A sauropod foot from the Early Cretaceous of Western Siberia, Russia

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We describe a reasonably complete sauropod foot from the Early Cretaceous (Aptian–Albian) Ilek Formation at the Shestakovo locality in Western Siberia, Russia. It shows some primitive characters, such as slender metatarsals, a relatively long second pedal ungual, and three claws. In the likely presence of the laterodistal process on the first metatarsal the Shestakovo sauropod is similar with diplodocoids, but its more elongated and gracile first metatarsal resembles brachiosaurids (*Brachiosaurus*, *Pleurocoelus*, and *Cedarosaurus*), titanosaurids (*Laplatasaurus*), and *Euhelopus*. *Pleurocoelus*-like isolated teeth from the Shestakovo assemblage may support the brachiosaurid affinities of the Shestakovo sauropod, but a strongly procoelous mid-caudal vertebra from another locality in the same formation establishes the presence of a titanosaurid in the fauna. The foot described is referred here to as Titanosauriformes gen. et sp. indet.

Key words: Sauropoda, Titanosauriformes, postcranial skeleton, Cretaceous, Siberia, Russia.

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Introduction

Sauropods are one of the most fascinating and successful groups of dinosaurs, known now from the Late Triassic until the very end of the Cretaceous, and from all continents except Antarctica. However, our knowledge of sauropods has serious gaps, both stratigraphic and geographic. The real *terra incognita* for sauropod evolution is Siberia, from where only very imperfect sauropod remains had previously been reported.

There are very few localities for sauropod remains in the vast territory of Siberia (Fig. 1). Three of them are known in the Early Cretaceous of Transbaikalia (Nessov and Starkov 1992; Nessov 1995), all producing only isolated and very fragmentary sauropod remains. The most productive of Transbaikalian sites is the late Barremian–middle Aptian Mogoito locality in Buryatia, from which scapular and rib fragments, caudal vertebrae, and isolated teeth of a titanosaurid sauropod are known (Dmitriev and Rozhdestvensky 1968; Nessov and Starkov 1992; Nessov 1995; Averianov and Skutschas 2000). A camarasaurid sauropod (Rich et al. 1997: 563), or cf. *Camarasaurus* sp. (Kurzanov et al. 2000: 356) was cited for the Late Jurassic–Early Cretaceous? Kempendyay locality in Yakutia. The latter determination is based on two isolated spatulate teeth lacking denticles and seems doubtful. Judging from the description by these authors these teeth might be compared also with those in *Euhelopus* (Wiman 1929: pl. 2) and may well belong to an euhelopodid rather than to a camarasaurid.

Another sauropod occurrence in Siberia is the Early Cretaceous Shestakovo complex of localities in Kemerovo Region, Western Siberia (Fig. 1), which previously yielded partial skeletons of *Psittacosaurus* (Rozhdestvensky 1960). More recently, this locality has yielded a diverse and important vertebrate assemblage including palaeonisciform and sinamiid fishes, the "macrobaenid" turtle *Kirgizemys* sp., xenosaurid, paramacellodid and an indeterminate scincomorphan lizards, the protosuchian crocodile *Tagarosuchus kulemzini* Efimov, 1999, the shartegosuchid crocodile *Kyasuchus saevi* Efimov and Leshchinskiy, 2000, dromaeosaurid and troodontid theropod dinosaurs, a sauropod, the ceratopsian *Psittacosaurus sibiricus* Voronkevich and Averianov, 2000, the tritylodontid *Xenocretosuchus sibiricus* Tatarinov and Maschenko, 1999, amphilestid "triconodonts" *Gobiconodon borissiaki* Trofimov, 1978, *G. hoburensis* (Trofimov, 1978), and *Gobi-*

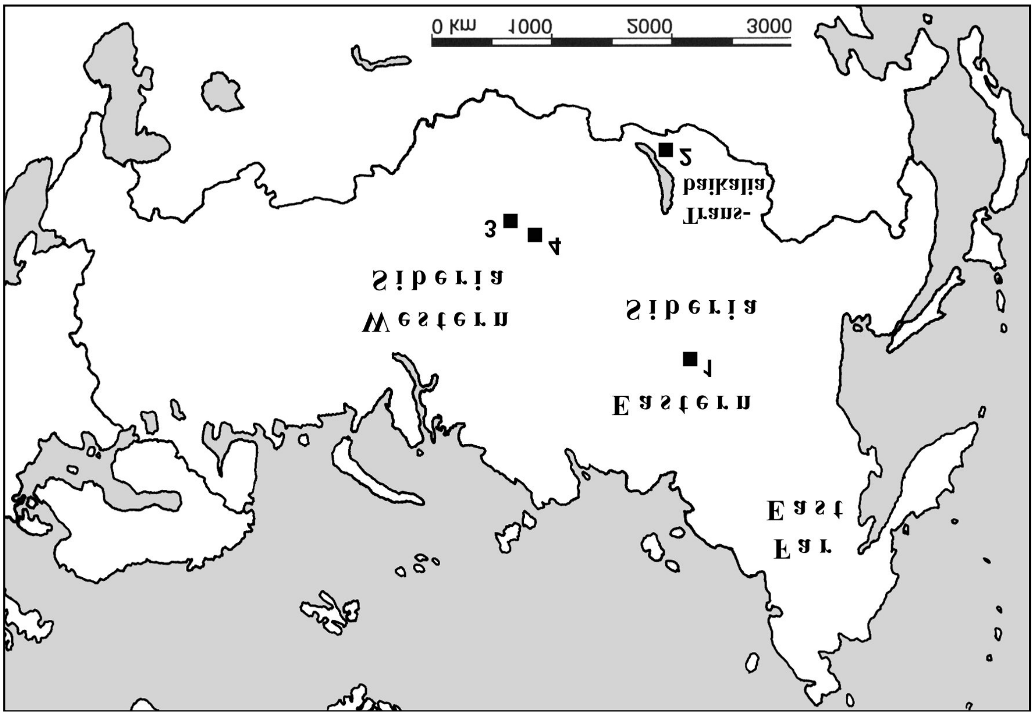

Fig. 1. Map of Russia showing position of sauropod localities discussed in the text: 1, Kempendyay; 2, Mogoito; 3, Shestakovo; 4, Bol'shoi Kemchug.

conodon sp. n., and a new more derived mammal (Leshchinskiy *et al*. 1997; Saev and Leshchinskiy 1997; Maschenko and Lopatin 1998; Voronkevich 1998; Alifanov *et al*. 1999; Tatarinov and Maschenko 1999; Efimov and Leshchinskiy 2000; Leshchinskiy *et al*. 2000).

