



УДК 57.072:551.762.2

A NEW BASAL COELUROSAUR (DINOSAURIA: THEROPODA) FROM THE MIDDLE JURASSIC OF SIBERIA

A.O. Averianov^{1*}, S.A. Krasnolutski² and S.V. Ivantsov³

¹Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia;
e-mail: lepus@zin.ru

²Шарыпово Regional Museum, 2nd microrayon 10, Шарыпово, 662311 Krasnoyarsk Territory, Russia;
e-mail: krasnolucki.ser@mail.ru

³Department of Palaeontology and Historical Geology, Geological-Geographical Faculty, Tomsk State University, Lenina Pr. 36, 634050 Tomsk, Russia; e-mail: stepan_ivantsov@mail.ru

ABSTRACT

Kileskus aristotocus gen. et sp. nov. from the Middle Jurassic (Bathonian) Itat Formation at Berezovsk Quarry, Krasnoyarsk Territory (West Siberia, Russia), is based on an associated maxilla and premaxilla, a mandible fragment, and some possible associated postcranial elements. *Kileskus* gen. nov. is referred together with the Middle Jurassic *Proceratosaurus* from England and the Late Jurassic *Guanlong* from China to Proceratosauridae fam. nov. (Tyrannosauroida, Coelurosauria) which is characterized by sagittal nasal crest (unknown for *Kileskus* gen. nov.), enlarged external nares, short ventral margin of premaxilla, and depth of the antorbital fossa ventral to the antorbital fenestra that is much greater than the depth of the maxilla below the ventral margin of the antorbital fossa. *Kileskus* gen. nov. is more similar to *Proceratosaurus* than to *Guanlong* in having anterodorsal process of the premaxilla inclined slightly anterodorsally and nares inclined posterodorsally, but differs from these two genera by having ascending process of the maxilla confluent with anterior rim of maxillary body and gently sloping posterodorsally. *Kileskus* gen. nov. has a basal position within the Proceratosauridae. *Dilong* from the Early Cretaceous of China with a parasagittal nasal crests is the sister taxon for the Proceratosauridae. The new taxon is one of the oldest members of Coelurosauria and Tyrannosauroida in the fossil record.

Key words: Coelurosauria, Dinosauria, Middle Jurassic, Russia, Theropoda, Tyrannosauroida, West Siberia

БАЗАЛЬНЫЙ ЦЕЛУРОЗАВР (DINOSAURIA: THEROPODA) ИЗ СРЕДНЕЙ ЮРЫ СИБИРИ

А.О. Аверьянов^{1*}, С.А. Краснолуцкий² и С.В. Иванцов³

¹Зоологический институт Российской академии наук, Университетская наб. 1, 199034 Санкт-Петербург, Россия;
e-mail: lepus@zin.ru

²Шарыповский краеведческий музей, 2-й микрорайон 10, Шарыпово, 662311 Красноярский край, Россия;
e-mail: krasnolucki.ser@mail.ru

³Кафедра палеонтологии и исторической геологии, Геолого-географический факультет, Томский государственный университет, пр. Ленина 36, 634050 Томск, Россия; e-mail: stepan_ivantsov@mail.ru

РЕЗЮМЕ

Kileskus aristotocus gen. et sp. nov. из среднеюрской (батский ярус) итатской свиты Березовского карьера в Красноярском Крае (Западная Сибирь, Россия) описан по верхнечелюстной кости (голотип), предчелюстной кости, фрагменту нижней челюсти и, возможно, некоторым ассоциированным костям посткраниального ске-

* Corresponding author / Автор-корреспондент.

лета. *Kileskus* gen. nov. вместе со среднеюрским *Proceratosaurus* из Англии и позднеюрским *Guanlong* из Китая выделен в новое семейство Proceratosauridae fam. nov. (Tyrannosauroida, Coelurosauria) которое характеризуется сагиттальным черепным гребнем, образованным носовыми костями (неизвестен для *Kileskus* gen. nov.), увеличенными носовыми отверстиями, коротким вентральным краем предчелюстной кости, анторбитальной ямкой под анторбитальным отверстием, превышающей по высоте участок верхнечелюстной кости под этой ямкой. *Kileskus* gen. nov. ближе к *Proceratosaurus* чем к *Guanlong* по наклону антеродорсального отростка предчелюстной кости вперед и вверх и носовых отверстий — назад и вверх, но отличается от этих двух родов входящим отростком верхнечелюстной кости, не отделенным выемкой от основной части кости. *Kileskus* gen. nov. занимает базальное положение в семействе Proceratosauridae. *Dilong* из раннего мела Китая с парасагиттальным черепным гребнем является сестринским таксоном для Proceratosauridae. Новый таксон является одним из древнейших представителей Coelurosauria и Tyrannosauroida в геологической летописи.

Ключевые слова: Coelurosauria, Dinosauria, средняя юра, Россия, Theropoda, Tyrannosauroida, Западная Сибирь

INTRODUCTION

A diverse assemblage of vertebrates, including fishes, salamanders, turtles, choristoderes, lizards, crocodyliforms, pterosaurs, dinosaurs, tritylodontids, and diverse mammals has recently been recovered from the Middle Jurassic (Bathonian) Itat Formation, exposed in the Berezovsk Quarry in the south of the Krasnoyarsk Territory, West Siberia (Alifanov et al. 2001; Averianov et al. 2005, 2008; Lopatin and Averianov 2005, 2006, 2007, 2009; Skutschas et al. 2005; Averianov and Lopatin 2006; Skutschas 2006; Averianov and Krasnolutskii 2009).

Here we report on a new faunal element from the Itat Formation, a new coelurosaurian theropod. It is based on an associated maxilla and premaxilla, a mandible fragment, and some postcranial bones that were scattered on area of 1 to 2 m² and likely represent the remains of a single individual.

Measurements. Teeth: BW, basal width; FABL, fore-aft-basal length. Metapodials and phalanges: L – length; PW – maximum width of proximal end; DW – maximum width of distal end. All measurements are in mm unless otherwise indicated.

Institutional abbreviation. ZIN PH – Paleoherpological Collection, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

SYSTEMATICS

Dinosauria Owen, 1842

Saurischia Seeley, 1888

Theropoda Marsh, 1881

Coelurosauria Huene, 1914

Tyrannosauroida Osborn, 1905

Proceratosauridae fam. nov.

Proceratosauridae [nomen nudum]: Rauhut et al., 2010: 187.

Type genus. *Proceratosaurus* Huene, 1926. Middle Jurassic of England, United Kingdom.

Differential diagnosis. Differs from other groups of theropod dinosaurs by the following unique combination of characters: 1) sagittal cranial crest formed by the nasals and starting at the premaxilla-nasal junction; 2) extremely elongated external naris with the length exceeding 20% of the skull length; 3) short ventral margin of the premaxilla; 4) depth of the antorbital fossa ventral to the antorbital fenestra is much greater than the depth of the maxilla below the ventral margin of the antorbital fossa.

Included genera. Type genus, *Guanlong* Xu et al., 2006 (Late Jurassic of Xingjiang, China), and *Kileskus* gen. nov. (Middle Jurassic of West Siberia, Russia).

Comments. Rauhut et al. (2010: 187) established a new “monophyletic clade” Proceratosauridae for *Proceratosaurus* and *Guanlong*, defining it as a stem based taxon including “all theropods that are more closely related to *Proceratosaurus* than to *Tyrannosaurus*, *Allosaurus*, *Compsognathus*, *Coelurus*, *Ornithomimus*, or *Deinonychus*.” The term “monophyletic clade” is a tautology because the clade is a monophyletic group by definition. In traditional systematics the family group taxa are subject of the International Code of Zoological Nomenclature. According to this Code, every new name published after 1930 must be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon (Article 13.1.1). Thus the name Proceratosauridae as it appeared in Rauhut et al. (2010) is a

nomen nudum. Here we provide a diagnosis for the Proceratosauridae and validate usage of this name as a family group taxon. The clade Proceratosauridae is defined here as a node based taxon including *Proceratosaurus*, *Kileskus* gen. nov., their most recent common ancestor, and all its descendants. This definition is preferred here to the having priority stem based definition by Rauhut et al. (2010) because it defines a more natural group of organisms. According to the stem based definition the Early Cretaceous *Dilong* should be included in the Proceratosauridae, but this taxon is markedly different in having the parasagittal cranial crests compared with the sagittal cranial crest characteristic for the Proceratosauridae.

The cranial crest is currently unknown for *Kileskus* gen. nov. but the presence of a cranial crest formed by the nasals is inferred for this taxon by its phylogenetic position between *Dilong* and the clade comprising *Guanlong* and *Proceratosaurus* (see below).

