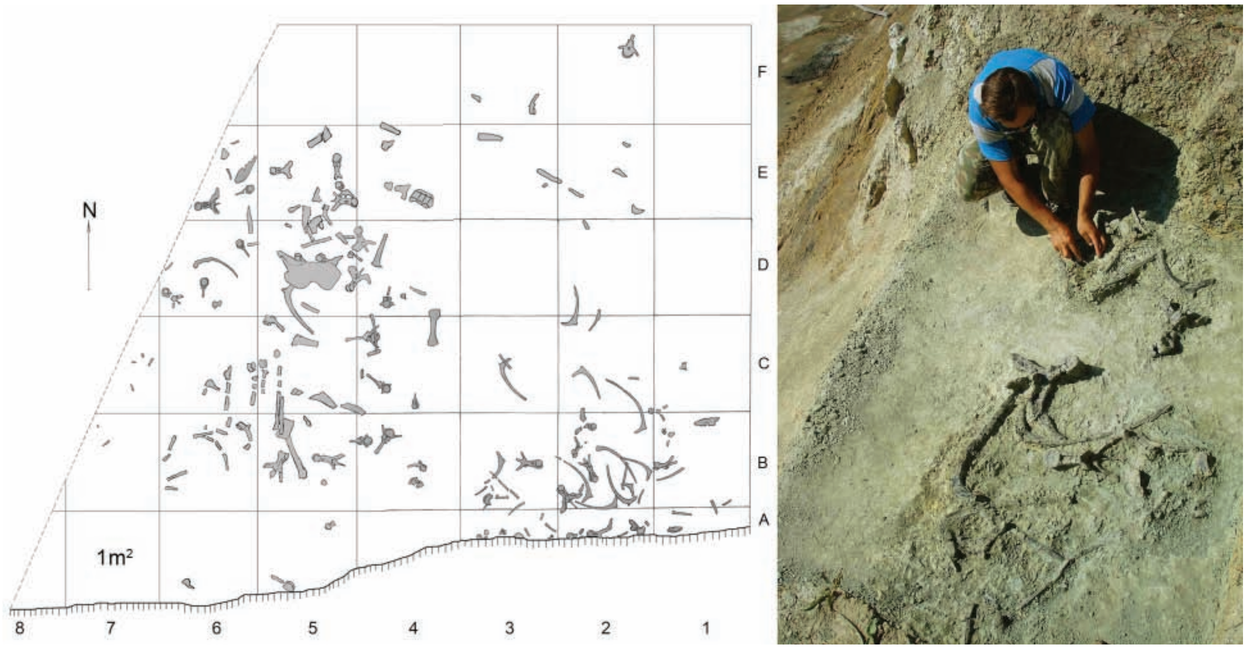

Fig. 2. Stegosaur Quarry map (left) and S.A. Krasnolutskii excavating the stegosaur bones at this site (right) in the Berezovsk Quarry, Krasnoyarsk Territory, Russia.

ZIN PH, Paleoherpetological collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

SYSTEMATICS

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Stegosauria Marsh, 1877

Stegosauria indet.
(Figs. 3–13)

Material. ZIN PH 1–2/117 and numerous uncatalogued specimens, isolated teeth; SHRM 205/1, posterior cervical(?); SHRM 203–204/1, anteriormost dorsals; SHRM 8/1, 9/1, 11/1, 103/1, 104/1, 122/1, 123/1, 206/1, dorsals; SHRM 3/1, 5/1, 6/1, 14/1, 15/1, 28/1, 109/1, dorsal neural arches; SHRM 12/1, dorsal neural arch with ankylosed rib; SHRM 52–56/1, 58/1, 59/1, 63/1, dorsal ribs; SHRM 17–26/1, 95–99/1, 106/1, 120/1, 121/1, caudals; SHRM 10/1, 30/1, 200/1, 201/1, 207/1, caudal centra; SHRM 31/1, 208/1, chevrons; SHRM 210/1 and 211/1, fragmented ilio-sacral blocks; SHRM 45/1, fragment of right anterior process of ilium; SHRM 214/1, fragment of left anterior process of ilium; SHRM 40/1, ungual phalanx; SHRM 212/1, dorsal dermal plate.

Description. Several dozens of isolated stegosaur teeth were found during screen-washing at various microvertebrate sites within the fossiliferous bed of the Itat Formation; no teeth have been found at the Stegosaur Quarry. The tooth morphology is typical for stegosaurs (Fig. 3; Galton and Upchurch 2004). The crown is covered with enamel on both sides and slightly asymmetrical. The mesial side is more convex and bears a greater number of denticles, five to eight compared with three to five on the distal side. As a result, the median cusp is slightly posterior to the midline of the crown. The cingulum is robust and almost complete, except a short interval on one side of the crown (labial or lingual), where it is very weak or absent. The median cusp is closer to this crown side than the lateral denticles, giving to the denticulated ridge a wide V-shape in occlusal view (Fig. 3A, D). On this crown side there is a “complex network of secondary ridges” (Fig. 3B), which among stegosaurs was noted previously only for *Stegosaurus* (Galton and Upchurch 2004, p. 350). Also the enamel appears to be more wrinkled on this side (compare Fig. 3E, F). On the opposite side, there are fewer ridges,