Skeletal remains of a big dinosaur (sauropod?) from the Shestakovo 1 locality were reported by Bulynnikova and Trushkova (1967). These materials were apparently lost. In 1994, one of us (EM) found a sauropod pedal claw in Shestakovo 1. In 1995 more sauropod pedal elements were recovered in Shestakovo 1 by the paleontological team from Tomsk State University led by V.I. Saev. Altogether three metatarsals (I, II, and V), metatarsal III proximal fragment, metatarsal III or IV distal fragment, two proximal phalanges (I-1 and II-1) and three unguals (I-2, II-3, and III-4) were found, but two elements (second metatarsal and third digit ungual) were subsequently lost. Furthermore, a badly preserved opisthocoelous dorsal centrum (Leshchinskiy et al. 2000: fig. 2) was excavated at Shestakovo 1 in 1996, some 100 m downstream from the site yielding the pedal elements. All identifiable pedal elements come from the left side and were found in close proximity, although not in articulation. Thus it is quite likely that all these elements came from the single individual. There is some probability that the large dinosaur bones reported by Bulynnikova and Trushkova (1967) belonged to a sauropod skeleton exposed in the Kiya River precipice (Shestakovo 1 locality) in early sixties and washed away by the river during the following 30 years. The foot and the vertebra may be among the last remaining portions of this skeleton, if it was buried with its back facing towards the river.

Alifanov et al. (1999: 492) referred to Titanosauridae one peg-like and round in cross-section sauropod tooth from Shestakovo. Leshchinskiy et al. (2000: 364) reported from Shestakovo 1 a spatulate, possibly juvenile sauropod tooth crown lacking denticles. Two isolated *Pleurocoelus*-like teeth were found at Shestakovo 1 in 2000. Finally, a strongly procoelous mid-caudal vertebra was found by S.L. Leshchinskiy and his colleagues at a new vertebrate locality in the Ilek Formation along the Bol'shoi Kemchug River in Krasnoyarsk Territory in 2000 (Fig. 1). The aim of this note is to describe the preserved sauropod pedal elements from Shestakovo 1 and discuss their possible affinities.

Institutional abbreviation.—PM TGU, Paleontological Museum, Tomsk State University, Tomsk, Russia.

Other abbreviations.—U, a character from Upchurch (1998); WS, a character from Wilson and Sereno (1998).

Systematic palaeontology

Sauropodomorpha Huene, 1932

Sauropoda Marsh, 1878

Neosauropoda Upchurch, 1995

Titanosauriformes Salgado, Coria, and Calvo, 1997

Titanosauriformes gen. et sp. indet.

Figs. 2–7.

Material.—PM TGU 16/0-81, metatarsal I; PM TGU 16/0-82, proximal fragment of metatarsal III(?); PM TGU 16/0-83, distal fragment of metatarsal III or IV; PM TGU 16/0-84, meta-

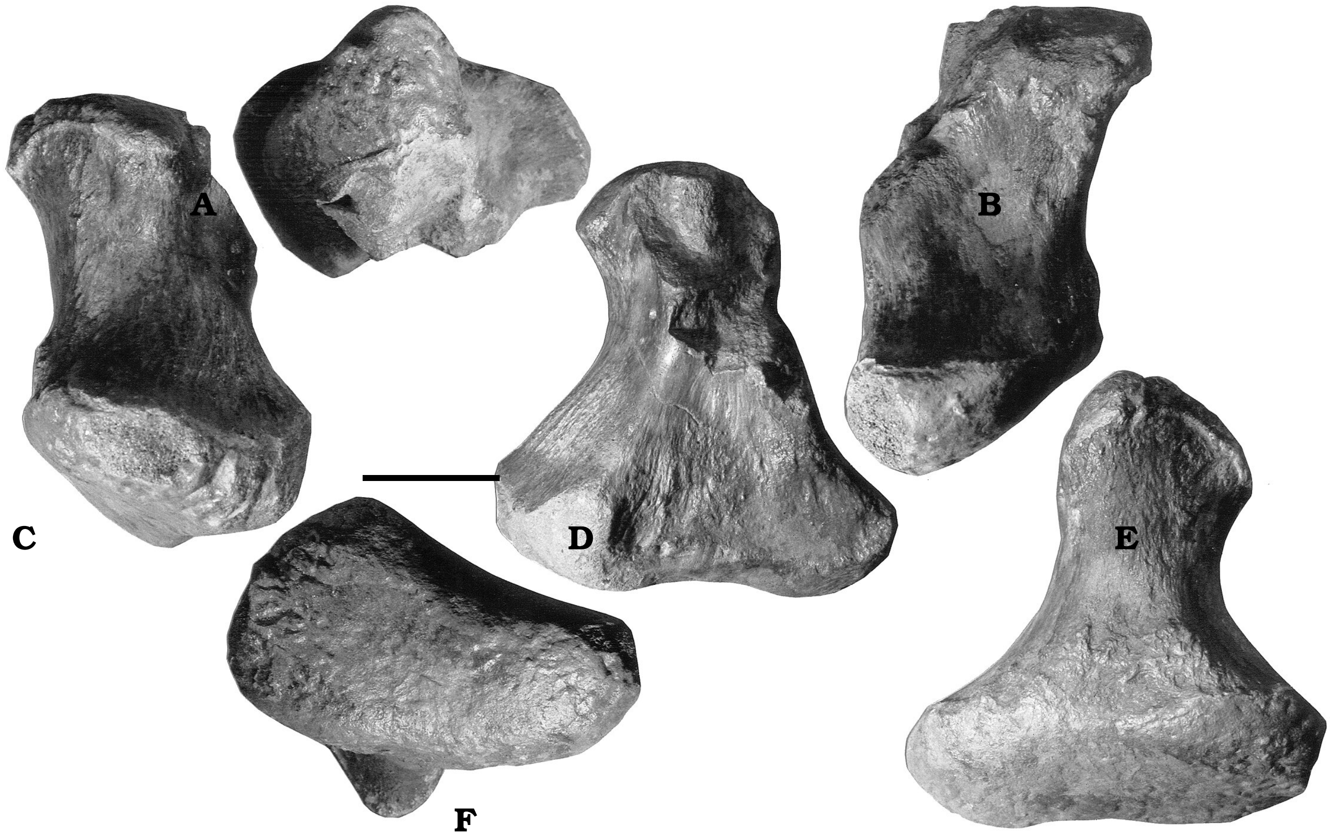

Fig. 2. Titanosauriformes gen. et sp. indet., PM TGU 16/0-81, metatarsal I, in proximal (**A**), medial (**B**), anterior (**C**), lateral (**D**), posterior (**E**), and distal (**F**) views. Locality Shestakovo 1, Ilek Formation (Aptian–Albian), Kemerovo Region, Russia. Scale bar 5 cm.