A potentially diagnostic for Proceratosauridae might be structure of the posterior caudal vertebrae. In *Guanlong* posterior caudals have “deep, longitudinal sulci on both ventral and dorsal surfaces” (Xu et al. 2006: 715). Similar posterior caudals with elongated centrum and sulci along dorsal side of the neural arch and ventral side of the centrum are common among isolated dinosaur bones from the Itat Formation and may belong to *Kileskus* gen. nov. This peculiar morphology of posterior caudals was independently evolved in troodontids (Xu et al. 2006).

***Kileskus* gen. nov.**

Type species. *Kileskus aristotocus*, sp. nov.

Differential diagnosis. Differs from *Proceratosaurus* and *Guanlong* by ascending process of the maxilla confluent with anterior rim of maxillary body and gently sloping posterodorsally. Additionally differs from *Proceratosaurus* by premaxillary teeth with subequal mesial and distal serrations, by fewer maxillary tooth positions (17 compared with 22), by antorbital fossa of the maxilla that does not extend anterior and ventral to the promaxillary fenestra, by promaxillary foramen lower dorsoventrally than the maxillary fenestra. Similar with *Proceratosaurus* and differs from *Guanlong* in having anterodorsal process of the premaxilla inclined slightly anterodorsally and nares inclined posterodorsally at $\sim 40^\circ$ to the skull longitudinal axis.

Etymology. From Khakas *kileskus*, a lizard.

***Kileskus aristotocus* sp. nov.**

(Figs. 1–8)

Holotype. ZIN PH 5/117, incomplete right maxilla.

Type locality and horizon. Berezovsk Quarry, 2 km south of Nikol'skoe village, Sharypovo District, Krasnoyarsk Territory, West Siberia, Russia. Grey clays of the upper part of Itat Formation, Middle Jurassic, Bathonian (see Averianov et al. 2005 for details).

Material. ZIN PH 6/117, left premaxilla. ZIN PH 7/117, posterior fragment of left surangular. ZIN PH 8/117, left metacarpal II. ZIN PH 9/117, left manual phalanx II-1. ZIN PH 10/117, left metatarsal I. ZIN PH 11/117, left metatarsal III. ZIN PH 12/117, left second phalanx of the second pedal digit. ZIN PH 13/117, pedal ungual phalanx.

Etymology. From Greek ἀριστότοκος, of noble origin, in allusion to the phylogenetic position of *Kileskus* gen. nov. within the clade of derived theropods (Coelurosauria).

DESCRIPTION

Premaxilla. The premaxilla (ZIN PH 6/117; Fig. 1) is a delicate triradiate bone with a relatively small body housing four tooth positions and with two slender processes, the anterodorsal (narial) process and the posterodorsal (subnarial) process. The anterior and posterior margins of the premaxillary body are broken and the medial alveolar wall is largely missing. The alveoli increase in size posteriorly, with the fourth alveolus more than twice as large as the first. The crown of a replacement tooth is preserved in situ in the second tooth position. It is asymmetrical, D-shaped, with finely striated medial and distal carinae. This tooth is only about half as large as the maxillary teeth (see below). The maxillary (palatal) process of the premaxilla is a distinct, leaf-like flange at the base of the posterodorsal process. Its lateroventral side, which contacts the maxilla, is slightly concave and smooth. Anterodorsal to the maxillary process there is a large foramen. The slightly curved posterodorsal process is very thin anteroposteriorly and its basal third is about twice as wide mediolaterally as the more distal portion. Along the lateroventral margin of the process there is a short groove with a striated surface representing the con-

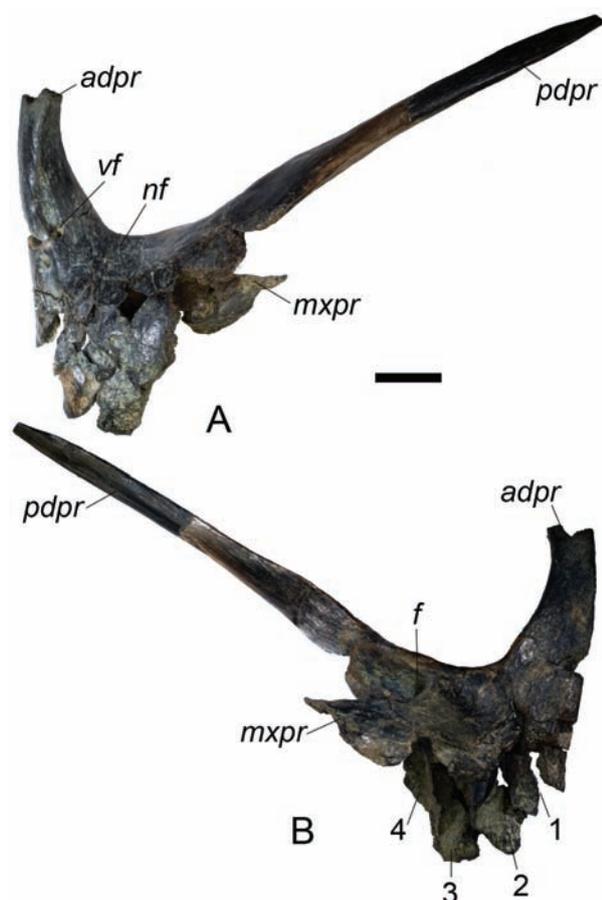


Fig. 1. ZIN PH 6/117, left premaxilla of *Kileskus aristotocus* gen. et sp. nov., from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in lateral (A) and medial (B) views.

Abbreviations: *f* – foramen; *adpr* – anterodorsal process; *mxpr* – maxillary process; *nf* – narial fossa; *pdpr* – posterodorsal process; *vf* – vascular foramen. Numbers 1 to 4 denote tooth positions. Scale bar = 1 cm.

tact area with the maxilla. The anterodorsal process is dorsally directed at the base, almost perpendicular to the posterodorsal process, but its missing distal portion evidently extended posteriorly, more or less parallel to the posterodorsal process. The process is triangular in cross-section, with a flat and striated medial side for contact with the opposite premaxilla, a convex (ventrally) to concave (dorsally) posterolateral side forming the wall of the narial fossa, and a convex anterior side. On the lateral side about half of the body is covered by a narial fossa, which extends onto the anterodorsal and posterodorsal processes. Some distance above the alveolar border there is a

row of vascular foramina, which extends dorsally towards the base of the anterodorsal process.

Maxilla. The holotype maxilla has been deformed postmortem and broken into several pieces. It has been repaired into three blocks: anterior, middle, and posterior (Fig. 2). The anterior fragment is missing the dorsal portion of the dorsal ramus and some other smaller pieces. The dorsal margin of the middle fragment is destroyed. The piece preserves the contact with the anterior fragment on the lateral side, but on the medial side the contact is obscured by postmortem distortion of the palatal shelf. The posterior fragment preserves the ventral and anterior margins of the antorbital fenestra and is nearly complete posteriorly. The contact area between the middle and posterior fragments is not preserved but it is unlikely that a considerable portion of bone, housing an additional tooth position, is missing. The total length of the maxilla is approximately 29 cm.

The maxilla is elongated and relatively low. In lateral view the alveolar margin is distinctly concave. In ventral view the bone is slightly sinusoidal, with a laterally convex middle portion. The posterior portion of the maxilla is laterally deflected. There are 17 alveoli in the maxilla. The postalveolar portion of the bone is more than 6 cm long. The first alveolus is only slightly smaller than the second alveolus. Alveoli 15 to 17 are about half the size of the fourteenth alveolus. The other alveoli are similar in size. The antorbital fenestra is large and extends anteriorly up to the tenth tooth position. Its anterior margin is nearly vertical. The shallow antorbital fossa is extensive, extending anteriorly up to the fourth tooth position. Its ventral margin is a low ridge, which closely approaches the alveolar margin at the posterior end of the bone. Anteriorly the ventral margin of the antorbital fossa gradually extends dorsally from the alveolar margin. The anterior and anterodorsal margins of the antorbital fossa are sharp ridges, with a pocket-like extension of the fossa beneath the anterior margin. The large oval maxillary fenestra is close to the anterior border of the antorbital fossa. Its long axis extends at an angle of 15° to the alveolar margin. The greatest diameter of the maxillary fenestra is ca. 4.5 cm. Ventral to the maxillary fenestra at the anterior corner of the antorbital fossa there is a relatively large promaxillary fenestra (vertical diameter is ca. 1.4 cm). The promaxillary fenestra opens into a small pneumatic excavation within the anterior ramus of maxilla. Although the medial margin of the promax-