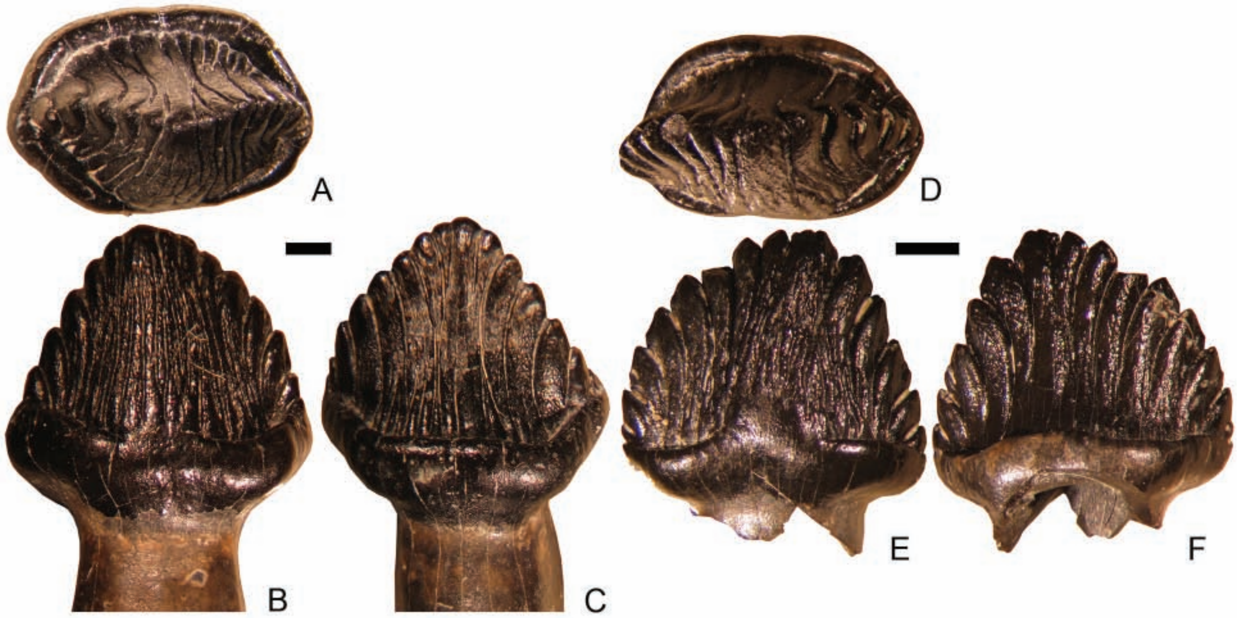

Fig. 3. Isolated teeth of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic) in occlusal (A, D) and two side (other figures) views: A–C — ZIN PH 1/117; D–F — ZIN PH 2/117. Scale bar = 1 mm.

and groves between denticles are more consistent, extending to the base of the crown (Fig. 3F). But on other specimens (Fig. 3C) there are secondary ridges on this side also, which are, however, confined to the basal and central part of the crown. The root is cylindrical, distinctly narrower than the crown and slightly constricted below the cingulum. Some teeth have facets on the cingulum closer to the mesial or distal side caused apparently by occlusion with the neighboring teeth and indicating some overlap of the teeth in the dental series. The largest complete tooth in the sample (ZIN PH 1/117; Fig. 3A–C) has FABL 6.7, BCW 4.5, and TCH 6.4. There are many teeth of various sizes and with different states of dental wear, some of which are completely eroded. Apparently, these teeth were swallowed and digested by the animal. Some teeth were in use until the crown was completely worn dawn and represent fungus-like structures with a thin apically concave cap.

In all dorsal vertebrae the centra are spool-shaped and amphiplatyan. The vertebrae SHRM 203–205/1 (Fig. 4) differ from the typical dorsals by an asymmetrical centrum in lateral view. In SHRM 204/1 the anterior intercentral articulation surface projects ventrally below the posterior intercentral articulation surface, while two other specimens show the reversal condition. Specimens SHRM 204/1 and SHRM 205/1 were found in association, but SHRM 203/1 was found in a different place and may not belong to the same individual. The parapophysis is not clearly discernible on these specimens, but in SHRM 205/1 it is possible just below the neurocentral suture. If this is correct, this vertebra would be a posterior cervical. Two other specimens are likely the most anterior dorsals. The neural arch in SHRM 203/1 is high, as in typical dorsals (the height of pedicel is ~1.4 times the height of the centrum). In two other specimens the neural canal is wider, and in SHRM 205/1 the neural arch is relatively low, as in the anterior dorsal of *Huayangosaurus* (Maidment et al. 2006, fig. 2A, B). The centrum is relatively short; the centrum length is approximately equal to centrum width in SHRM 204/1 and SHRM 205/1 and little smaller in SHRM 203/1. In SHRM 204/1 and SHRM 205/1 the intercentral articulation surfaces are more squarish compared to the rounded surfaces in SHRM 203/1 and typical dorsals. The anterior margin of the neural arch pedicel is with level with the centrum anterior surface and vertical with or slightly overhanging the latter. The posterior margin of the neural arch pedicel is sloping towards the posterior centrum surface. The transverse process, preserved completely on right side of SHRM 203/1 (Fig. 4G–I), is short and oriented at

70° to the sagittal plane. The prezygapophyseal articulation surfaces are not fused ventrally and are oriented at about 45° to the sagittal plane. The postzygapophysis, best preserved in SHRM 203/1 (Fig. 4G, H), is anteroposteriorly elongate and projects posteriorly beyond the posterior intercentral articulation surface. The neural spine, preserved in SHRM 203/1 (Fig. 4G–I), is a low plate triangular in lateral view and not widened dorsally.

The other dorsals (Figs. 5–6) show typical stegosaurian morphology (Galton and Upchurch 2004). The ventral margin of the centrum is slightly concave or almost straight in lateral view. The lateral side of the centrum is smooth, without a longitudinal ridge or depression. The neural canal varies in width and height (the latter is 29–71% of the centrum height, measured along the anterior side). In most specimens it is relatively low and tear-drop shaped (Fig. 5). In some specimens with a broken thin plate above the canal it appears very high and narrow