tarsal V; PM TGU 16/0-85 and 16/0-86, proximal pedal phalanges, possibly I-1 and II-1 respectively; PM TGU 16/0-87, ungual phalanx of first digit (I-2); PM TGU 16/0-88, ungual phalanx of second digit (II-3). Shestakovo 1 (approximately 55°53′N, 87°55′E), Kemerovo Region, Western Siberia, Russia; Lower Cretaceous: Asptian–Albian.

Description.—The metatarsal I (Fig. 2) is relatively slender and elongate. Its proximal condyle is crescent-shaped, slightly concave in the center of the proximal surface, and markedly elongated anteroposteriorly. Its long axis is oriented perpendicularly to that of the distal end. The medial and lateral surfaces of the shaft are gently concave and the anterior and posterior surfaces are deeply concave. On the lateral surface, close to the proximal margin, there is a distinct rugosity, which represents the articular surface for the second metatarsal. The laterodistal portion of the metatarsal I is broken off, but the preserved portion suggests that this region formed a well-developed laterodistal process. The distal end is transversely elongated, more than twice smaller than the proximal end. It is globular and subtriangular in outline.

PM TGU 16/0-82 (Fig. 3A–E) is the proximal fragment of a third or fourth metatarsal (the lost second metatarsal was much more robust). Its proximal surface is subrectangular in outline rather than wedge-shaped, and, by analogy with *Apatosaurus* (Gilmore 1936: fig. 25B), is interpreted here as metatarsal III. The proximal condyle is greatly elongated anteroposteriorly, being almost twice as long as the transverse diameter. The condyle protrudes farther beyond the bone shaft posteriorly than anteriorly, as in *Apatosaurus* (Gilmore 1936: fig. 27B). The medial and lateral surfaces of the shaft are almost flat.

PM TGU 16/0-83 (Fig. 3F–J) is the distal portion of a third or fourth metatarsal; it has no contact with the proximal fragment described above. The distal condyle is ball-like, almost round in distal view, some 1.5 times larger than the most proximal portion of the bone shaft preserved.

Metatarsal V (Fig. 4) has an enormously anteroposteriorly expanded proximal condyle, its diameter exceeding the anteroposterior diameter of the distal condyle by about 1.7 times. Both condyles are strongly convex. The proximal condyle is wedge-shaped, triangular in outline, wide anteriorly and tapering posteriorly. At its widest point it has an anteromedial projection, continuing into a distinct ridge along the anteromedial margin of the bone. The lateral surface of the shaft is almost flat. The medial surface is concave, and the bone is tapering towards the distal end. Both the anterior and posterior surfaces of the shaft are deeply concave. The posterior surface is restricted to a narrow band. The distal condyle is subrectangular in outline, greatly compressed transversely and elongated anteroposteriorly.

PM TGU 16/0-85 and 16/0-86 (Fig. 5) are clearly proximal phalanges, judging from their size and structure. Being