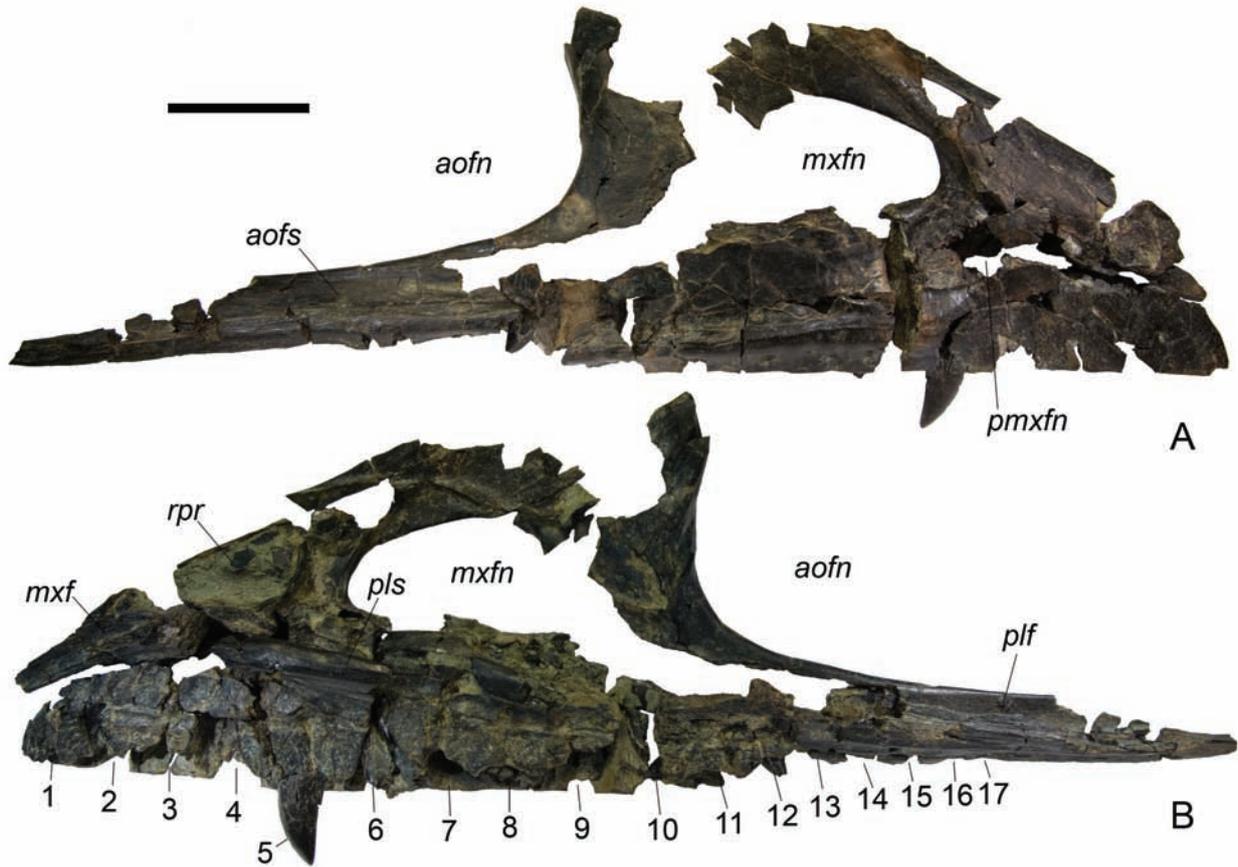


Fig. 2. ZIN PH 5/117, holotype, right maxilla of *Kileskus aristotocus* gen. et sp. nov., from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in lateral (A) and medial (B) views.

Abbreviations: *aofn* – antorbital fenestra; *aofs* – antorbital fossa; *mxfl* – maxillary facet; *mxfn* – maxillary fenestra; *plf* – palatine facet; *pls* – palatal shelf; *pmxfn* – premaxillary fenestra; *rpr* – recessus promaxillaris. Numbers 1 to 17 denote tooth positions. Scale bar = 3 cm.

illary fenestra is destroyed, this opening was likely visible in lateral view. The lateral surface of the bone outside the antorbital fossa is smooth or very finely striated. There is a single row of supralabial vascular foramina, which extends close to the alveolar border. These openings are most pronounced in the middle part of the bone. They become smaller and shallower anteriorly, where they sometimes continue as faint grooves directed towards the alveolar margin. Posteriorly, where the ventral ridge delimiting the antorbital fossa closely approaches the alveolar border, the vascular foramina are absent. The anterior margin of the maxilla is convex at the alveolar level and straight along the posteriorly inclined dorsal ramus. The rostral ramus is quite short and not separated by a concavity from the dorsal ramus. A small piece of

bone preserved along the anterior margin anterior to the maxillary fenestra has a flattened and rugose dorsal surface. Along the dorsal part of this piece there is a pocket-like excavation within the dorsal ramus. These features apparently form the contact area with the nasal. The long posterodorsal process of premaxilla extends exactly to this area, suggesting that the maxilla was completely excluded from the border of external nares by the nasal and premaxilla.

Medially, the maxilla is divided into two parts by a horizontal ridge, with the maxillary facet (for the opposing maxilla) anteriorly and the palatal shelf posteriorly. The maxillary facet is relatively short (ca. 4.5 cm) and obliquely oriented, converging on the dorsal margin of the bone anteriorly. The area contacting the opposite maxilla is excavated dorsally by a deep groove,

which is bordered ventrally and dorsally by sharp ridges. Ventrally on this area there are two much shallower longitudinal ridges. The palatal shelf is placed about 3 cm above the alveolar margin anteriorly but gradually extends toward this margin posteriorly. At the posterior end of the alveolar row the palatal shelf reaches its greatest width and becomes confluent with the alveolar margin. There the palatal shelf is transversely as broad as the alveolar row. In this region, a small piece of a rugose area representing the palatine facet is preserved. This facet is set perpendicular to the alveolar surface. The other preserved pieces of the palatal shelf between the maxillary and palatine facets are smooth, suggesting no bony contact in this area. The vertical bony lamina with the palatine facet on the medial side is very thin and forms the medial wall of a deep and wide channel-like groove along the dorsal surface of the bone at the antorbital fenestra. The lateral wall of this groove is formed by the thin ventral margin of the antorbital fenestra. The posterior part of this groove has a rugose bottom and apparently represents the contact areas with the lacrimal and jugal. The jugal facet is a small strap-like groove lateral to the lacrimal facet and is separated from the latter by a distinct ridge. The triangular interdental plates are well developed. Their medial surfaces are finely sculptured whereas the remainder of the medial surface of the maxilla is smooth. The interdental plates decrease in size posteriorly.

The dorsal ramus of the maxilla is very thin and excavated from the medial side by three pneumatic recesses. The anterior one is the recessus promaxillaris (Witmer 1997), a triangular depression above the maxillary facet and anterior end of the palatal shelf. The more posterior recess extends around the maxillary fenestra. The two depressions are separated by a sharp vertical ridge that forms the margin of a large opening between the two chambers. At the bottom of the recessus promaxillaris at the posterior end of the maxillary facet there is a small foramen leading to the promaxillary fenestra. The third pneumatic recess is in the posterior part of the dorsal maxillary process, forming the anterior margin of the antorbital fenestra.

A complete functional tooth is preserved in the fifth tooth position. It is labiolingually compressed (FABL = 11.5; BW = 5.1; BW/FABL = 0.44), with finely serrated mesial and distal carinae. There are completely or partially preserved replacement teeth in the second, fourth, sixth, eighth, tenth, and twelfth

alveoli. In the sixth position, a replacing crown is preserved above the root of the functional tooth.

Surangular. ZIN PH 7/116 is a posterior fragment of the left surangular (Fig. 3). It preserves most of the surangular portion of the mandibular glenoid and retroarticular process and a part of the bone anterior to the glenoid. The glenoid fossa is relatively narrow and deeply U-shaped in lateral view. It is oblique relative to the longitudinal axis of the bone. The thin bony plate of the retroarticular process is directed posteromedially. Its medial side contacting the articular is flat and rugose. On the lateral side of the retroarticular process there is a rugosity possible representing attachment area for *m. pterygoideus ventralis*. An alternative but less likely interpretation of this rugosity is that it is an attachment area for the angular extending to the posterior end of the retroarticular process (as in *Proceratosaurus* but not in *Guanlong*). There is a robust ridge (lateral shelf) along the dorsolateral margin of the bone extending anteriorly from the glenoid. This ridge separates a shallow dorsal depression from a somewhat deeper lateral depression (fossa for *M. adductor mandibulae externus*). Within the dorsal depression the dorsal border of a small posterior surangular foramen is preserved. The foramen continues into a faint groove on the medial side of the bone, which forms the lateral wall of the internal mandibular fenestra.

