

Karpinskiosaurus ultimus (Seymouriamorpha, Parareptilia) from the Upper Permian of European Russia

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Abstract—The genus *Raphanodon* Ivachnenko, 1987 (Leptorophidae, Seymouriamorpha) is not a valid taxon, since its type species *Nycteroleter ultimus* Tchudinov et Vjuschkov, 1956 is assigned to the genus *Karpinskiosaurus*. The cranial anatomy of *K. ultimus* is described in the present paper with newly collected material from the Babintsevo locality. The genus *Karpinskiosaurus* is assigned to the subfamily Karpinskiosaurinae, which is affiliated to the Lower Permian Discosauriscinae (*Discosauriscus* and *Ariekanerpeton*) to form the family Karpinskiosauridae.

INTRODUCTION

In 1956, Tchudinov and Vjuschkov described a new species of the genus *Nycteroleter*, *N. ultimus* based on jaw material from the Pron'kino locality (Orenburg Region) (Tchudinov and Vjuschkov, 1956). Later, Ivachnenko separated this form from the nycteroleters and placed it in the family Leptorophidae (Seymouriamorpha, Parareptilia) under a new name, *Raphanodon*. This paper included reconstructions of the skull roof and palatal complex of *R. ultimus*. However, these were only based on the material from the Babintsevo locality, which yielded several incomplete skulls together with the jaws morphologically similar to those previously known from the Pron'kino locality (Ivachnenko, 1987).

Revision of the material demonstrated that a part of specimens from Babintsevo referred to as *R. ultimus* and all of the jaw material from Pron'kino, including the holotype *Nycteroleter* (= *Raphanodon*) *ultimus*, belong to the genus *Karpinskiosaurus*. This is supported by the presence of such peculiar features of the genus *Karpinskiosaurus* as numerous jaw teeth, deep otic notches, the retention of premaxillary fontanels, the pitted nature of dermal ornament, and a number of other characters. This assemblage of features strongly distinguishes this form from the other *Raphanodon* species, *R. tverdochlebovae*, described on the basis of cranial material from the Donguz-6 locality (Ivachnenko, 1987). As far as *Nycteroleter ultimus* being a type species of the genus *Raphanodon*, the latter cannot be regarded as a valid taxon. The new generic name *Raphaniscus* for the form from the Donguz-6 locality was established earlier (Bulanov, 2000).

A significant part of the collection from Babintsevo actually belongs to a seymouriamorph that is morphologically close to *Raphaniscus tverdochlebovae* and obviously belongs to the same genus. Information on

the skull structure of this form will be published in the future.

The genus *Karpinskiosaurus* was established by Sushkin (1925) based on two specimens (an incomplete skeleton and a skull) described by Amalitsky (1921) as *Kotlassia secunda* from the excavations at the Malaya Severnaya Dvina River (Sokolki locality). Sushkin ranked this genus as a new family, Karpinskiosauridae, based on its distinctions from *Kotlassia* proper (*Kotlassia prima*) such as a different number of presacral and sacral vertebrae, the shape of the neural processes, and the relative depth of the otic notches.

Later, Sushkin (1926, p. 339) mentioned another species of *Karpinskiosaurus*, *K. neglectus*, which was established on the basis of a skull from the same locality. This skull differs from that of *K. secundus* by slightly different proportions, the shape of postparietals (dermosupraoccipitals), and by the pattern of the dermal ornament. Unfortunately, there were no figure image, complete description, and collection number of the specimen in this paper; thus, this specimen is unidentifiable. Currently, only one skull of *Karpinskiosaurus*, belonging to holotype *K. secundus* from the Sokolki locality, is housed at the Paleontological Institute of the Russian Academy of Sciences (PIN). The specimen named *K. neglectus* is probably presented in the paper by Watson (1954, text-figs. 31 and 32); however, schematic sketches do not make possible the establishment of distinctions between the two species of *Karpinskiosaurus*, including the characters mentioned by Sushkin. Thus, the validity of *K. neglectus* as a separate species remains doubtful.