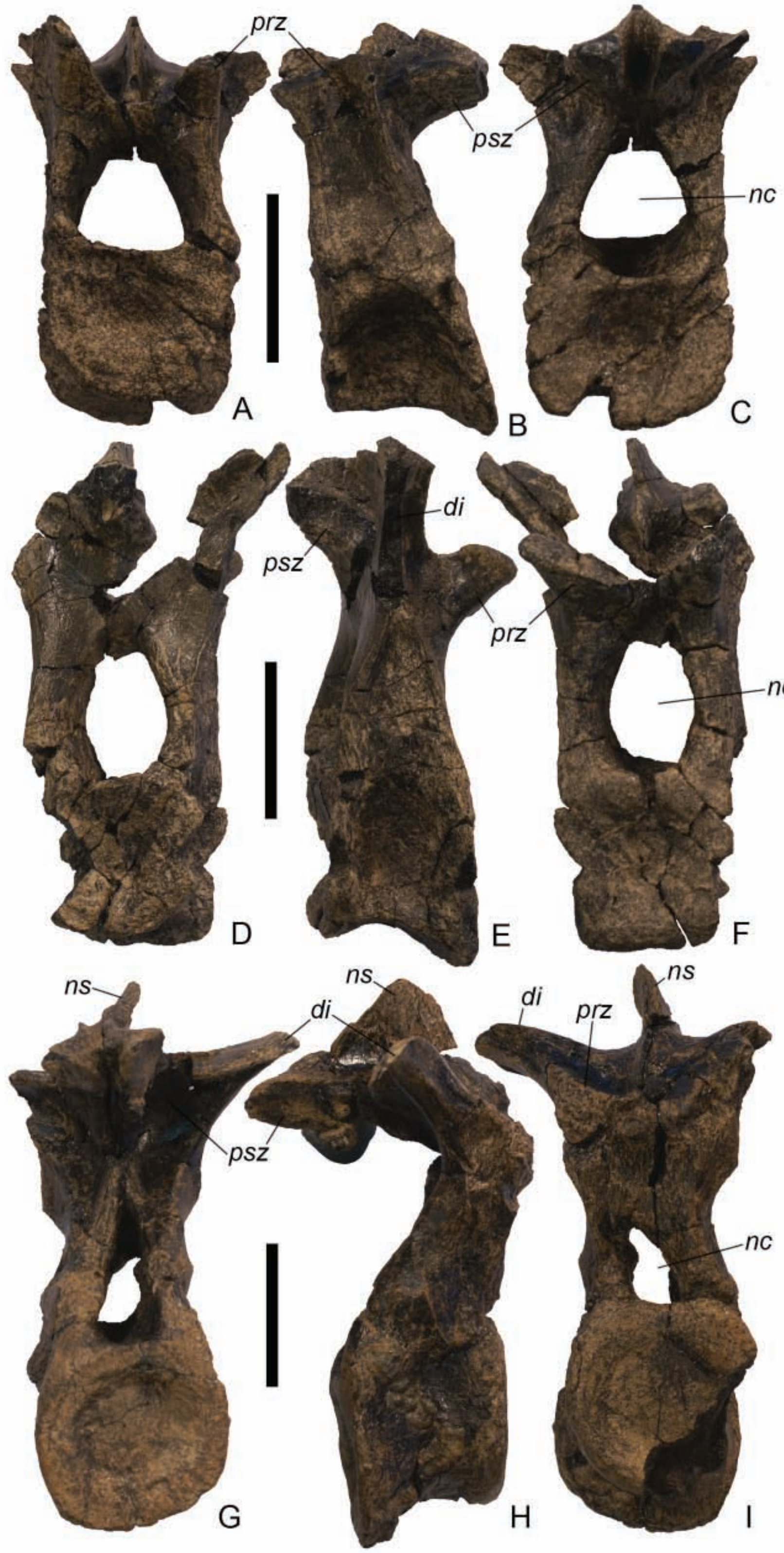

Fig. 4. Posterior cervicals or anterior dorsals of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): A–C — SHRM 205/1, in anterior (A), lateral (B), and posterior (C) views; D–F — SHRM 204/1, in posterior (D), lateral (E), and anterior (F) views; G–I — SHRM 203/1, in posterior (G), lateral (H), and anterior (I) views.
Abbreviations: *di* — diapophysis; *nc* — neural canal; *ns* — neural spine; *prz* — prezygapophysis; *psz* — postzygapophysis. Scale bar = 5 cm.

Fig. 5. Dorsals of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): A–D — SHRM 11/1, in posterior (A), ventral (B), lateral (C), and anterior (D) views; E–H — SHRM 8/1, in posterior (E), ventral (F), lateral (G), and anterior (H) views.
Abbreviations: *di* — diapophysis; *nc* — neural canal; *ns* — neural spine; *pa* — parapophysis; *prz* — prezygapophysis; *psz* — postzygapophysis. Scale bar = 5 cm.

Fig. 6. Dorsals of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): A–C — SHRM 123/1, in posterior (A), lateral (B), and anterior (C) views; D–F — SHRM 206/1, in posterior (D), lateral (E), and anterior (F) views.
Abbreviations: *di* — diapophysis; *nc* — neural canal; *ns* — neural spine; *pa* — parapophysis; *prz* — prezygapophysis; *psz* — postzygapophysis. Scale bar = 5 cm.