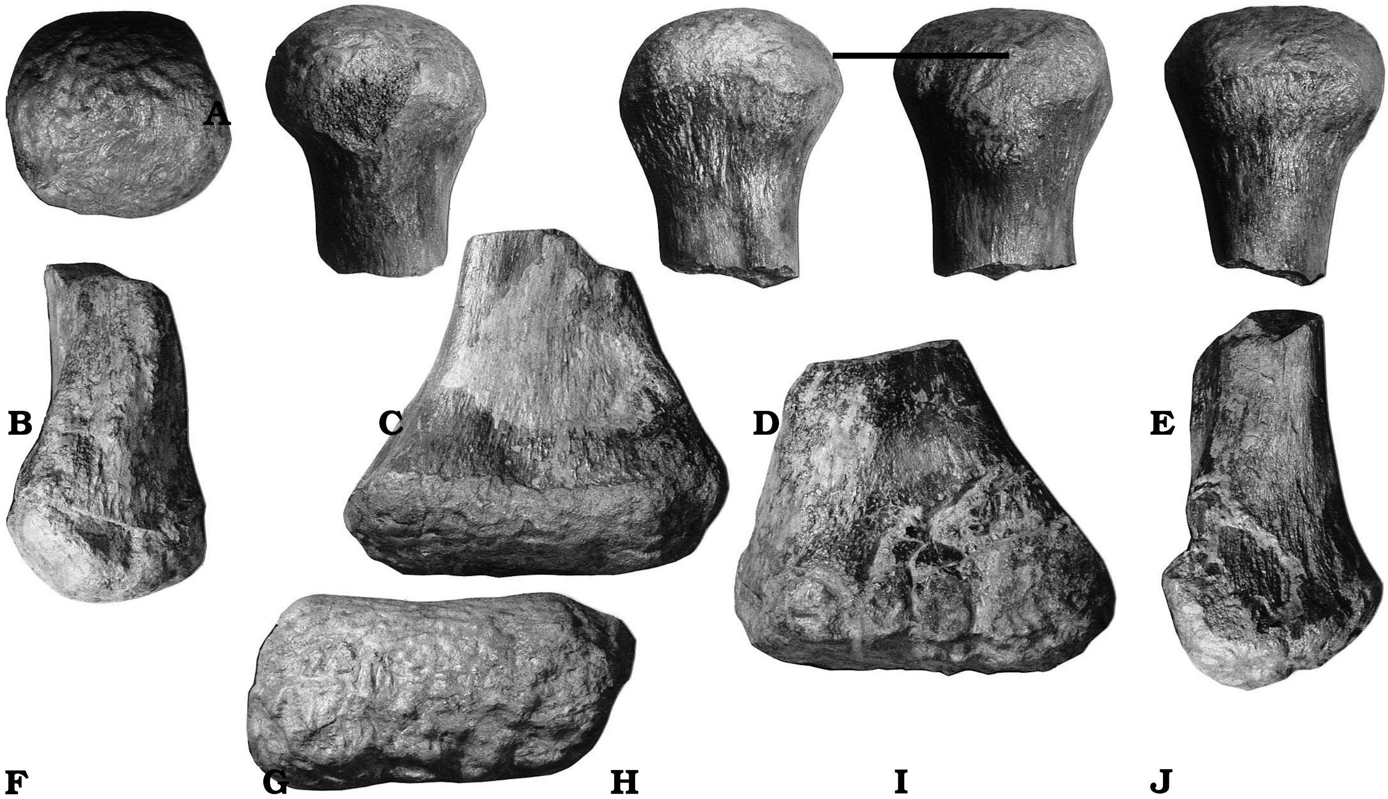

Fig. 3. Titanosauriformes gen. et sp. indet., PM TGU 16/0-82, proximal fragment of metatarsal III(?) (**A**–**E**), in proximal (**A**), posterior (**B**), medial (**C**), lateral (**D**), anterior (**E**), and PM TGU 16/0-83, distal fragment of metatarsal III or IV (**F**–**J**), in distal (**F**) and four other views (**G**–**J**). Locality Shestakovo 1, Ilek Formation (Aptian–Albian), Kemerovo Region, Russia. Scale bar 5 cm.

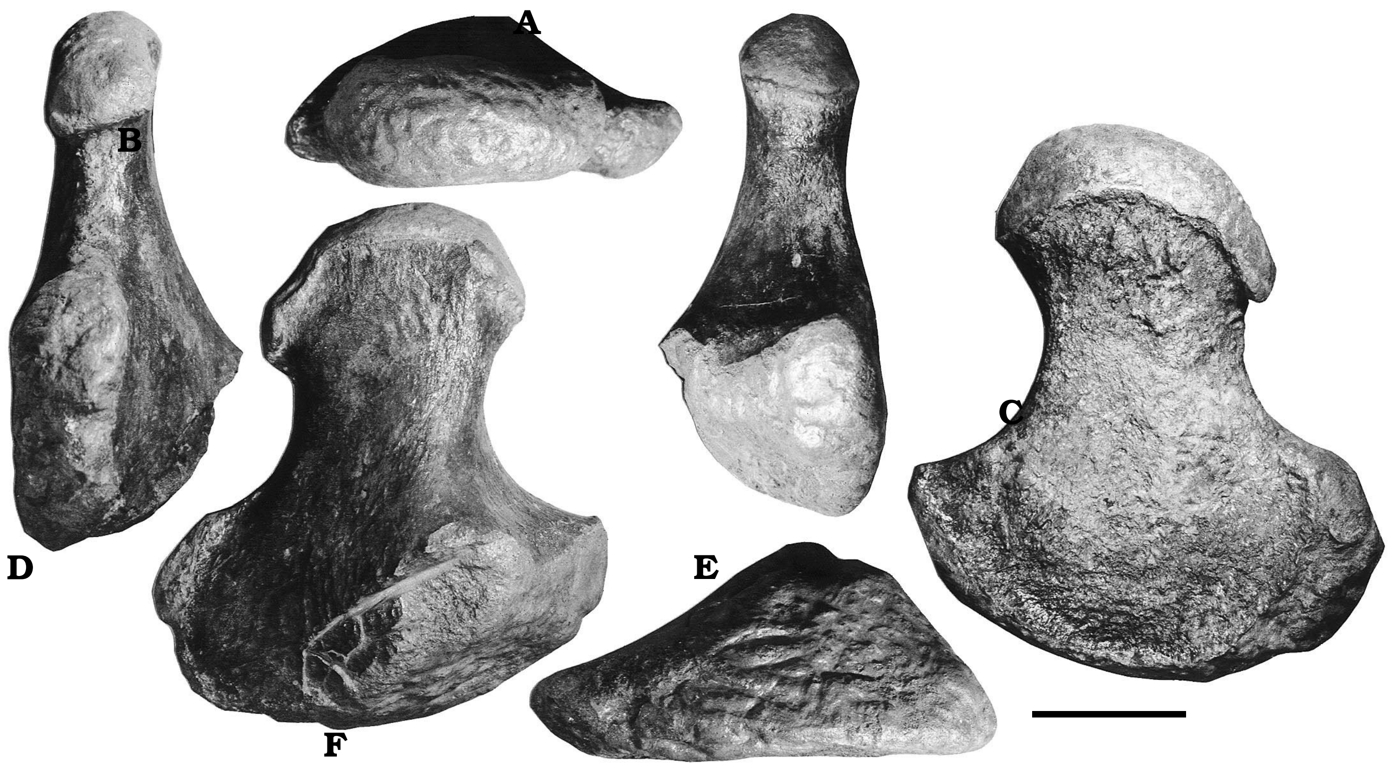

Fig. 4. Titanosauriformes gen. et sp. indet., PM TGU 16/0-84, metatarsal V, in proximal (**A**), medial (**B**), lateral (**C**), posterior (**D**), anterior (**E**), and distal (**F**) views. Locality Shestakovo 1, Ilek Formation (Aptian–Albian), Kemerovo Region, Russia. Scale bar 5 cm.

quite large, they probably do not belong to III–V digit, which is characterised by having the smallest proximal phalanges. PM TGU 16/0-86 is somewhat transversely broader than PM TGU 16/0-85 and thus could be ascribed to the second digit, because II-1 is usually the largest proximal phalanx in the sauropod pes. PM TGU 16/0-85 is interpreted here as the I-1 phalanx. Both known proximal phalanges are stout bones, markedly broader than long, and lack ligament pits. The proximal condyle is oval and more subtriangular in I-1. Its proximal surface is concave both transversely and anteroposteriorly; this concavity is better developed in I-1. The posterior surface is shallowly concave in I-1 and almost flat in II-1. The anterior surface is concave in both phalanges. Both the proximal and distal articular surfaces are exposed in the