Bystrow (1944) regarded *Karpinskiosaurus* specimens as juveniles of *Kotlassia prima* and presented mixed description of both forms. Later, his reconstructions combining the characters of *Kotlassia* and *Karpinskiosaurus* were used by the majority of authors

who developed seymouriamorph systematics. Only Watson (1954), who owned one of *Karpinskiosaurus* skulls (*K. neglectus?*), insisted on the taxonomic autonomy of this genus (Watson, 1954).

The genus *Karpinskiosaurus* was only recently introduced anew in the seymouriamorph systematics as a valid taxon (Ivakhnenko, 1987; Ivakhnenko *et al.*, 1997); however, it was placed in the same family as *Kotlassia*. The latter appeared to have much in common with *Raphaniscus* in skull structure (the depth of the otic notches, the presence of well-developed postchoanal rows of large palatine teeth, the shape and pattern of parasphenoid dentition, the form and size of the squamosal, etc.). In this connection, it is appropriate to regard this genus as a leptorophid, placing it in a separate subfamily together with *Raphaniscus*.

The description of *Karpinskiosaurus ultimus* using new material from the Babintsevo locality collected by the author during the 1997–1998 field seasons is presented below.

SYSTEMATIC PALEONTOLOGY

Family Karpinskiosauridae Sushkin, 1925

Subfamily Karpinskiosaurinae Sushkin, 1925

Karpinskiosauridae: Sushkin, 1925, p. 179; Ivakhnenko *et al.*, 1997, p. 15.

Type genus. *Karpinskiosaurus* Sushkin, 1925.

Diagnosis. Skull of adults more than 70 mm long. Canals of seismosensory system absent and endocranium well ossified in adults. Dorsal processes of premaxillae high; fontanel between them retained. Base of jaw teeth elongated and slightly folded. Postorbital region of jugal enlarged. Cellular surface sculpturing rapidly formed in ontogeny.

Comparison. The subfamily Karpinskiosaurinae differs from the Discosauriscinae by its larger size, the absence of the seismosensory grooves at the late developmental stages, well-ossified endocranium in adults, longer dorsal processes of the premaxillae, the retention of a fontanel between them, the elongation and slightly folded pattern of the jaw tooth bases, the larger extension of the postorbital division of the jugals, and a rapid formation of cellular ornament in the course of ontogeny.

Genus *Karpinskiosaurus* Sushkin, 1925

Kotlassia: Amalitzky, 1921, p. 1 (partim); Efremov, 1940, p. 379 (partim); Bystrow, 1944, p. 380 (partim); Efremov and Vjuschkov, 1955, p. 18 (partim); Konzjukova, 1964, p. 141 (partim); Tatarinov, 1972, p. 71 (partim); Tverdokhlebova and Ivakhnenko, 1994, p. 124; Ivakhnenko *et al.*, 1997, p. 15.

Karpinskiosaurus: Sushkin, 1925, p. 179; 1926, p. 339; Watson, 1954, p. 407; Kalandadze *et al.*, 1968, p. 81 (partim); Ivakhnenko, 1987, p. 33; Ivakhnenko *et al.*, 1997, p. 15.

Nycteroleter: Tchudinov and Vjuschkov, 1956, p. 547; Kalandadze *et al.*, 1968, p. 81 (partim).

Raphanodon: Ivakhnenko, 1987, p. 41 (partim); Ivakhnenko *et al.*, 1997, p. 15 (partim).

Type species. *Kotlassia secunda* Amalitzky, 1921; Upper Permian, Upper Tatarian Substage, Vyatkian Regional Stage, *Scutosaurus karpinskii* Zone; Russia, Arkhangelsk Region, Kotlas District, Sokolki locality.

Diagnosis. The genus forms monotypical subfamily.

Species composition. The genus includes two species: *K. ultimus* (Tchudinov and Vjuschkov, 1956) and *K. secundus* (Amalitzky, 1921); Upper Permian, Upper Tatarian Substage, North Dvinian and Vyatkian Regional stages; European Russia, Orenburg, Arkhangelsk and Vladimir regions.

Karpinskiosaurus ultimus (Tchudinov et Vjuschkov, 1956)

Nycteroleter ultimus: Tchudinov and Vjuschkov, 1956, p. 547; Kalandadze *et al.*, 1968, p. 81.