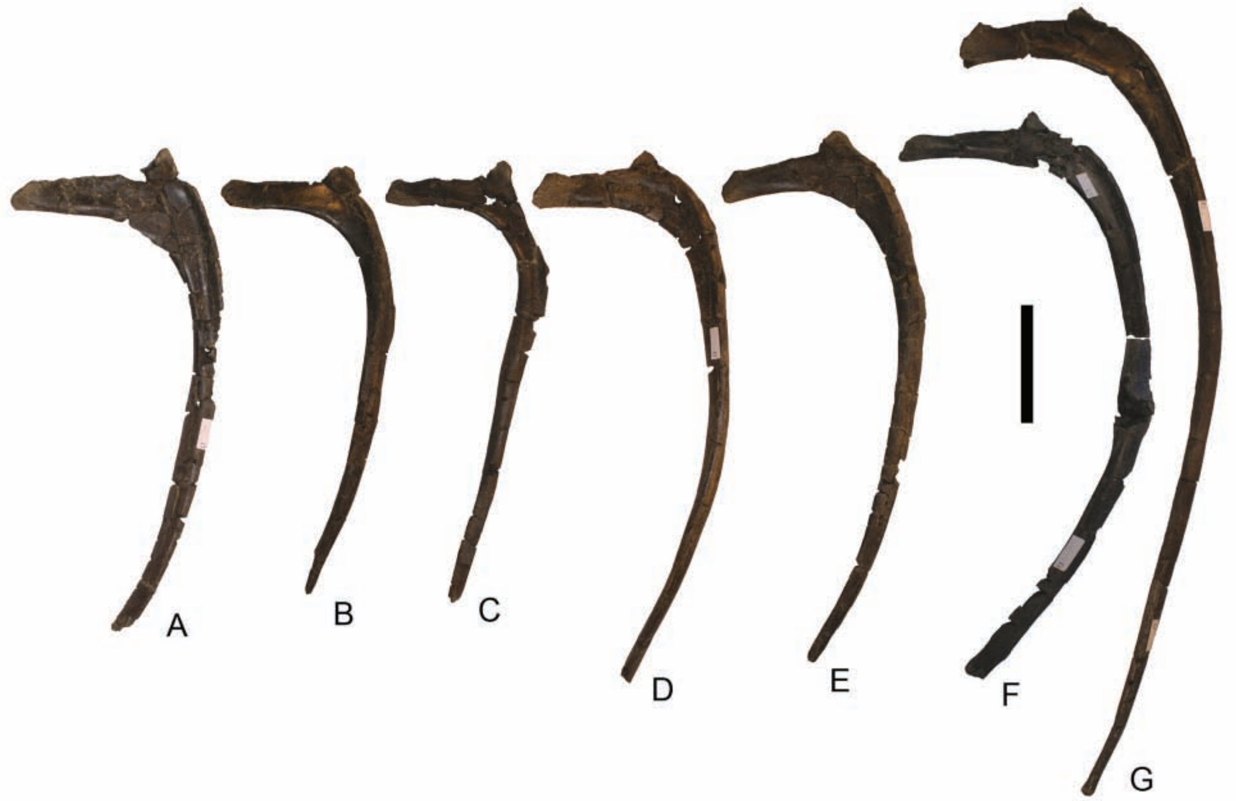

Fig. 7. Isolated dorsal ribs of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic) in anterior or posterior views: A — SHRM 63/1; B — SHRM 53/1; C — SHRM 54/1; D — SHRM 58/1; E — SHRM 55/1; F — SHRM 59/1; G — SHRM 52/1. Scale bar = 10 cm.

(e.g., SHRM 206/1; Fig. 6D, F), which is an artifact of preservation (some postmortem compression of vertebrae is also likely). The height of the pedicel varies from 138% to 204% of the centrum height (the mean value is 170% for nine measurements). There is a deep pocket-like depression on the posterior side of the neural arch pedicel above the neural canal and between the lateral columnar buttresses supporting the postzygapophyses. The anterior side of the pedicel above the neural canal is flat and with level with the lateral buttresses supporting the prezygapophyses. The parapophysis is placed approximately at the level of prezygapophyses. It has a short pedicel in SHRM 5/1 and SHRM 8/1 (Fig. 5E, H). The transverse processes are robust and T-shaped in cross section, with the longitudinal supporting ridge extending ventrally between the parapophysis and the diapophysis. As typical for stegosaurs, the transverse processes are united between the prezygapophyses and the neural spine. The orientation of the transverse processes to the sagittal plane varies from 20° to 65°; in the specimens with the low angle they are almost as high as the neural spine. These specimens possibly come from the middle of the dorsal series. The prezygapophyses are joined ventrally and form a U-shaped common articulation surface in most specimens but are separated by a deep groove in SHRM 109/1. The articulation surfaces are oriented from 31° to 55° to the sagittal plane. Usually there is a prominent ridge between the prezygapophyseal articular surface and the base of the neural spine. The anterior base of the neural spine is positioned level with the centrum midline. The anterior and posterior margins of the neural arch pedicel converge towards the base of the diapophysis and zygapophyses, in contrast with the anteriormost dorsals described above, where the anterior margin is subvertical. The postzygapophysis is elongated and projects posteriorly beyond the centrum. The postzygapophyseal articular surfaces are separated by a ventral groove.

The vertical ridge between the postzygapophyses and the top of the neural canal is variably developed. The neural spine is completely preserved in SHRM 8/1 and SHRM 123/1 (Figs. 5E, G, H and 6A–C). It is a plate like-structure extending between the posterior ends of the prezygapophyses and postzygapophyses and slightly tapering dorsally.

There are several isolated dorsal ribs (Fig. 7). SHRM 63/1 (Fig. 7A) with a relatively large and massive capitular process and wider rib shaft could be among first dorsal ribs or even the posterior cervical ribs. The tuberculum is relatively small in all specimens. SHRM 52/1 (Fig. 7G) with the longest and straightest shaft apparently comes from the middle of dorsal series. The rib shaft has a T-shape in cross section as in *Stegosaurus* (Gilmore 1914; Ostrom and McIntosh 1999, pl. 20), with a perpendicular lateral lamina in the proximal part forming a ridge in anterior view.

The sacral vertebrae are known from two fragmentary ilio-sacral blocks (SHRM 210/1 and SHRM 211/1). In SHRM 210/1 there are six coosified centra (Fig. 8), the two anterior of which are apparently dorsosacrals. The second dorsosacral appears to share the sacral rib with the first sacral, as in *Stegosaurus* (Ostrom and McIntosh 1999, pl. 24). The first dorsosacral has a round intercentral articulation surface which is flattened dorsally. The second dorsosacral centrum has a prominent ventral keel. The sacral centra are longer than wide and are approximately equal in length. The sacral neural arches are better preserved in SHRM 211/1. The neural arch is transversely about twice as wide in the third vertebra (sacral 1) compared with the first vertebra (dorsosacral 1), indicating widening of the sacral neural canal, similarly to that of *Stegosaurus* and *Kentrosaurus*. SHRM 211/1 preserves four sacral ribs and one dorsosacral rib attached to the ilium (Fig. 12C). Stegosaurs usually have four robust sacral ribs, but in some there is an additional slender dorsosacral rib (Gilmore 1914, fig. 23; Galton and Upchurch 2004, p. 353). SHRM 211/1 agrees with this condition: the dorsosacral rib is slender and anteromedially directed, while the remaining sacral ribs are more robust and directed more medially.