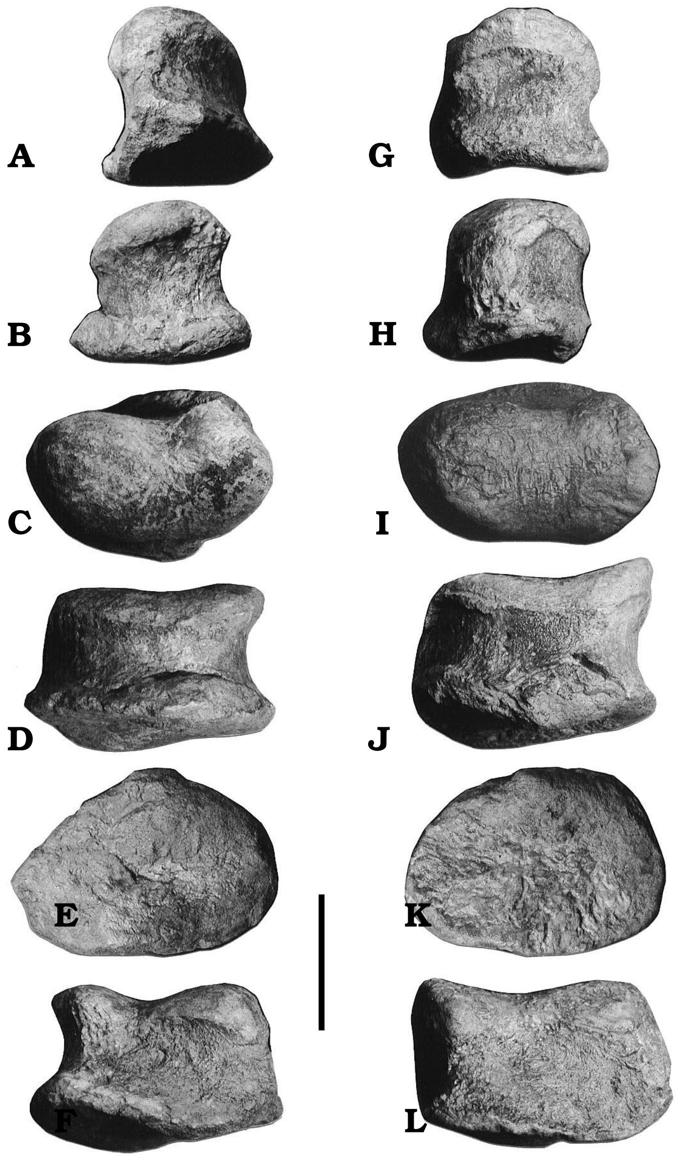

Fig. 5. Titanosauriformes gen. et sp. indet., PM TGU 16/0-85 and 16/0-86, proximal pedal phalanges, possibly I-1 (**A**–**F**) and II-1 (**G**–**L**) respectively, in posterior (**A**, **G**), proximal (**B**, **H**), anterior (**C**, **I**), distal (**D**, **J**), medial (**E**, **K**), and lateral (**F**, **L**) views. Locality Shestakovo 1, Ilek Formation (Aptian–Albian), Kemerovo Region, Russia. Scale bar 5 cm.

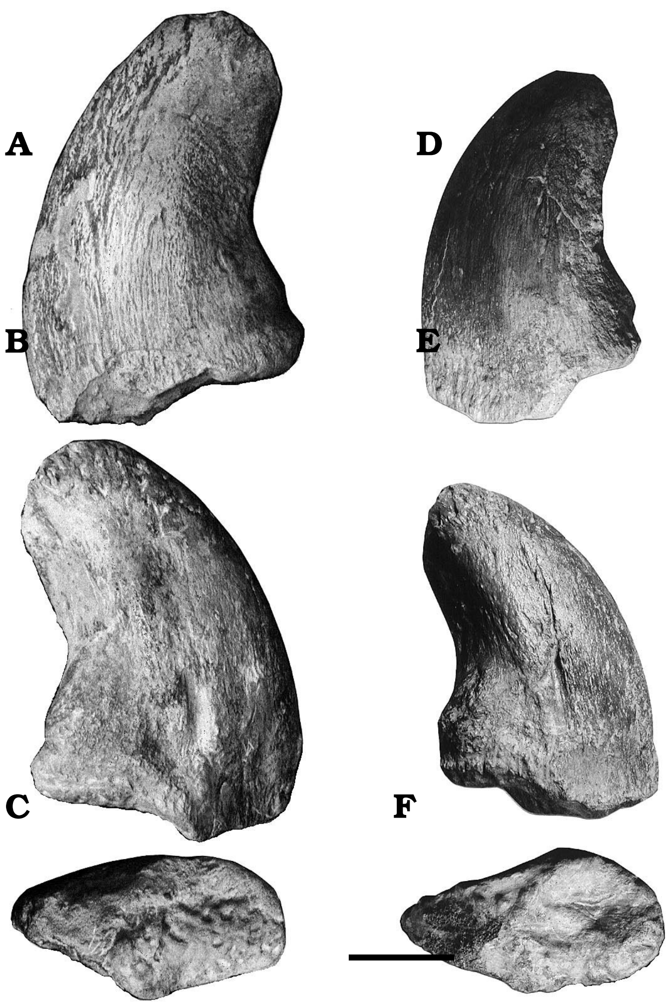

Fig. 6. Titanosauriformes gen. et sp. indet., PM TGU 16/0-87, ungual phalanx of first digit (I-2) (**A**–**C**) and PM TGU 16/0-88, ungual phalanx of second digit (II-3) (**D**–**F**), in proximal (**A**, **D**), medial (**B**, **E**), and lateral (**C**, **D**) views. Locality Shestakovo 1, Ilek Formation (Aptian–Albian), Kemerovo Region, Russia. Scale bar 5 cm.

anterior view. In both phalanges the proximal condyle is anteroposteriorly longer than the distal condyle. The distal condyle is globular in side view and kidney-shaped in distal view, slightly subdivided and with distinct concavity along the posterior margin. The distal surface is slightly concave transversely.