Raphanodon ultimus: Ivakhnenko, 1987, p. 41 (partim); Ivakhnenko *et al.*, 1997, p. 15 (partim).

Holotype. PIN, no. 521/104, dentary; Orenburg Region, Sorochinsk District, Pron'kino locality; Upper Permian, Upper Tatarian Substage, Vyatkian Regional Stage, Sarma Formation.

Diagnosis. Intertemporal large and elongated. Ascending lamina of maxilla not developed. The marginal tooth apices only slightly curved lingually.

Description (Figs. 1–5). The skulls studied range from 15 mm to 40 mm of length. In the specimens of *K. ultimus*, at the stage of the 30- to 40-mm-long skull (specimens PIN, no. 4617/158; SGU, nos. 104V/2008 and 104V/2009), the orbits are displaced slightly anteriorly (Figs. 1a, 1b, 2a, and 2b). The parietals are small; a tiny rounded pineal foramen is located anterior to the ossification centers of these bones, close to the suture with the frontals. The frontals are narrow; their length is approximately equal to the orbital length; the nasals are of the same width but slightly shorter. The prefrontal is longer than the postfrontal. The lachrymal is deep in the postnasal region; it expands far posteriorly below the orbit. The lachrymonasal duct begins like a narrow funnel in the anterior wall of the orbit and opens on the anteroventral edge of the lachrymal.

A spoon-shaped septomaxilla is displaced inside the nasal cavity; the septomaxillary opening is apparently closed.

The postorbital is triangular. The intertemporal is large and elongated, larger than the supratemporal. In all available skulls, the postparietals and tabulars are lost; however, in specimens PIN, no. 4617/158 and SGU, no. 104V/2009, the posterolateral edges of the parietals bear special platforms for their contact (Figs. 1b and 2a). In other seymouriamorphs, in which the correspondence of the dorsal and ventral bone margins of the skull roof in this area is known (*Discosaurus austriacus*: Klembara, 1997; *Raphaniscus tverdokhlebovae*: Bulanov, 2000), the overlapping pattern is the opposite and the parietals overgrow the tabulars.