Caudal vertebrae are common at the Stegosaur Quarry. The specimens SHRM 95–99/1 were found in association and apparently represent a continuous caudal section of one individual. The vertebrae SHRM 22/1 and SHRM 120/1 (Fig. 9A–C) are among the first three or four caudals. They are similar to the third caudal of *Stegosaurus* (Ostrom and McIntosh 1999, pl. 25) in having a short and wide centrum and long transverse processes directed vent-

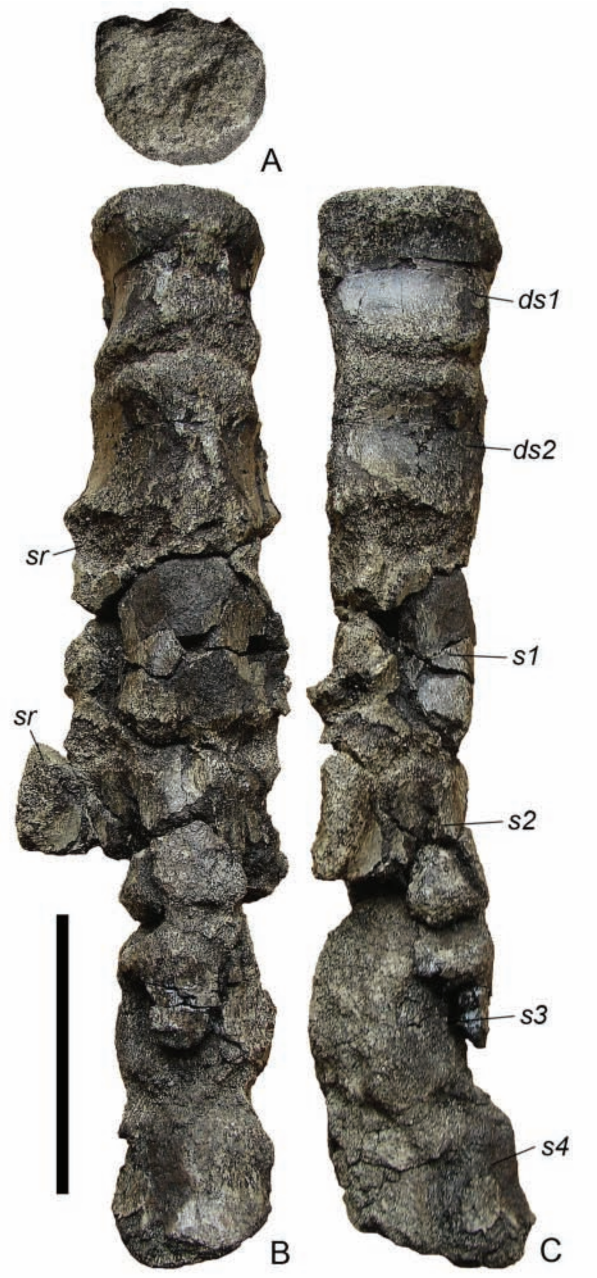

Fig. 8. SHRM 210/1, coosified dorsosacral and sacral centra of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic) in anterior (A), ventral (B), and lateral (C) views.
Abbreviations: *ds1–ds2* — dorsosacrals one and two; *s1–s4* — sacrals one to four; *sr* — sacral rib. Scale bar = 10 cm.