The ungual phalanges (Fig. 6) are typically sickle-shaped, transversely greatly compressed and lack flattened ventral surfaces. PM TGU 16/0-87 is about 16% larger than PM TGU 16/0-88 (greatest length 192 mm vs. 165 mm), and thus the former is regarded here as the ungual of the first digit and the latter as that of the second digit. Both unguals are almost identical in structure, the second digit claw only being more pointed distally, and thus are described together. The unguals are asymmetrical, with the proximal articular surface somewhat exposed in medial view (Fig. 6B, E). The dorsal intercondylar process occupies little less than half of the proximal surface. The medial and lateral surfaces are covered by nu-

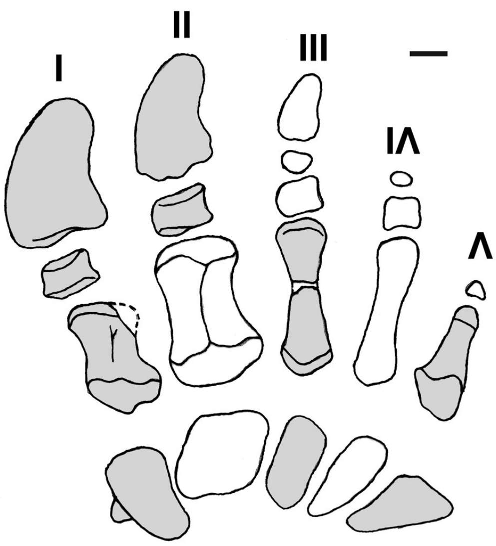

Fig. 7. Titanosauriformes gen. et sp. indet., composite reconstruction of the left pes in anterior view and metatarsals in proximal view (top row). Locality Shestakovo 1, Ilek Formation (Aptian–Albian), Kemerovo Region, Russia. Known elements shown in grey. The outline of the currently lost second metatarsal is based on the photograph preserved. The Roman numerals denote fingers. Scale bar 5 cm.

merous groves and pits for nutrient vessels, with a distinct nail groove on the medial surface, similar to that in *Camarasaurus* (Wilson and Sereno 1998: fig. 35B). An additional sauropod claw, found together with the pedal elements reported here but subsequently lost, was distinctly smaller than unguals described, but was also sickle-shaped. Most probably it belonged to the third digit.

Discussion

The sauropod pes described is the most complete associated sauropod material from the Mesozoic of Siberia known to date. It clearly belongs to a sauropod based on the following derived characters: metatarsals I and V with proximal ends subequal in area to that of metatarsals II and IV (WS 14), length of metatarsal V 70 percent or more that of metatarsal IV (WS 15) [the fourth metatarsal is unknown, but the fifth metatarsal is long enough and has a greatly increased proximal area to suppose the derived state for the characters WS 14 and 15], ungual of pedal digit I enlarged (WS 16), and ungual of pedal digit I deep and narrow (WS 17). The Shestakovo sauropod may be placed in Eusauropoda based on the following characters: metatarsals with spreading configuration (WS 52), pedal phalanges (other than unguals) broader than long (WS 53), pedal digit I ungual as long as, or longer than, metatarsal I (WS 54), pedal digits II–III with sickle-shaped unguals (WS 56), and pedal phalanges with collateral ligament pits greatly reduced or absent (U 202). The more derived traits of the Shestakovo sauropod includes pedal unguals asymmetrical (canted ventrolaterally in articulation) (WS 64), metatarsals III and IV with minimum transverse shaft diameters 65 percent or less those of metatarsals I or II (WS 73) [only metatarsals I and III could be compared, this ratio is 50%], laterodistal process on metatarsal I present (U 199) [actually broken off but likely present], and proximal pedal phalanges narrow towards their lateral and palmar margins (U 204). WS 64 is a synapomorphy for the *Barapasaurus* + *Omeisaurus* + Neosauropoda clade and WS 73 is a synapomorphy for the *Omeisaurus* + Neosauropoda clade in the analysis by Wilson and Sereno (1998). U 204 is a synapomorphy for Neosauropoda *sensu* Upchurch (1998). These features suggest that the Shestakovo sauropod is a member of Neosauropoda. The phylogenetic position of this taxon cannot be determined more precisely based on the currently known material. The presence of the laterodistal process on metatarsal I (U 199) was cited as a synapomorphy for the unnamed node U [Diplodocidae + Dicraeosauridae] in the analysis by Upchurch (1998: 102), but was stated that it is convergently acquired in Brachiosauridae, *Shunosaurus* and *Omeisaurus*. Assessment of this character in sauropods is quite controversial. The presence of this process is doubtful for *Shunosaurus*. The only published photograph of the pes of *S. lii* available for us (Saunders and Engesser 1990: fig. on p. 11) shows no laterodistal process on the metatarsal I. According to McIntosh (1990: tab. 4.1) this process is absent in *Brachiosaurus*, but a short laterodistal process can be seen in the metatarsal I of *B. brancai* (Janensch 1961: pl. for p. 218, figs. 1, 2a, 2c). A better developed laterodistal process may be seen on the metatarsal I from Maryland referred to *Pleurocoelus* (Marsh 1896: pl. 41: 3, 4), but is lacking in the materials from Texas originally referred to the same genus (Gallup 1989: fig.1) [now these materials could be determined only as Titanosauriformes indet., pers. com. from Dr. M. Wedel]. In the Early Cretaceous brachiosaurid *Cedarosaurus* the metatarsal I is apparently lacking laterodistal process (Tildwell et al. 1999: fig. 11B). McIntosh et al. (1992: 164) believed that "the prominent projection on the posterodistal corner of the lateral face of Mt I is a unique derived character of the Diplodocidae". Indeed, this process is a very distinctive character of diplodocids, most clearly developed in *Dyslocosaurus* (e.g., Marsh 1896: pl. 28: 2; Gilmore 1936: fig. 27A; Janensch 1961: pl. for p. 224, figs. 1a, 6a; McIntosh et al. 1992: fig. 5D–F). The pes from Shestakovo differs from the diplodocid pedes mainly by more slender and elongated first metatarsal and by less transformed first digit proximal phalanx. The elongated metatarsal I resembles that in *Brachiosaurus* (Janensch 1961: pl. for p. 218, figs. 1, 2), *Pleurocoelus* (Marsh 1896: pl. 41: 3, 4), and *Cedarosaurus* (Tildwell et al. 1999: fig. 11B). *Cedarosaurus* had three claws in the pes (Tildwell et al. 1999: fig. 11C), and the first claw is only 11% longer than the second claw (16% longer in the Shestakovo sauropod). The Texas titanosauriform was reconstructed with four claws (Gallup 1989: fig. 1). The foot of *Brachiosaurus* is only known from isolated elements; possibly it had only two claws. In *Brachiosaurus* the proximal condyle of the metatarsal V is much less anteroposteriorly expanded (Janensch 1961: pl. for p. 220, figs. 5, 7) than in the Shestakovo sauropod. In *Pleurocoelus* the distal portion of the metatarsal I is greatly expanded mediolaterally with a well-developed laterodistal process, and the medial margin of the proximal surface is distinctly concave, as in the Shestakovo sauropod. However, *Pleurocoelus* differs from the latter by the anteroposteriorly shorter distal condyle of the metatarsal I.