Metacarpal II. The left metacarpal II ZIN PH 8/117 is a relatively gracile and elongate bone, with the proximal end transversely expanded ~2.5 times

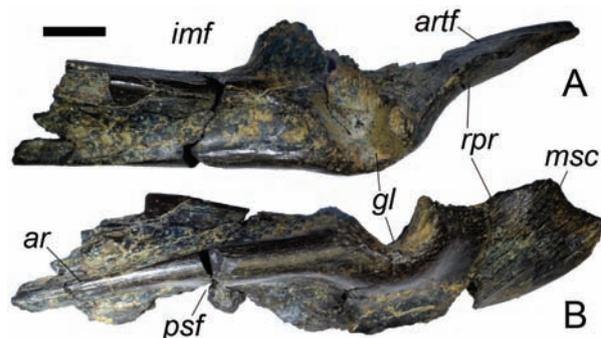


Fig. 3. ZIN PH 7/117, posterior fragment of left surangular of *Kileskus aristotocus* gen. et sp. nov., from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in dorsal (A) and lateral (B) views.

Abbreviations: *ar* – adductor ridge; *artf* – articular facet; *gl* – glenoid fossa; *imf* – internal mandibular fenestra; *msc* – muscle scar; *psf* – posterior surangular foramen; *rpr* – retroarticular process. Scale bar = 1 cm.



relative to the minimum shaft width (Fig. 4A–F; L=110.9; PW = 39.8; DW = 28.2). Its proximal end is trapezoidal in proximal view, with slightly concave and subparallel anterior and posterior margins and strongly concave medial and lateral margins. The proximal surface is convex posterolaterally and flattened anteromedially. In anterior view, the proximal end is distinctly skewed medially. There is a sharp ridge in the proximal half of the bone between the medial and posterior sides. On the medial side within the proximal concavity housing metacarpal I there is a distinct circular area possibly for a ligament attachment (Fig. 4F). This ligament scar suggests that the metacarpal I

Fig. 4. ZIN PH 8/117, left metacarpal II (A–F), and ZIN PH 9/117, left manual phalanx II-1 (G–L), of *Kileskus aristotocus* gen. et sp. nov., from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in proximal (A, G), distal (B, H), anterior (C, D), lateral (D, J), posterior (E, K), and medial (F, L) views.

Abbreviation: ls – ligament scar. Scale bar = 2 cm.

was closely appressed to the proximal part of metacarpal II. The attachment area for metacarpal I occupies less than one third of the shaft length of metacarpal II. On the lateral concavity at the proximal end there is no distinct facet for metacarpal III, and the two bones apparently contacted each other only at their bases. The shaft surface is striated proximally, especially on the posterior side, and smooth otherwise. The distal end of metacarpal II is asymmetrical, with the distal surface of the medial condyle about twice as large as that of lateral condyle. The distal articular surface lacks a groove between condyles. The medial condyle protrudes slightly farther distally than the lateral condyle. Both condyles are flared posteriorly. The lateral condyle is flared further posteriorly and is more gracile than the medial condyle. The pits for the collateral ligaments are quite deep and equally well developed on both condyles. The anterior surface of the shaft immediately proximal to the distal condyle is slightly concave and rugose but there is no distinct extensor pit.

Manual phalanx II-1. The phalanx ZIN PH 9/117 articulates well with metacarpal II and evidently is the left proximal phalanx of the second manual digit of the same specimen (Fig. 4G–L; L = 74.3; PW = 27.5; DW = 22.9). It is expanded proximally, with the proximal anteroposterior diameter only slightly larger than the mediolateral width. The proximal end is asymmetrical, with the medial articular surface about twice as large as and more concave than the lateral surface. The posterior side of the shaft is flattened whereas the anterior side is rounded. The distal end lacks a distinct groove between the condyles. It is about 1.3 times wider posteriorly than anteriorly. As on the metacarpal, the medial condyle protrudes slightly farther distally than the lateral condyle. Both condyles are also flared posteriorly. Again, the lateral flaring is somewhat more pronounced and more gracile. The collateral ligament pit is large and deep on the medial condyle and very shallow, and almost indistinct on the lateral condyle. On the anterior surface there is a deep short crescentic groove between the distal edges of both condyles.

Metatarsal I. ZIN PH 10/117 is a complete left metatarsal I or the distal portion of that bone if it comprised two separate parts as in some other theropods (Fig. 5; L = 46.6; DW = 14.7). The proximal end of this metatarsal is reduced and pointed, with the flattened lateral surface contacting metatarsal II. Its medial surface is broadly convex. The distal end

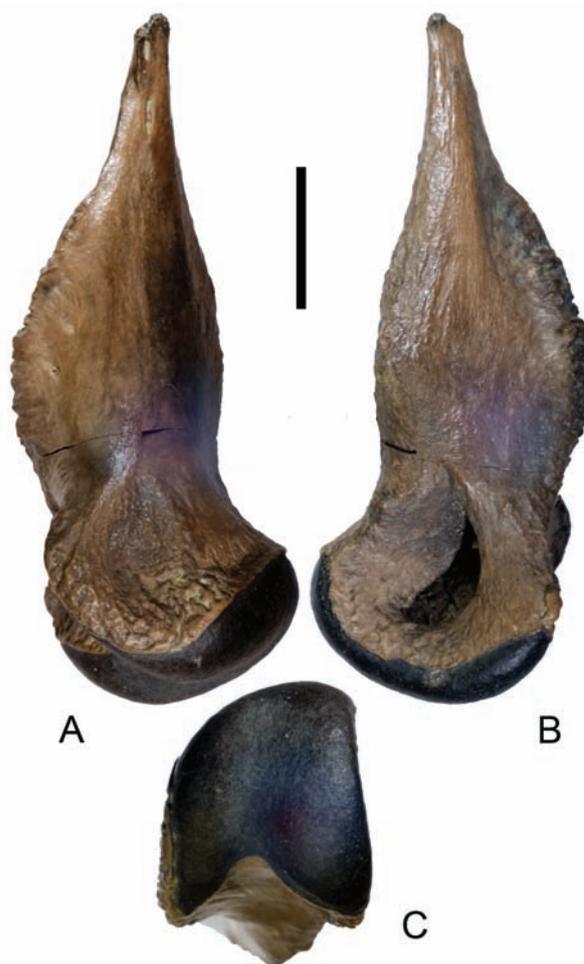


Fig. 5. ZIN PH 10/117, left metatarsal I of *Kileskus aristotocus* gen. et sp. nov., from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in medial (A), lateral (B), and distal (C) views. Scale bar = 1 cm.

is globular and slightly deflected medially from the shaft of the bone. A well developed distal articular surface suggests mobility for pedal digit I. The articular surface is subdivided posteriorly by an incision and a short shallow groove. The pit for the collateral ligament is large and deep on the lateral condyle but shallow on the medial condyle.

Metatarsal III. ZIN PH 11/117 is an almost complete left metatarsal III (Fig. 6; L = 219.0; PW = 15.5; DW = 25.6). The bone is gracile and long, with the proximal end expanded anteroposteriorly. The angle between the long axes of the proximal and distal ends of the metatarsal is $\sim 47^\circ$. The proximal end is hourglass-shaped in proximal view, with a re-



markably flat attachment area for the metatarsal II and a median concavity along the attachment area for metatarsal IV. Its proximal articular surface is depressed at the center. The anteroposterior diameter of the shaft suddenly decreases just distal to the proximal end and is more or less uniform through the rest of the shaft. The shaft is somewhat wider mediolaterally at the distal end compared with the proximal end. The distal half of the shaft is triangular in cross-section, with a flat anterior side and a pointed posterior margin. The distal end is slightly expanded mediolaterally relative to the shaft. It is subrectangular in distal view with a distal articular surface lacking a distinct groove between the condyles. The condyles are subdivided only along the posterior edge by a shallow incision. The pit for the collateral ligament is distinctly larger on the medial condyle than on the lateral condyle.

Pedal phalanges. ZIN PH 12/117 is possibly a left second phalanx of the second pedal digit (Fig. 7;

Fig. 6. ZIN PH 6/117, left metatarsal III of *Kilekus aristotocus* gen. et sp. nov., from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in anterior (A), lateral (B), posterior (C), medial (D), distal (E), and proximal (F) views. Scale bar = 3 cm.