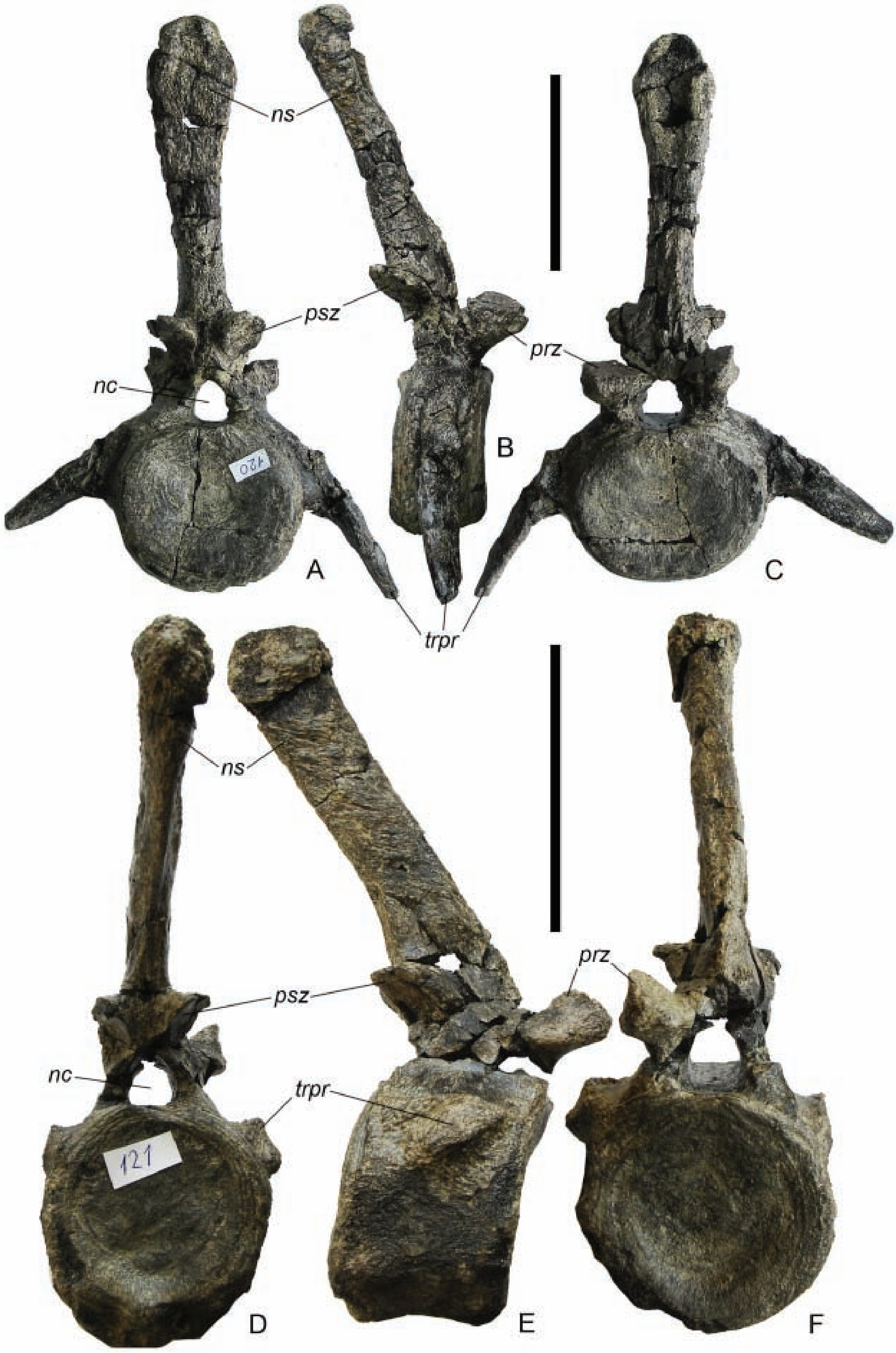

Fig. 9. Anterior caudals of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): A–C — SHRM 120/1, in posterior (A), lateral (B), and anterior (C) views; D–F — SHRM 121/1, in posterior (D), lateral (E), and anterior (F) views.
Abbreviations: *nc* — neural canal; *ns* — neural spine; *prz* — prezygapophysis; *psz* — postzygapophyses; *trpr* — transverse process. Scale bar = 10 cm.

Fig. 10. SHRM 31/1, chevron of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): dorsal (A), posterior (B), anterior (C), and lateral (D) views. Scale bar = 5 cm.

rolaterally, but differ in lacking the dorsal process on the transverse process, and the neural spine is much less expanded distally. The neural spine gradually widens laterally towards the distal end. It is concave anteriorly and flat posteriorly. The zygapophyses are widely separated and have flat articulation surfaces. In more posterior caudals (e.g., SHRM 121/1; Fig. 9D–F) the centrum is longer and transversely narrower, with very short transverse processes. The neural spine bears a club-like structure on the top. In still more posterior caudals the transverse process disappears and the neural spine club is variably developed. There are few fragmented posterior caudals. The centrum SHRM 201/16 is longer anteroposteriorly than transversely wide and hexagonal in cross section, with distinct median ridges on lateral sides. For the measurements of vertebrae see Table 1.

The chevrons are represented by two specimens, among which SHRM 31/1 is more complete (Fig. 10). They are similar to those of *Stegosaurus* (Gilmore 1914, fig. 29). The articular heads are expanded and globular, but not united. The haemal canal is high and oval-shaped. The shaft is long and a little curved, with a ridge along the anterior surface and a groove posteriorly.

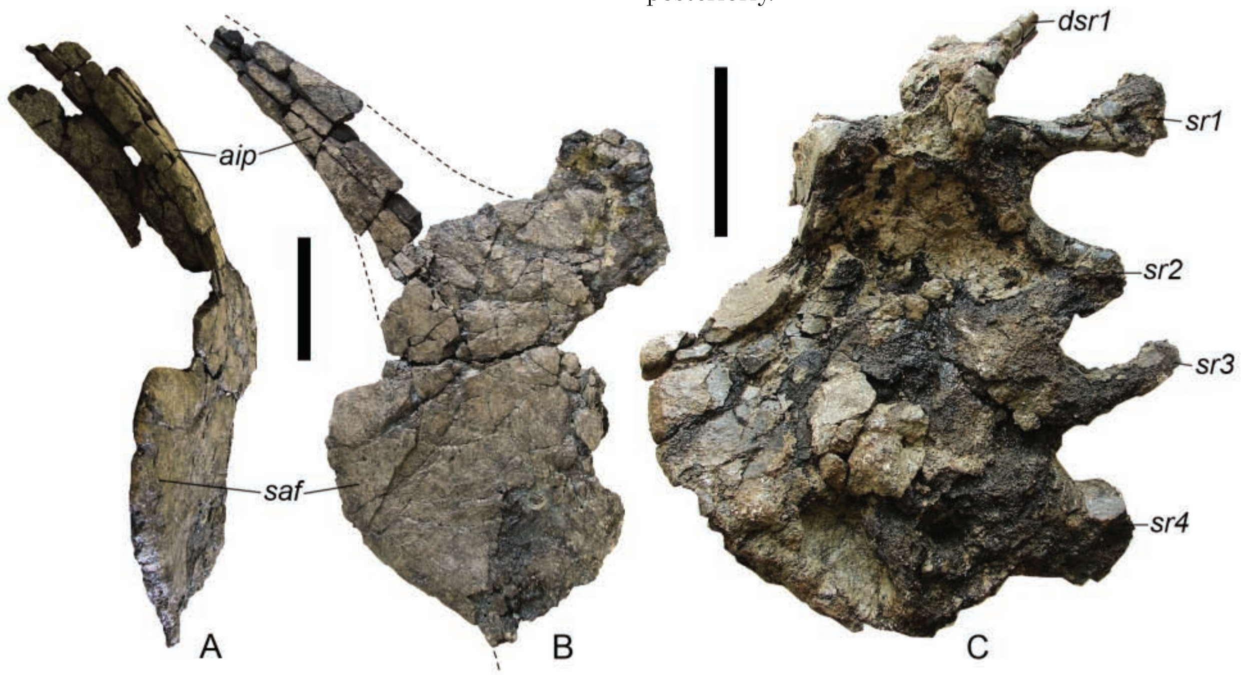

Fig. 11. Fragments of ilio-sacral block of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic): A, B — SHRM 210/1, left ilium in lateral (A) and dorsal (B) views; C — SHRM 211/1, right ilium and attached sacral ribs in ventral view.
Abbreviations: *aip* — anterior iliac process; *dsr1* — dorsosacral rib 1; *saf* — supraacetabular flange; *sr1–sr4* — sacral ribs one to five. Scale bar = 10 cm.