The pes in titanosaurids is imperfectly known. In the Maastrichtian *Opisthocoelicaudia* from Mongolia the metatarsals are very robust, metatarsal I being short and stout, and the distal metatarsal condyles nearly as wide as the proximal condyles (Borsuk-Białynicka 1977: pl. 14). This condition is markedly different from that of the Shestakovo sauropod. In the Campanian–Maastrichtian *Laplatasaurus* from Argentina metatarsal I is quite elongated (Huene 1929: fig. 22; primitive character), as in the Shestakovo specimen, but apparently lacks a laterodistal process. Metatarsal V in *Laplatasaurus* (Huene 1929: figs. 21?, 25?, 27) has a relatively unexpanded proximal condyle which is not triangular in outline in proximal view, unlike that of the Shestakovo specimen.

In the Early Cretaceous *Euhelopus* from China (Wiman 1929: pl. 4: 11–14; McIntosh et al. 1992: fig. 5B) metatarsal I is primitively elongated, with a mediolaterally widened distal condyle. *Euhelopus* further resembles the Shestakovo specimen in having relatively unexpanded anteroposteriorly distal condyles and in the shape of proximal condyles in metatarsals I and III, but differs by lacking the laterodistal process of metatarsal I and by having a more curved first digit ungual. This similarity in the pes structure between *Euhelopus*, Brachiosauridae, and Titanosauria supports placement of *Euhelopus* within the Titanosauriformes (Wilson and Sereno 1998) and suggests attribution of the Shestakovo sauropod to that group.

Concluding, the Shestakovo pes resembles that in brachiosaurids (*Brachiosaurus*, *Pleurocoelus*, and *Cedarosaurus*), titanosaurids (*Laplatasaurus*), and *Euhelopus* in the presence of slender metatarsals, especially the gracile and elongated first metatarsal, which differs markedly from the shortened and robust first metatarsal of diplodocids. This may support attribution of the Shestakovo sauropod to Titanosauriformes (Brachiosauridae + *Euhelopus* + Titanosauria).

The presence in the Shestakovo assemblage of both Titanosauria and Brachiosauridae is likely. A genuine titanosaurid is known from the Early Cretaceous Mogoito locality in Transbaikalia (Averianov and Skutschas 2000). The Brachiosauridae were reported, but not described, from several Early Cretaceous localities in Japan and China (e.g., Azuma and Tomida 1995: 128; Dong 1992: 100, 104, 110), but reference of sauropod materials to this family by Chinese authors may be based on older, broader concept of the family.

The presence of a brachiosaurid in the Shestakovo may be suggested also by the compressed cone-chisel-like isolated teeth (terminology of Calvo 1994), characteristic for brachiosaurids *Brachiosaurus*, *Pleurocoelus* (= *Astrodon*), *Bothriospondylus*, and also for the enigmatic Asian *Asiatosaurus* (Osborn 1924). However, a strongly procoelous mid-caudal vertebra with a nearly hemispherical posterior articular “ball” from the Bol’shoi Kemchug locality in the Ilek Formation in (Fig. 1) undoubtedly indicates also the presence of a true titanosaurid in the Ilek fauna.

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References

Alifanov, V.R., Efimov, M.B., Novikov, I.V., and Morales, M. 1999. A new psittacosaur complex of tetrapods from the Lower Cretaceous Shestakovo locality (southern Siberia) [in Russian]. *Doklady Akademii Nauk* 369: 491–493.

Averianov, A.O. [Aver’ânov, A.O.] and Skutschas, P.P. [Skučas, P.P.] 2000. A vertebrate assemblage from the Early Cretaceous of Transbaikalia (locality Mogoito) [in Russian]. *In*: A.V. Komarov (ed.), *Materialy regional’noj konferencii geologov Sibiri, Dal’nego Vostoka i Severo-Vostoka Rossii*. Tom II, 357–358. GalaPress, Tomsk.

Azuma, Y. and Tomida, Y. 1995. Early Cretaceous dinosaur fauna of the Tetori Group in Japan. *In*: A. Sun and Y. Wang (eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, 125–131. China Ocean Press, Beijing.

Borsuk-Białynicka, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologica Polonica* 37: 1–64.

Bulynnikova, A.A. and Trushkova, L.Ya. [Truškova, L.Â] 1967. Continental Cretaceous deposits of eastern and central parts of the Western Siberian lowland [in Russian]. *In*: G.G. Martinson (ed.), *Stratigrafiâ i paleontologiâ mezozojskih i paleogen-neogenovyh kontinental’nyh otloženij aziatskoj časti SSSR*, 40–46. Nauka, Leningrad.

Calvo, J.A. 1994. Jaw mechanics in sauropod dinosaurs. *In*: M.G. Lockley, V.F. dos Santos, C.A. Meyer and A. Hunt (eds.), Aspects of Sauropod Paleobiology. *Gaia* 10: 183–193.

Dmitriev, A.G. and Rozhdestvensky, A.K. [Roždestvenskij, A.K.] 1968. Bone bearing facies of lacustrine-fluvial deposits of the upper Mesozoic of Buryatia [in Russian]. *In*: N.A. Florensov (ed.), *Mezozojskie i kajnozojskie ozëra Sibiri*, 39–48. Nauka, Moskva.

Dong, Z. 1992. *Dinosaurian Faunas of China*. 188 pp. China Ocean Press & Springer-Verlag, Beijing.

Efimov, M.B. and Leshchinskiy, S.V. [Leŝinskij, S.V.] 2000. First finding of the fossil crocodile skull in Siberia [in Russian]. *In*: A.V. Komarov (ed.), *Materialy regional’noj konferencii geologov Sibiri, Dal’nego Vostoka i Severo-Vostoka Rossii.* Tom II, 361–363. GalaPress, Tomsk.