Fig. 7. ZIN PH 12/117, possible left pedal phalanx II-2 of *Kileskus aristotocus* gen. et sp. nov., from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in proximal (A), distal (B), medial (C), anterior (D), lateral (E), and posterior (F) views. Scale bar = 1 cm.

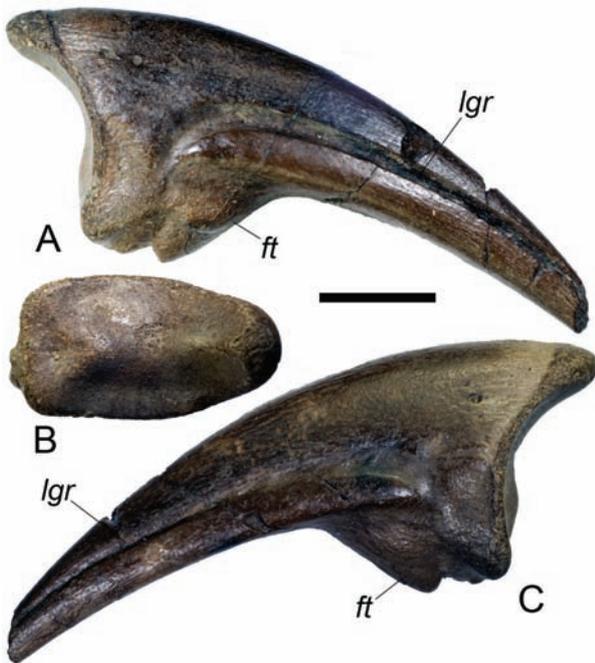


Fig. 8. ZIN PH 12/117, pedal unguinal phalanx of *Kileskus aristotocus* gen. et sp. nov., from Berezovsk Quarry, Krasnoyarsk Territory, Russia (Itat Formation, Middle Jurassic), in two side views (A, C) and in proximal view (B).

Abbreviations: *ft* – flexor tubercle; *lgr* – lateral groove. Scale bar = 1 cm.

L = 37.5; PW = 20.2; DW = 20.6). Its proximal end is expanded anteroposteriorly, with the slightly asymmetrical proximal articular surface divided by a prominent ridge into two roughly equal and deeply concave portions. The proximal articular surface is pointed anteriorly and flattened posteriorly. The shaft is short and stout. The distal articular surface is also slightly asymmetrical, with the surface of the lateral condyle extending further proximally than that of the medial condyle. The two condyles are separated by a distinct distal groove. The pit for the collateral ligament is deep on both sides, but somewhat larger laterally.

ZIN PH 13/117 is apparently a pedal unguinal phalanx (Fig. 8; PW = 13.1). It is almost perfectly symmetrical and could belong to the third pedal digit. Its proximal articular surface is broadly convex and subdivided by a ridge. It is separated from the rest of the bone by a distinct groove marking the proximal extension of the claw sheath. The phalanx is moderately curved, with distinct lateral grooves for the claw sheath. On the ventral side, close to the proximal end, there is a relatively small tubercle for insertion of a flexor tendon.

PHYLOGENETIC ANALYSIS

The phylogenetic interrelationships within Theropoda have been the subject of numerous cladistic analyses in recent years. For our purposes the most appropriate, comprehensive, and up-to-date character-taxon matrix is that published by Smith et al. (2007, 2008), because it includes multiple representatives of the major clades of basal theropods (“Coelophysoidea”, Abelisauroidea, Spinosauroidea, Allosauroidea, and Coelurosauria). We did not include the *Megaraptor*-like ulna from Australia described by Smith et al. (2008), which is not pertinent to our work, and the poorly known *Tugulusaurus* from the Early Cretaceous of China (Rauhut and Xu 2005). We included in the analysis two additional taxa, the Middle Jurassic *Proceratosaurus* and the Late Jurassic *Guanlong* (coding is based on information provided in Xu et al. 2006, 2009; Rauhut et al. 2010):

Proceratosaurus: 1(0), 3(2), 4(0), 5(0), 6(0), 7(0), 8(1), 9(0), 10(1), 13(0), 14(0), 15(0), 16(0), 17(0), 18(2), 19(1), 20(1), 21(0), 22(0), 23(1), 24(2), 25(1), 26(1), 27(1), 28(0), 29(1), 30(0), 31(1), 32(1), 34(1), 35(1), 36(0), 37(0), 40(1), 42(1), 43(0), 46(2), 47(1), 49(0), 50(0), 51(1), 59(0), 60(1), 69(0), 71(0), 72(1),

73(1), 81(1), 82(2), 83(1), 84(0), 85(0), 86(0), 87(0), 88(0), 89(0), 98(0), 99(0), 100(0), 101(0), 102(0), 103(0), 104(2), 114(1), 118(2), 121(0), 124(0), 125(0), 126(0), 127(0), 128(0), 129(1), 132(1), 137(0), 138(1), 139(1), and 140(1);

Guanlong: 1(0), 2(0), 3(2), 4(0), 5(0), 6(0), 7(0), 8(1), 9(0), 10(1), 14(0), 15(0), 16(0), 17(0), 18(2), 19(1), 20(1), 21(0), 22(0), 23(1), 24(2), 25(1), 26(1), 27(1), 28(0)*, 29(1), 30(0), 32(1), 35(0), 36(0), 38(1), 40(1), 42(1), 43(0), 44(0), 45(0), 46(2), 47(1), 50(0), 51(1), 52(0), 53(0), 54(1), 55(0), 56(1), 57(0), 58(0), 59(0), 60(1), 61(2), 64(1), 65(0), 67(0), 68(0), 69(0), 70(0), 71(0), 72(1), 73(1), 75(-), 76(0), 77(0), 78(0), 79(0), 80(0), 81(1), 82(2), 83(1), 84(1), 85(0), 86(0), 87(1), 90(0), 91(1), 99(0), 100(0), 101(0), 102(0), 103(0), 118(3), 121(0), 122(1), 123(0), 124(0), 125(0), 126(0), 127(0), 128(0), 129(1), 132(1), 136(1), 137(1), 139(1), 140(1), 147(1), 148(1), 149(1), 151(0), 156(1), 159(1), 170(1), 175(1), 176(0), 179(1), 182(2), 187(0), 191(1), 193(0), 194(1), 195(0), 197(1), 198(0), 199(1), 201(1), 202(1), 212(1), 213(0), 214(0), 215(0), 217(1), 218(0), 219(0), 220(0), 221(0), 222(0), 223(0), 227(1), 229(0), 233(0), 234(1), 235(0), 236(1), 237(1), 238(0)*, 239(1), 240(1), 241(0), 242(1), 243(1), 244(1), 245(0), 246(0), 247(0)*, 248(0), 249(0), 250(0), 251(0), 252(0), 253(1), 254(1), 255(1), 256(0), 257(1), 259(0), 260(0), 261(0), 262(0), 265(1), 266(1), 267(0), 276(0), 277(0), 280(1), 281(1), 283(0), 284(0), 286(0), 287(0), 288(0), 289(0), 290(0), 292(0), 293(1), 296(1), 297(2), 298(1), 300(0), 301(0), 302(1), 305(1), 307(1), 308(2), 310(1), 311(2), 316(1), 317(0), 319(1), 320(1), 321(2), 322(1), 324(1), 325(1), 327(0), 328(2), 329(0), 330(0), 331(1), 332(0), 333(1), 342(1), 343(2), 345(0), and 347(0) (asterisk denotes coding different from that in Xu et al., 2006).

The data set modified as described above consists of 58 taxa scored for 353 characters. *Kileskus* gen. nov. could be scored by 46 characters from this data set (13.0%). The scored character states are listed and briefly discussed below.

Character 3(2): Tooth row completely antorbital, ends anterior to the vertical strut of the lacrimal. This character state is inferred from the holotype maxilla, where the tooth row terminates well anterior to the lacrimal facet. This state is a tetanuran synapomorphy under ACCTRAN optimization.

Character 5(0): Height/length ratio of premaxilla below external naris 0.5 – 1.25. The reversal to this

primitive state is an unambiguous synapomorphy for Tetanurae. Among this group, the more derived condition is characteristic for Tyrannosauridae.

Character 6(0): Premaxillary body in front of external nares shorter than body below the nares and angle between anterior margin and alveolar margin more than 75°. The derived condition is characteristic for some coelophysoids and the Spinosauroida.

Character 7(0): Ventral process at the posterior end of premaxillary body absent. The derived condition is developed in parallel in *Sinraptor*, *Compsognathus*, and some coelophysoids.