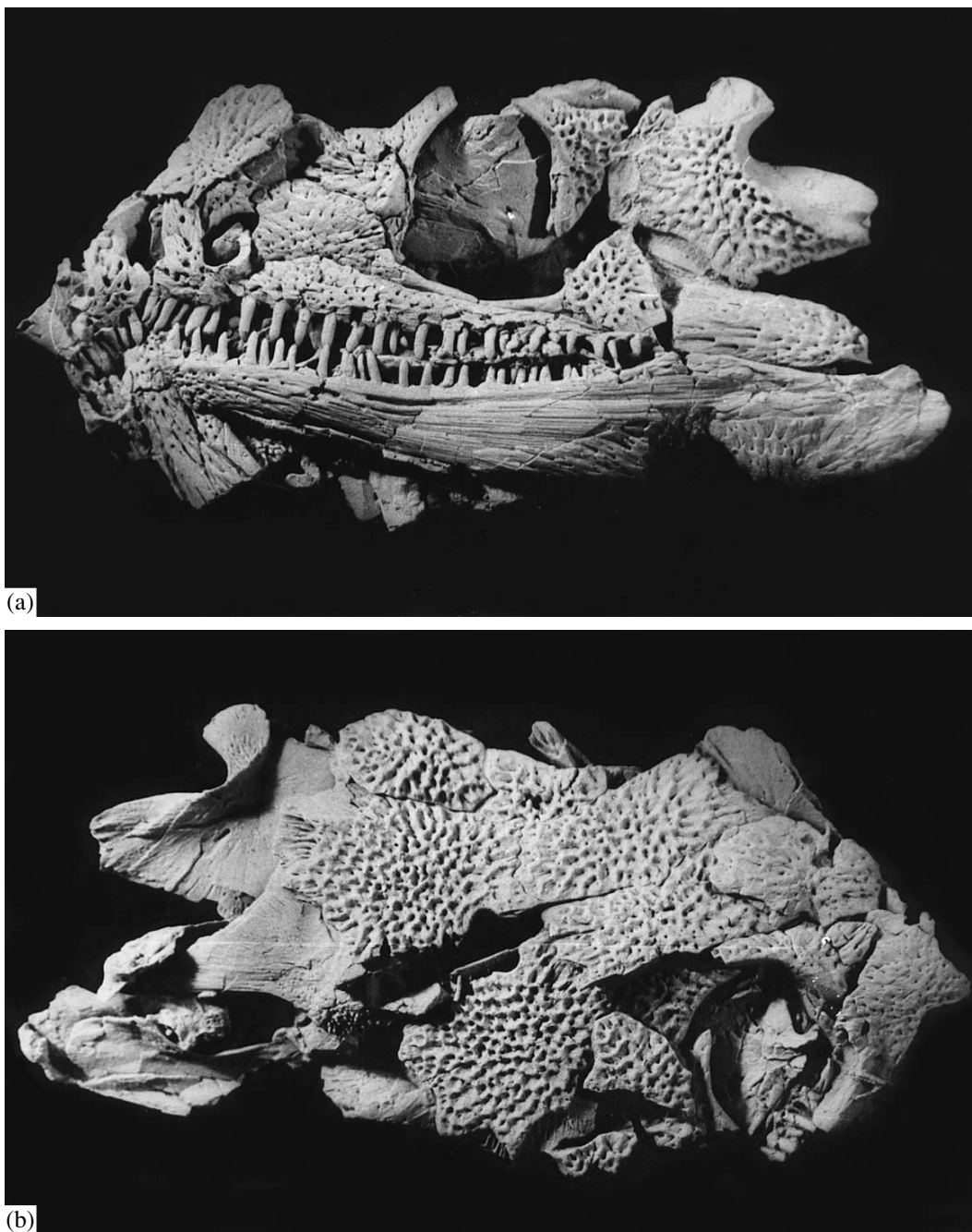


Fig. 1. *Karpinskiosaurus ultimus* (Tchudinov et Vjuschkov, 1956); specimen PIN, no. 4617/158, skull, Russia, Orenburg Region, Babintsevo locality; Upper Permian, Upper Tatarian Substage, North Dvinian Regional Stage; $\times 2.5$: (a) laterally and (b) dorsally.

The postparietals of the *K. ultimus*, on the contrary, are overlapped by the parietals.

The jugal strongly extends posteriorly in the postorbital region. The otic notch extends as far anteriorly as the anterior edge of the supratemporal; it is bordered laterally by a plate extending backwards and formed by the occipital edge of the squamosal. Medially, the squamosal forms a platelike process extending below the temporal area. This process formed the articulation between the jugal division and the parietal shield.

The premaxillae have high dorsal processes separately contacting the nasals. A wide fontanel is retained between these processes (Figs. 1a and 2a). The premaxilla bears six tooth positions (specimens SGU, nos. 104V/2031 and 104V/2034; specimen PIN, no. 4617/158).

The maxilla is low, and its ascending lamina is not developed (Figs. 3a and 3b). A notch at the anterior edge of the maxilla formed by the nasal opening is flat, and the whole lateral wall of the narial opening is