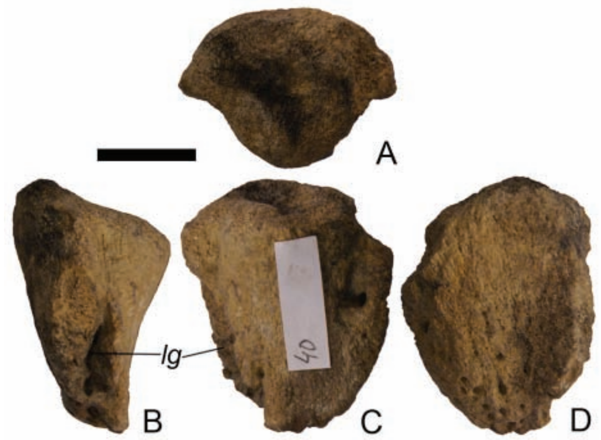

Fig. 12. SHRM 40/1, ungual phalanx of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic) in proximal (A), side (B), dorsal (C), and ventral (D) views.
Abbreviation: *lg* — lateral groove. Scale bar = 2 cm.

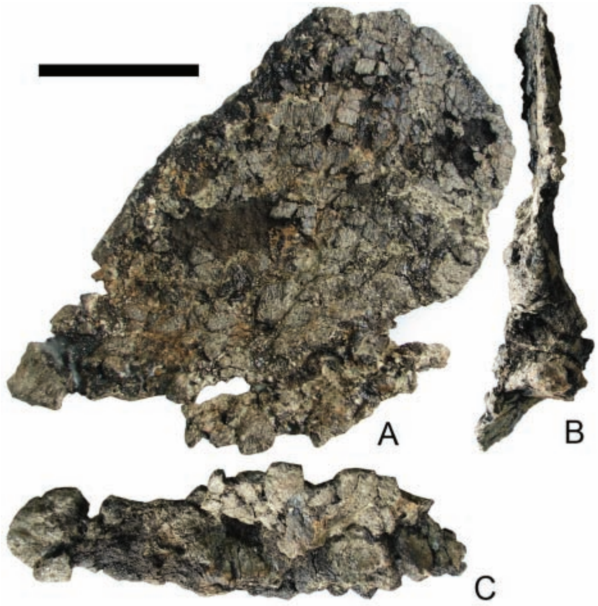

Fig. 13. SHRM 212/1, dorsal dermal plate of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic) in lateral (A), posterior (B), and ventral (C) views. Scale bar = 10 cm.

The pelvic bones are present by fragmentary ilia from two individuals (two ilio-sacral blocks SHRM 210/1 and SHRM 211/1). The acetabulum is poorly preserved on all specimens. The most complete is the left ilium SHRM 210/1 (Fig. 11A, B). It has a partially complete anterior iliac process. The process is gently curved laterally and slightly ventrally, as usually for stegosaurs (Galton and Upchurch 2004, fig. 16.7; Maidment et al. 2008, fig. 2). Its anterior end, known from two isolated specimens (SHRM 45/1 and SHRM 214/1) is deep vertically and mediolaterally thick along the dorsal margin. The ilium is expanded laterally above the acetabulum as in other stegosaurs, with a distinct supraacetabular flange. The angle between the supraacetabular flange and the anterior iliac process is close to 90° (a character considered an autapomorphy for *Stegosaurus* by Maidment et al. [2008]). The posterior iliac process is not complete but seems to be prominent. The dorsal surface of the ilium is flat.

The ungual SHRM 40/1 (Fig. 12) is the only known identifiable limb bone from the Stegosaur Quarry (there is also a poorly preserved shaft fragment possible from the tibia which is not catalogued and not described here). The ungual is hoof-like, with the proximal articular surface facing posteroventrally, convex dorsal and concave ventral surfaces. It is asymmetrical in dorsal/ventral view suggesting that it comes from a side digit. Along one side there is a deep cleft for the claw sheath (lateral groove on Fig. 12B), not present on the opposite side. The distal end is blunt and truncated. There are several relatively large vascular foramina concentrated at the distal part of the ungual.

SHRM 212/1 is a poorly preserved but relatively complete dorsal dermal plate (Fig. 13). It is a very thin transversely triangular asymmetrical plate with a somewhat thicker ventral base. The ventral surface is slightly concave. There are some vascular grooves on the lateral sides but they are obscured by numerous cracks.

DISCUSSION

The comparison of the stegosaur remains from Berezovsk Quarry with other stegosaurs is limited by fragmentary nature of these remains. Based on the recent phylogenetic work by Maidment et al. (2008) these remains show the following phylogenetically informative characters: 1) horizontal lateral enlargement of the ilium present (unambiguous synapomorphy for Thyreophora); 2) dermal armor, including scutes, spines and/or plates present (unambiguous synapomorphy for Thyreophora); 3) transverse processes of dorsal vertebrae project at a high angle to the horizontal (synapomorphy for Thyreophoroidea + *Emasaurus* or for Thyreophoroidea depending on op-

Table 1. Measurements (in mm) of vertebrae of Stegosauria indet. from Berezovsk Quarry, Krasnoyarsk Territory, Russia; upper part of the Itat Formation, Middle Jurassic (Bathonian). *Abbreviations*: ACH, anterior height of centrum; ACW, anterior width of centrum; ANW, anterior width of neural arch (between lateral margins of prezygapophyses); CL, centrum length (ventral); NAL, neural arch length (between anterior and posterior margins of ventral floor of neural canal); NSL, neural spine length (maximum); PCH, posterior height of centrum; PCW, posterior width of centrum; PNW, posterior width of neural arch (between lateral margins of postzygapophyses).