Character 8(1): Four premaxillary teeth. This state is characteristic for the majority of theropods except for some aberrant taxa.

Character 9(0): Premaxillary tooth row ends ventral to naris. In Spinosauridae, *Acrocanthosaurus*, and some coelophysoids it ends anterior to the naris.

Character 10(1): Subnarial process of the premaxilla strongly reduced in width, but still contacting the nasals. This is unambiguous synapomorphy for Allosauroida + Coelurosauria.

Character 11(0): Maxillary/palatal process of premaxilla large flange. An opposite state (the process is a blunt triangle) is characteristic for some ceratosaurs.

Character 12(1): Foramen on the medial side of the premaxillary body, below the narial margin present. This is an unambiguous synapomorphy for Theropoda.

Character 13(0): Slot-shaped foramen on the lateral face of the premaxilla, located at the base of the nasal process absent. This foramen is present in some coelophysoids.

Character 17(0): Serrations on premaxillary teeth present. The serrations are absent on premaxillary teeth in some derived coelurosaurs.

Character 18(2): Premaxillary teeth D-shaped in cross-section. This derived state is present in tyrannosauroids and *Ornitholestes*. A coelurosaur synapomorphy according to Norell et al. (2001: character 93[1]).

Character 19(1): Premaxillary teeth labiolingually asymmetrical. This state is characteristic for some coelophysoids, ceratosaurs and all tetanurans, except *Torvosaurus* and spinosaurids.

Character 20(1): Rostroventral narial fossa expanded, well-developed on the premaxilla in the rostroventral corner of the naris. This character is sporadically distributed among Theropoda and was

identified as phylogenetically uninformative by Winclada.

Character 21(0): Constriction between articulated premaxillae and maxillae absent. An alternative condition is found in some coelophysoids and in Spinosauridae.

Character 22(0): Premaxilla and maxilla in contact at alveolar margins. The alveolar margins of these bones are not in contact in *Eoraptor* and some 'coelophysoids'.

Character 24(0): Ascending process of the maxilla confluent with anterior rim of maxillary body and gently sloping posterodorsally. There is a complex pattern of distribution of the three states of this character on the cladogram. In derived ceratosaurs the ascending process is offset from anterior rim of maxillary body, with anterior projection of maxillary body shorter than high. It is also offset in basal tetanurans, but there the anterior projection of maxillary body is as long as high or longer. This structure of maxilla, with a long rostral ramus and a concavity between the rostral and dorsal rami is sometimes considered a synapomorphy for Tetanurae (Holtz 1998; Holtz et al. 2004). The Coelurosauria are characterized by reversal to the primitive state of this character. The plesiomorphic state is also present in the some carcharodontosaurids.

Character 25(1): Maxillary antorbital fossa shallow, margins formed by low ridges, a sharp rim may be present only in front of the promaxillary foramen. This is an unambiguous synapomorphy for Theropoda that is reversed in Spinosauridae.

Character 26(1): Maxillary antorbital fossa in front of the internal antorbital fenestra more than 40 percent of the length of the external antorbital fenestra. Although the full extent of the external antorbital fenestra is not known for *Kileskus* gen. nov., it is coded as the derived state by comparison with similarly coded taxa such as *Ornitholestes* (Carpenter et al. 2005), which has the antorbital fossa similarly extended anteriorly. This is an unambiguous synapomorphy for Coelurosauria according to the present analysis and the analysis by Holtz (1998: character 15.1). This character is the only unambiguous synapomorphy for Coelurosauria in the analysis by Rauhut (2003: character 14[1]). We changed the coding of this character to the derived state for *Dilong*, *Sinornithomimus*, and *Deinonychus*. In *Dilong* the anterior extension of antorbital fossa looks relatively small on the skull reconstruction, but on the photograph of the specimen it is more than 50%

of the length of the external antorbital fenestra (Xu et al. 2004: fig. 1a, b). It is also large in *Sinornithomimus* (Kobayashi and Lü 2003) and in dromaeosaurids including *Deinonychus* (Norell and Makovicky 2004). In non-coelurosaurian theropods the antorbital fossa has a distinctly shorter anterior extension.

Character 27(1): Depth of the ventral antorbital fossa much greater than the depth of the maxilla below the ventral margin of the antorbital fossa. This character is a synapomorphy for Proceratosauridae fam. nov. It was independently developed in some coelophysoids, whereas the majority of tetanurans have the opposite condition, with the ventral antorbital fossa less than or subequal to the depth of the maxilla below the ventral margin of the antorbital fossa.

Character 28(0): Horizontal ridge on the maxilla absent. The ridge is present in *Eoraptor* and some coelophysoids.

Character 29(1): Maxillary fenestra present. This is an unambiguous synapomorphy for the clade Allosauroidae + Coelurosauria + *Monolophosaurus*. We corrected the coding for *Afrovenator*, *Dubreillosaurus*, *Sinornithomimus*, and *Monolophosaurus* as having maxillary fenestra based on the original descriptions of these taxa (Sereno et al. 1994; Zhao and Currie 1994; Allain 2002; Kobayashi and Lü 2003).

Character 30(0): Maxillary fenestra situated at anterior border of antorbital fossa. In Maniraptora (*Ornitholestes*, Dromaeosauridae, and Aves) it is situated posterior to anterior border of fossa. The derived state is also considered a maniraptoran synapomorphy by Norell et al. (2001: character 6[1]).

Character 31(1): Pneumatic excavation/antrum in maxillary anterior ramus present. This is an unambiguous synapomorphy for Tetanurae.

Character 32(1): Promaxillary fenestra present. This fenestra is present in derived ceratosaurs and Tetanurae.

Character 33(0): Palatal process of maxilla ridged flange. A more derived condition (reduced, simple process or long, and plate-shaped process) is found in some ceratosaurs and Spinosauridae.

Character 34(1): Secondary palate formed premaxilla, maxilla, and vomer. This derived state was acquired in parallel by Spinosauridae and Coelurosauria. This character was also found to be a synapomorphy for Coelurosauria by Norell et al. (2001: character 31[1]) and Makovicky et al. (2005: character 25[1]).

Character 35(0): Maxillary tooth count 12 – 18 (17 in *Kileskus* gen. nov.). This state is characteristic

for the majority of Theropoda. A lower or higher tooth count is found in some Ceratosauria, Spinosauridae, and in *Proceratosaurus* (22 tooth positions in the latter taxon; Rauhut et al., 2010).

Character 36(0): Maxillary and dentary teeth serrated (for *Kileskus* gen. nov. known only for maxillary teeth). Also a condition found in the majority of theropods. Unserrated teeth are found in Spinosauridae and some derived coelurosaurs.

Character 37(0): Medial surface of paracanthals plates smooth. Striated interdental tooth plates are characteristic for derived abelisaurids.

Character 39(0): Dorsal rim of antorbital fossa below nasal suture, or formed by this suture. The antorbital fossa is extending onto the lateroventral side of the nasals in “Dilophosauridae,” *Monolophosaurus*, and Allosauroidea. The family group name “Dilophosauridae” appeared as a nomen nudum in Charig and Milner, 1990; here it is used for the clade including *Dilophosaurus*, *Dracovenator*, and *Cryolophosaurus*.

Character 133(1): Horizontal shelf on the lateral surface of the surangular rostroventral to the mandibular condyle prominent and extending laterally. This morphology is characteristic for the majority of theropods, with a “reversal” to the alternate state (ridge absent or faint) in some derived coelurosaurs.

Character 134(0): Laterally inclined flange along dorsal edge of surangular for articulation with lateral process of lateral quadrate condyle absent. This flange is present in Ornithomimidae.

Character 135(0): No lateral groove along posterior end of surangular, just dorsal to articulation with posterior splint of angular. This groove is present in some members of “Dilophosauridae.”

Character 136(1): Well-developed anterior wall to lateral glenoid on surangular, resulting in a lateral glenoid fossa that is at least weakly U-shaped in lateral aspect. This condition is characteristic for some coelophysoids, ceratosaurs and all Tetanurae except Dromaeosauridae and Aves.

Character 236(1): Metacarpal I closely appressed to proximal half of metacarpal II. The condition for *Kileskus* gen. nov. is inferred from the attachment facet for metacarpal I on metacarpal II. This is a tetanuran synapomorphy under ACCTRAN optimization.

Character 238(0): Medial side of metacarpal II expanded proximally. It is unexpanded in derived coelurosaurs. We corrected coding of this character for *Tyrannosaurus*, in which metacarpal II is clearly expanded proximally in medial view (Brochu 2003).