Gallup, M.R. 1989. Functional morphology of the hindfoot of the Texas sauropod *Pleurocoelus* sp. indet. *In*: J.O. Farlow (ed.), Paleobiology of the Dinosaurs. *Geological Society of America Special Paper* 238: 71–74.

Gilmore, C.W. 1936. Osteology of *Apatosaurus* with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum* 11: 175–300.

Huene, F. von. 1929. Los saurisquios y ornitisquios del Cretácico Argentino. *Anales del Museo de La Plata* 2 (Serie 3): 1–194.

Huene, F. von. 1932. Die fossil Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaeontologie* (1) 4: 1–361.

Janensch, W. 1961. Die Gliedmaszen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. *Palaeontographica* 3 (Supplement 7, 1): 177–235.

Kurzanov, S.M., Efimov, M.B., and Gubin, Yu.M. [Gubin, Û.M.] 2000. Dinosaurs of Yakutia [in Russian]. *In*: A.V. Komarov (ed.), *Materialy regional'noj konferencii geologov Sibiri, Dal'nego Vostoka i Severo-Vostoka Rossii*. Tom II, 356–357. GalaPress, Tomsk.

Leshchinskiy, S.V. [Leŝinskij, S.V.], Voronkevich, A.V. [Voronkevič, A.V], Fayngertz, A.V. [Fajngerc, A.V], and Schikhovtzeva, L.G. [Šihovceva, L.G.] 1997. Some aspects of taphonomy and stratigraphic position of the localities of the Shestakovo complex of Early Cretaceous vertebrates [in Russian]. *In*: V.M. Podobina (ed.), *Voprosy geologii i paleontologii Sibiri*, 83–90. Tomskij Gosudarstvennyi Universitet, Tomsk.

Leshchinskiy, S.V. [Leŝinskij, S.V.], Fayngertz, A.V., Voronkevich, A.V. [Voronkevič, A.V], Maschenko, E.N. [Maŝenko, E.N.], and Averianov, A.O. [Aver'ânov, A.O.] 2000. Preliminary results of the investigation of the Shestakovo localities of Early Cretaceous vertebrates [in Russian]. *In*: A.V. Komarov (ed.), *Materialy regional'noj konferencii geologov Sibiri, Dal'nego Vostoka i Severo-Vostoka Rossii*. Tom II, 363–366. GalaPress, Tomsk.

McIntosh, J.S. 1990. Species determination in sauropod dinosaurs with tentative suggestions for their classification. *In*: K. Carpenter and P.J. Currie (eds.), *Dinosaur Systematics. Approaches and Perspectives*, 53–69. Cambridge University Press, Cambridge.

McIntosh, J.S., Coombs, W.P., Jr., and Russell, D.A. 1992. A new diplodocid sauropod (Dinosauria) from Wyoming, USA. *Journal of Vertebrate Paleontology* 12: 158–167.

Marsch, O.C. 1878. Principal characters of American Jurassic dinosaurs. Pt. I. *American Journal of Science* (3) 16: 411–416.

Marsh, O.C. 1896. The dinosaurs of North America. *Sixteenth Annual Report of the United States Geological Survey* 1: 135–244.

Maschenko, E.N. and Lopatin, A.V. 1998. First record of an Early Cretaceous triconodont mammal in Siberia. *Bulletin de l'Institute Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 68: 233–236.

Nessov, L.A. [Nesov. L.A.] 1995. *Dinozavry severnoj Evrazii: novye dannye o sostave kompleksov, ekologii i paleogeografii*. 156 pp. Izdatelstvo Sankt-Peterburgskogo Universiteta, Sankt Petersburg.

Nessov, L.A. [Nesov. L.A.] and Starkov, A.I. 1992. Cretaceous vertebrates of the Gusinoe Lake Depression in Transbaikalia and their contribution into dating and determination of sedimentation conditions [in Russian]. *Geologiâ i Geofizika* 6: 10–19.

Osborn, H.F. 1924. Sauropoda and Theropoda of the Lower Cretaceous of Mongolia. *American Museum Novitates* 128: 1–7.

Rich, T.H., Gangloff, R.A., and Hammer, W.R. 1997. Polar dinosaurs. *In*: P.J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*, 562–573. Academic Press, San Diego.

Rozhdestvensky, A.K. [Roždestvenskij, A.K.] 1960. Locality of Lower Cretaceous dinosaurs in Kuzbass [in Russian]. *Paleontologičeskij Žurnal* 2: 165.

Saev, V.I. and Leshchinskiy, S.V. [Leŝinskij, S.V.] 1997. New findings of dinosaurs in Siberia [in Russian]. *In*: V.M. Podobina, N.I. Savina, K.I. Kuznecova, and N.G. Muzylev (eds.), *Biostratigrafiâ i mikroorganizmy fanerozoâ Evrazii*, 268. Geos, Moskva.

Salgado, L., Coria, R.A., and Calvo, J.O. 1997. Evolution of titanosaurid sauropods. I. Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34: 3–32.

Saunders, J.B. and Engesser, B. 1990. Dinosaurier aus China. *Veröffentlichungen aus dem Naturhistorischen Museum Basel* 24: 1–33.

Tatarinov, L.P. and Maschenko, E.N. [Maŝenko, E.N.] 1999. Finding of an aberrant tritylodont in the Lower Cretaceous of Kemerovo Region [in Russian]. *Paleontologičeskij Žurnal* 4: 85–92.

Tildwell, V., Carpenter, K., and Brooks, W. 1999. New sauropod from the Lower Cretaceous of Utah, USA. *Oryctos* 2: 21–37.

Upchurch, P. 1995. Evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London B* 349: 365–390.

Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society* 124: 43–103.

Voronkevich, A.V. [Voronkevič, A.V.] 1998. A large representative of the genus *Psittacosaurus* from the locality Shestakovo-3 [in Russian]. *In*: I.A. Vylcan (ed.), *Aktual'nye voprosy geologii i geografii Sibiri. Materialy naučnoij konferencii 1*, 190–193. Tomskij Gosudarstvennyj Universitet, Tomsk.

Wiman, C. 1929. Die Kreide-Dinosaurier aus Shantung. *Palaeontologia Sinica* C6: 1–67.

Young, C.C. 1958. New sauropods from China. *Vertebrata PalAsiatica* 2: 1–28.

Wilson, J.A. and Sereno, P.C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology Memoir* 5: 1–68.