SHRM number	ACH	ACW	ANW	CL	NAL	NSL	PCH	PCW	PNW
				posterior cervical or anterior dorsal vertebrae					
205	40.5	50.5	–	46.3	–	–	42.0	55.5	–
204	50.8	–	–	41.8	–	–	45.0	–	–
203	58.0	–	–	46.4	–	–	57.0	59.5	–
				dorsal vertebrae					
18	84.3	93.0	67.1	36.8	–	35.4	83.5	97.7	49.8
26	84.8	92.0	–	42.1	–	–	81.2	89.4	–
24	81.5	78.1	–	44.0	44.9	29.8	81.3	75.5	46.5
22	83.4	95.4	75.4	45.9	–	33.5	84.4	101.6	60.5
19	84.0	92.4	82.3	47.4	45.4	33.1	82.4	84.5	50.1
21	81.0	80.5	–	47.5	–	33.0	79.8	75.3	–
23	78.1	72.9	–	47.8	–	–	77.4	73.8	–
20	61.4	57.4	–	50.2	–	35.0	63.2	56.5	–
17	66.6	61.1	39.0	52.2	45.5	35.6	66.1	59.9	35.3
123	63.3	53.2	72.4	60.8	62.0	59.5	53.2	50.6	67.1
9	–	–	–	67.0	–	–	52.3	62.3	51.3
7	65.9	66.9	60.2	67.9	108.6	55.2	66.3	68.2	51.3
103	72.8	70.9	72.0	68.9	65.0	–	69.9	68.9	–
206	69.5	55.8	76.8	71.6	67.4	–	72.6	66.3	–
8	65.2	66.3	58.0	73.1	114.5	–	64.3	68.4	–
122	67.3	63.6	–	74.8	–	–	65.4	65.4	–
11	52.5	56.6	48.3	75.4	–	–	–	–	–
104	65.7	64.4	–	77.3	79.9	–	64.5	61.9	56.7
5	–	–	51.2	–	116.7	53.4	–	–	39.9
16	–	–	–	–	–	–	82.4	–	57.3
12	–	–	–	–	–	–	–	–	51.0
109	–	–	69.6	–	–	–	–	–	60.8
				caudal vertebrae					
95	74.1	68.4	40.3	54.7	51.2	30.5	74.4	68.7	–
96	72.4	73.4	–	55.3	–	33.3	76.3	70.4	39.1
97	69.7	67.3	47.3	55.2	45.2	30.0	72.2	69.3	35.0
98	–	–	–	51.5	–	30.3	65.9	55.5	–
99	76.0	74.9	–	52.6	–	–	74.5	71.3	44.4
120	76.2	100.6	79.3	49.7	32.0	30.5	86.9	100.0	60.4
22	81.3	109.2	84.2	55.6	39.1	32.5	93.5	117.6	67.6
19	86.1	100.0	88.9	57.3	52.6	34.5	92.2	94.1	55.1
106	66.9	64.2	–	59.0	47.7	34.9	71.4	59.5	29.9
17	77.0	72.5	50.0	60.6	45.7	37.3	77.0	69.0	40.4
121	83.3	91.9	–	64.0	51.1	34.8	85.6	81.4	42.2
21	96.8	99.8	–	65.8	40.5	37.5	82.3	79.6	45.3

timization); 4) large horizontal lateral enlargement of the ilium present (synapomorphy for Thyreophoroidea + *Emasaurus* or for Thyreophoroidea depending on optimization); 5) supraacetabular flange present (synapomorphy for Thyreophoroidea + *Emasaurus* or for Thyreophoroidea, reversed in Ankylosauria; the same character is cited also as a DELTRAN synapomorphy for Stegosauria, convergent in *Scelidosaurus*); 6) anterior caudal neural spine height is greater than the height of the centrum (unambiguous synapomorphy for Thyreophoroidea); 7) prominent, ring-like cingulum present on maxillary teeth (unambiguous synapomorphy for Euryopoda; this cingulum present in all isolated teeth from Berezovsk Quarry, some of which should be maxillary teeth); 8) prezygapophyses fused on some dorsal vertebrae (unambiguous synapomorphy for Euryopoda); 9) manual and pedal unguals hoof-shaped (unambiguous synapomorphy for Euryopoda); 10) anterior iliac process projects at an angle that diverges widely from the parasagittal plane (unambiguous synapomorphy for Euryopoda); 11) parasagittal dorsal dermal armor is transversely thin except at the base (ACCTRAN synapomorphy for the clade C: *Loricatosaurus*, *Tuojiangosaurus*, *Paranthodon*, and *Stegosaurus*).

The Berezovsk stegosaur is not referable to the Jurassic Huayangosauridae from China (*Huayangosaurus* + *Chungkingosaurus*) because it lacks the autapomorphic reversal for this clade: anterior iliac process projects at an angle roughly parallel to the parasagittal plane (Maidment et al. 2008). In *Huayangosaurus* the maxillary teeth lack the ring-like cingulum (Sereno and Dong 1992; Galton and Upchurch 2004). As all isolated teeth from Berezovsk Quarry have such a cingulum, this character will further differentiate the Berezovsk taxon from *Huayangosaurus*.

The Berezovsk stegosaur lacks the dorsal process on transverse process of anterior caudal vertebrae. Presence of this process is an ACCTRAN synapomorphy for the clade Stegosauridae + Huayangosauridae (actually unknown for Huayangosauridae) or a DELTRAN synapomorphy for Stegosauridae (Maidment et al. 2008). Transverse width of tops of anterior caudal neural spines greater than anteroposterior width is an unambiguous synapomorphy for Stegosauridae according to Maidment et al. (2008). This character is found in SHRM 120/1 (Fig. 9A–C), but majority of anterior caudals from Berezovsk Quarry show the reversal condition (e.g., Fig. 9D–F). These two characters suggest the Berezovsk taxon is not referable to Stegosauridae. But on the other hand, the Berezovsk taxon possesses a synapomorphy for clade C within the Stegosaurinae: parasagittal dorsal dermal armor is transversely thin except at the base. Furthermore, the materials from Berezovsk Quarry show one character considered as an unambiguous synapomorphy for *Stegosaurus*: supraacetabular flange projects at 90° from the anterior iliac process. The stegosaur teeth from Berezovsk Quarry have a complex network of secondary ridges, a character previously considered unique for *Stegosaurus* (Galton and Upchurch 2004, p. 350).

The stegosaur material from Berezovsk Quarry show a unique combination of primitive and derived character states discussed above, not found in any other known taxon of Stegosauria. Presence of more than one taxon in this assemblage seems unlikely. The Bathonian Berezovsk stegosaur is among the oldest representatives of the group. Other Middle Jurassic stegosaurs are known currently from Europe, China, and Kyrgyzstan (Galton and Upchurch 2004; Averianov et al. 2007; Maidment et al. 2008). The Berezovsk stegosaur likely represents a new taxon and we hope that discovery of more complete materials from the Berezovsk Quarry will allow its formal description.

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