Character 243(1): Extensor pits on the dorsal surface of the distal end of metacarpals absent or poorly developed. This is an unambiguous synapomorphy for Coelurosauria.

Character 330(0): Metatarsals not co-ossified. Proximally co-ossified metatarsals are found in some coelophysids and in birds.

Character 331(1): Metatarsal I does not contact the ankle joint.

Character 332(1): Metatarsal I length < 50% metatarsal II length. This and the previous character state are unambiguous synapomorphies for Theropoda.

Character 335(1): Outline of proximal articular surface of metatarsal III hourglass-shaped. This is an unambiguous synapomorphy for Tetanurae.

Character 336(0): Proximal end of metatarsal III backing ventral sides of metatarsals II and IV, resulting in a “T”-shaped proximal profile: no. The derived condition (“antarctometatarsus”) is characteristic for some ceratosaurs.

Character 337(0): Proximal end of metatarsal III not ventrally enlarged. The derived condition is found in Coelophysidae.

Character 338(0): Distal end of metatarsal III smooth, not ginglymoid. The ginglymoid distal articulation of the metatarsal III is characteristic for Dromaeosauridae and Aves.

Character 344(0): Vascular grooves on pedal unguals single. Double vascular grooves are a synapomorphy for Abelisauridae.

The dataset modified as described above was analyzed using Winclada version 1.00.08 (Nixon 1999). Six characters were found to be phylogenetically uninformative (characters 20, 130, 209, 210, 316, and 350). They were deactivated for further analyses. We ran two analyses. In both analyses all characters were equally weighted and treated as unordered. The first analysis was performed using PAUP* version 4.0b10 (Swofford 2002). A heuristic search was performed with 10,000 random addition sequence replicates. Tree bisection and reconnection (TBR) was utilized as the branch-swapping algorithm for the heuristic search. This analysis produced 2,050 most parsimonious trees, each with a length of 874 steps with a consistency index of 0.47 and a retention index of 0.77. The second analysis was performed using NONA version 2.0 (Goloboff 1999) run with Winclada version 1.00.08 interface (Nixon 1999). One thousand repetitions of the parsimony ratchet (island hopper) algorithm produced 100 most

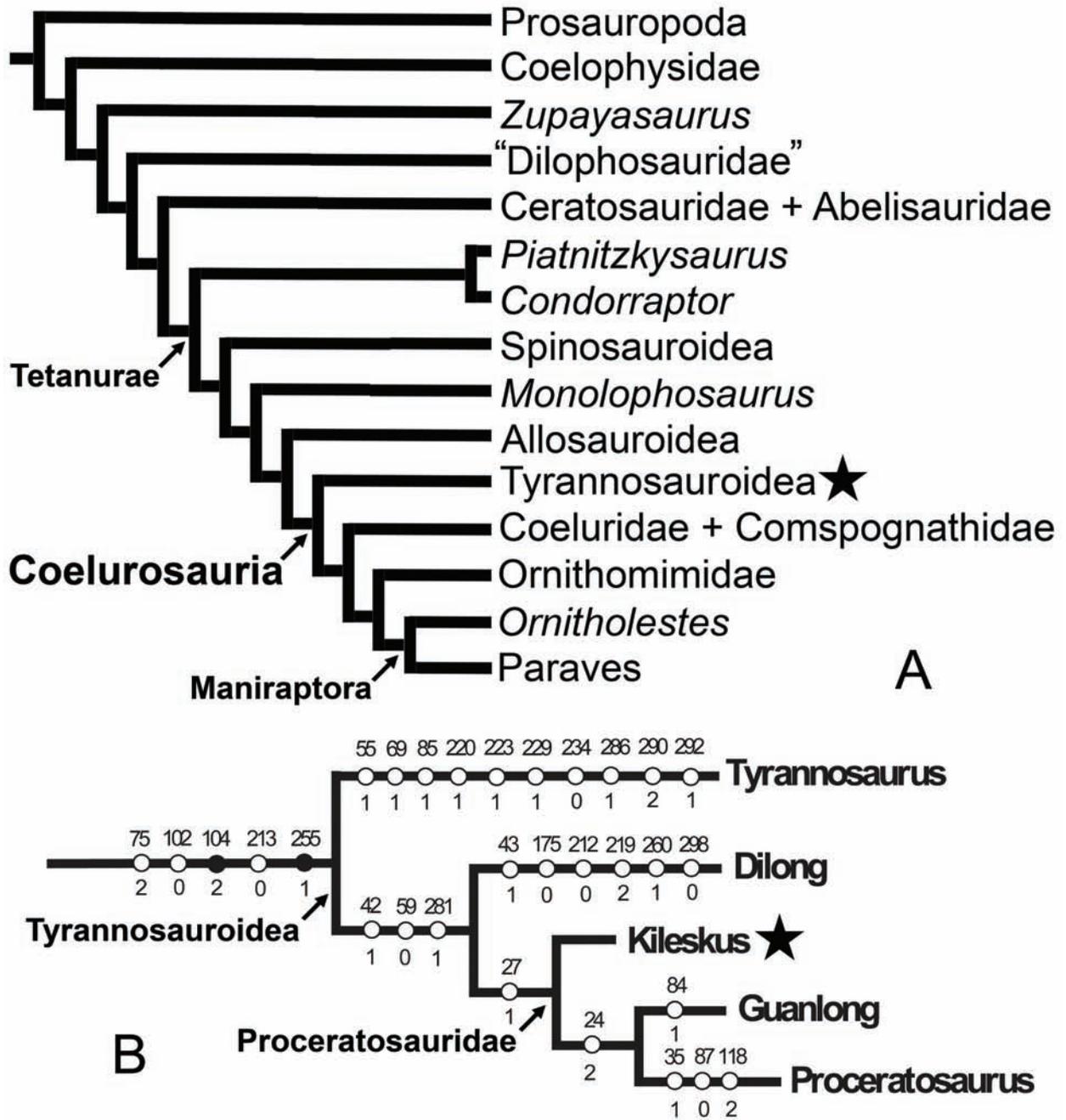


Fig. 9. Strict consensus tree produced by PAUP* version 4.0b10 and NONA 2.0 used a modified dataset by Smith et al. (2008) in simplified form, with some terminal taxa combined into the respective clades and part of cladogram basal to Prosauropoda omitted (A) and a more detailed fragment of this tree including Tyrannosauroidae (B). Position of *Kileskus* gen. nov. is highlighted by an asterisk in A and B. In B only unambiguously optimized characters are shown (black circles are nonhomoplasies and white circles are homoplasies). The numbers at the circles are characters (above) and states (below).

parsimonious trees each with a length of 879 steps with a consistency index of 0.47 and a retention index of 0.76. The strict consensus tree is identical in both analyses (Fig. 9). On this tree *Kileskus* gen. nov. is clustered together with *Proceratosaurus* and *Guanlong* in Proceratosauridae fam. nov. within the Tyrannosauroidae. *Dilong* from the Early Cretaceous of China (Xu et al. 2004) is the sister taxon to the Proceratosauridae fam. nov.

DISCUSSION

Kileskus gen. nov. from the Bathonian (Middle Jurassic) of Siberia is one of the oldest known members of Coelurosauria and Tyrannosauroidae. It is quite similar to the Bathonian *Proceratosaurus* from England (Rauhut et al. 2010 confusingly indicated both Bathonian and Callovian ages for this taxon). It is less derived compared with the contemporaneous *Proceratosaurus* and a somewhat younger *Guanlong* from the beginning of the Late Jurassic (Oxfordian; Xu et al. 2006). This may indicate Asiatic origin for the Proceratosauridae. The oldest currently known coelurosaur could be the problematic *Eshanosaurus*, known from a single dentary from the Early Jurassic of China (Zhao and Xu 1998; Xu et al. 2001; Barrett 2009).

ACKNOWLEDGEMENTS

We are grateful to S.B. Turko (Krasnoyarsk Regional Museum) for assistance during excavation. Support for our work was provided by the general director of OAO SUEK Krasnoyarsk A.V. Federov and by the chief manager of the Berezovsk Quarry M.V. Palshin. We thank D.V. Grigor'ev (Saint Petersburg State University) for photographing the specimens. We are grateful to N.D. Smith (Field Museum of Natural History, Chicago) for providing the NEXUS matrix file from Smith et al. (2008). We thank N.D. Smith and H.-D. Sues (National Museum of Natural History, Smithsonian Institution, Washington) for reviewing the paper and linguistic corrections.

REFERENCES

Alifanov V.R., Krasnolutskii S.A., Markov V.N. and Martynovich N.V. 2001. About discovery of the Middle Jurassic dinosaurs in the Krasnoyarsk Territory. Scientific-Practical Conference "Problems of the Struggle Against Illegal Excavations and Illegal Turnover of the Objects of Archaeology, Mineralogy, and Paleontology". Krasnoyarsk: 71–74. [In Russian]

- Allain R. 2002.** Discovery of megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal tetanurae. *Journal of Vertebrate Paleontology*, **22**(3): 548–563.
- Averianov A.O. and Krasnolutskii S.A. 2009.** Stegosaur remains from the Middle Jurassic of West Siberia. *Proceedings of the Zoological Institute RAS*, **313**: 59–73.
- Averianov A.O. and Lopatin A.V. 2006.** *Itatodon tatarinovi* (Tegotheriidae, Mammalia), a docodont from the Middle Jurassic of Western Siberia and phylogenetic analysis of Docodonta. *Paleontological Journal*, **40**: 668–677.
- Averianov A.O., Lopatin A.V., Skutschas P.P., Martynovich N.V., Leshchinskiy S.V., Rezvyi A.S., Krasnolutskii S.A. and Fayngerts A.V. 2005.** Discovery of Middle Jurassic Mammals from Siberia. *Acta Palaeontologica Polonica*, **50**: 789–797.
- Averianov A.O., Lopatin A.V. and Krasnolutskii S.A. 2008.** An amphilestid grade eutriconodontan from the Middle Jurassic of Russia. *Russian Journal of Theriology*, **7**: 1–4.
- Barrett P.M. 2009.** The affinities of the enigmatic dinosaur *Eshanosaurus deguchiianus* from the Early Jurassic of Yunnan Province, People's Republic of China. *Palaeontology*, **52**: 681–688.
- Brochu C.A. 2003.** Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis. *Society of Vertebrate Paleontology Memoir*, **7**: 1–138.
- Carpenter K., Miles C.A., Ostrom J.H. and Cloward K.C. 2005.** Redescription of the small maniraptoran theropods *Ornitholestes* and *Coelurus* from the Upper Jurassic Morrison Formation of Wyoming. In: K. Carpenter (Ed.). *The Carnivorous Dinosaurs*. Indiana University Press, Bloomington and Indianapolis: 49–71.
- Charig A.J. and Milner A.C. 1990.** The systematic position of *Baryonyx walkeri*, in the light of Gauthier's reclassification of the Theropoda. In: K. Carpenter and P.J. Currie (Eds.). *Dinosaur Systematics. Approaches and Perspectives*. Cambridge University Press, Cambridge, New York, Port Chester, Melbourne, Sydney: 127–140.
- Goloboff P. 1999.** NONA (ver. 1.9). Software published by the author, S.M. de Tucuman, Argentina. Available on-line at www.cladistics.org.
- Holtz T.R., Jr. 1998.** A new phylogeny of the carnivorous dinosaurs. *Gaia*, **15**: 5–61.
- Holtz T.R., Jr., Molnar R.E. and Currie P.J. 2004.** Basal Tetanurae. In: D.B. Weishampel, P. Dodson and H. Osmólska (Eds.). *The Dinosauria*. Second Edition. University of California Press, Berkeley, Los Angeles, London: 71–110.
- Kobayashi Y. and Lü J.-C. 2003.** A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica Polonica*, **48**: 235–259.

- Lopatin A.V. and Averianov A.O. 2005.** A new docodont (Docodonta, Mammalia) from the Middle Jurassic of Siberia. *Doklady Biological Sciences*, **405**: 434–436.
- Lopatin A.V. and Averianov A.O. 2006.** Mesozoic mammals of Russia. In: P.M. Barrett and S. E. Evans (Eds.). 9th International Symposium on Mesozoic Terrestrial Ecosystems and Biota. Abstracts and Proceedings Volume. Manchester: 67–70.
- Lopatin A.V. and Averianov A.O. 2007.** The earliest Asiatic pretribosphenic mammal (Cladotheria, Amphitheriidae) from the Middle Jurassic of Siberia. *Doklady Biological Sciences*, **417**: 432–434.
- Lopatin A.V. and Averianov A.O. 2009.** Mammals that coexisted with dinosaurs. Finds on Russian territory. *Herald of the Russian Academy of Sciences*, **79**: 268–273.
- Makovicky P.J., Apesteguia S. and Agnolin F.L. 2005.** The earliest dromaeosaurid theropod from South America. *Nature*, **437**: 1007–1011.
- Nixon K.C. 1999.** Winclada (Beta) version 0.9.9. Software published by the author, Ithaca, NY. Available on-line at www.cladistics.org.
- Norell M.A., Clark J.M. and Makovicky P.J. 2001.** Phylogenetic relationships among coelurosaurian theropods. In: J.A. Gauthier and L.E. Gall (Eds.). *New Perspectives on the origin and early evolution of Birds*, Proceedings of the International Symposium in Honor of John H. Ostrom. Yale Peabody Museum: 49–67.
- Norell M.A. and Makovicky P.J. 2004.** Dromaeosauridae. In: D.B. Weishampel, P. Dodson and H. Osmólska (Eds.). *The Dinosauria*. Second Edition. University of California Press, Berkeley, Los Angeles, London: 196–209.
- Rauhut O.W.M. 2003.** The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology*, **69**: 1–216.
- Rauhut O.W.M. and Xu X. 2005.** The small theropod dinosaurs *Tugulusaurus* and *Phaedrolosaurus* from the Early Cretaceous of Xinjiang, China. *Journal of Vertebrate Paleontology*, **25**: 107–118.
- Rauhut O.W.M., Milner A.C., Moore-Fay S. 2010.** Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society*, **158**: 155–195.
- Sereno P.C., Wilson J.A., Larsson H.C.E., Dutheil D.B. and Sues H.-D. 1994.** Early Cretaceous Dinosaurs from the Sahara. *Science*, **266**: 267–271.
- Skutschas P.P. 2006.** Mesozoic amphibians from Siberia, Russia. In: P.M. Barrett and S.E. Evans (Eds.). 9th International Symposium on Mesozoic Terrestrial Ecosystems and Biota. Abstracts and Proceedings Volume. Manchester: 123–126.
- Skutschas P.P., Leshchinskiy S.V., Rezvyi A.S., Fayngerts A.V. and Krasnolutskii S.A. 2005.** Remains of salamanders from the Middle Jurassic of the Krasnoyarsk Territory. In: A.Yu. Rozanov, A.V. Lopatin and P.Yu. Parkhaev (Eds.). *Modern Paleontology: Classical and Newest Methods*. Paleontological Institute RAS, Moscow: 121–124. [In Russian]
- Smith N.D., Makovicky P.J., Hammer W.R. and Currie P.J. 2007.** Osteology of *Cryolophosaurus ellioti* (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. *Zoological Journal of the Linnean Society*, **151**: 377–421.
- Smith N.D., Makovicky P.J., Agnolin F.L., Ezcurra M.D., Pais D.F. and Salisbury S.W. 2008.** A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the Mid-Cretaceous. *Proceedings of the Royal Society B: Biological Sciences*, **275**: 2085–2093.
- Swofford D.L. 2002.** PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0. Sunderland, Sinauer Associates.
- Witmer L.M. 1997.** The evolution of the antorbital cavity of archosaurs: A study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Society of Vertebrate Paleontology Memoir*, **3**: 1–73.
- Xu X., Zhao X.-J. and Clark J.M. 2001.** A new therizinosaur from the Lower Jurassic Lower Lufeng Formation of Yunnan, China. *Journal of Vertebrate Paleontology*, **21**: 477–483.
- Xu X., Norell M.A., Kuang X.-W., Wang X.-L., Zhao Q. and Jia C. 2004.** Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature*, **431**: 680–684.
- Xu X., Clark J.M., Forster C.A., Norell M.A., Erickson G.M., Eberth D.A., Jia C. and Zhao Q. 2006.** A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature*, **439**: 715–718.
- Xu X., Clark J.M., Mo J., Choiniere J., Forster C.A., Erickson G.M., Hone D.W.E., Sullivan C., Eberth D.A., Nesbitt S.J., Zhao Q., Hernandez R., Jia C., Han F. and Guo Y. 2009.** A Jurassic ceratosaur from China helps clarify avian digital homologies. *Nature*, **459**: 940–944.
- Zhao X.-J. and Currie P.J. 1994.** A large crested theropod from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**: 2027–2036.
- Zhao X.-J. and Xu X. 1998.** The oldest coelurosaurian. *Nature*, **394**: 234–235.

Submitted November 5, 2009; accepted January 12, 2010.