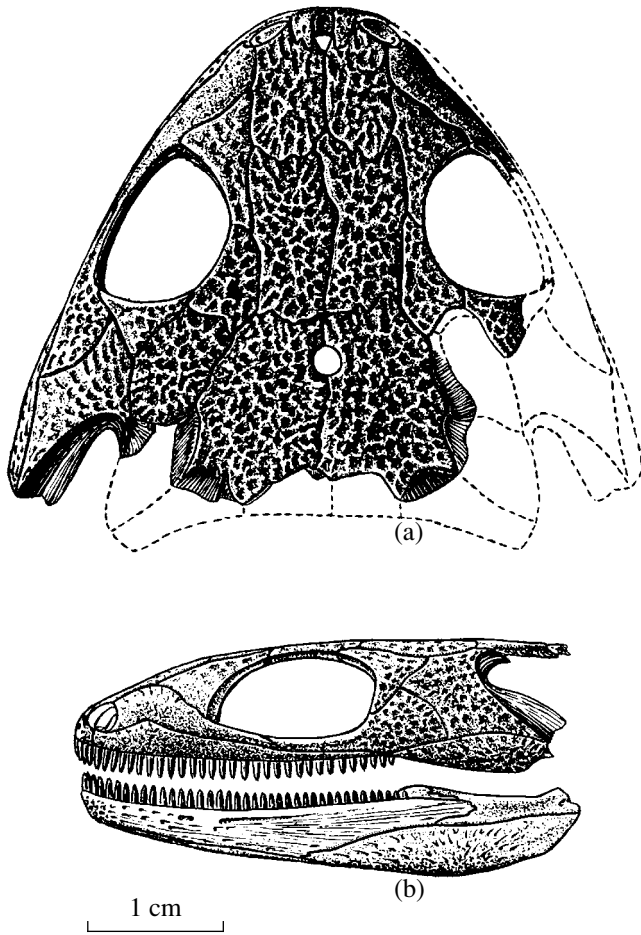


Fig. 2. *Karpinskiosaurus ultimus*; skull reconstruction based on specimen PIN, no. 4617/158: (a) dorsally and (b) laterally.

formed by the lachrymal). The posterior end of the maxilla probably contacted the quadratojugal and was overlapped by its anterior edge.

A groove for the infraorbital artery extends on the internal side of the maxilla from the posterior edge of the bone. The artery branched inside the maxilla and passed through 6–7 small foramina located at equal intervals from each other. The anterior foramen is placed opposite to the sixth or seventh marginal tooth and usually larger than the others, being frequently composed of several smaller foramina. Specimen SGU, no. 104V/2015 has four small foramina in this area. Ventrally, there is an elongated depression below a small ledge, which is similar to that present in the same position in *Discosauriscus austriacus* (Klembara, 1997; fig. 10) and in *Raphaniscus tverdochlebovae* (Bulanov, 2000; figs. 2b and 2d: *fpa*). Laterally, the anterior division of the maxilla is strongly perforated; one or two foramina that are larger than the others are, as a rule, present close to the naris. In the posterior half of the bone, the grooves extending from the upper labial foramina fuse to form a joint canal that follows backwards along the lower maxillary margin. The maxilla bears 30 tooth positions (specimen PIN, no. 4617/158).

The length of the postdentary part of the lower jaw is 3.5 times less than the length of the dentary itself. The coronoid process is only slightly developed (Figs. 1a and 2b). The splenials are equal in length. The splenial does not participate in the formation of the symphyseal surface. The angular is half as long as the jaw. The surangular bears only one small surangular foramen opening caudally and located at its posterior edge. The upper edge of the internal wall of the adductor fossa is formed by the prearticular and sharply curves medially to form a horizontal shelf.

The dentary is long; it attains the maximum depth in the middle of the jaw. The symphyseal division of the dentary is strongly perforated; the foramina open mainly backwards and are accompanied by extended grooves. Starting from the second third of the bone the grooves extending from the lower labial foramina fuse

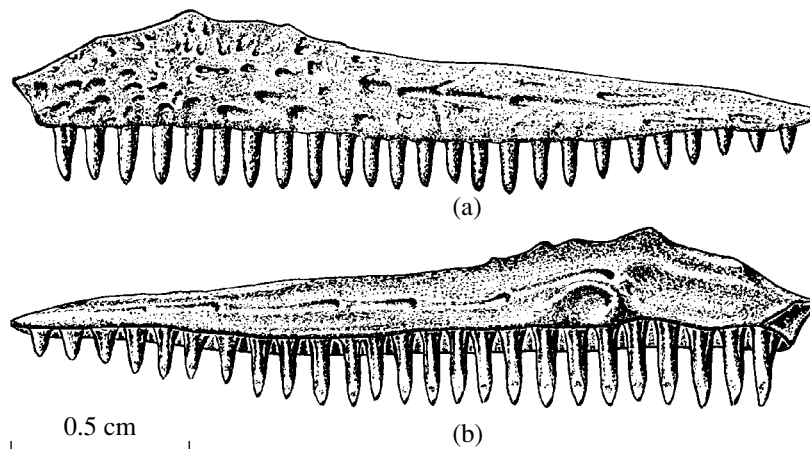


Fig. 3. *Karpinskiosaurus ultimus*; reconstruction of the left maxilla based on specimens SGU, nos. 104V/2011 and 104V/2013: (a) laterally and (b) medially.

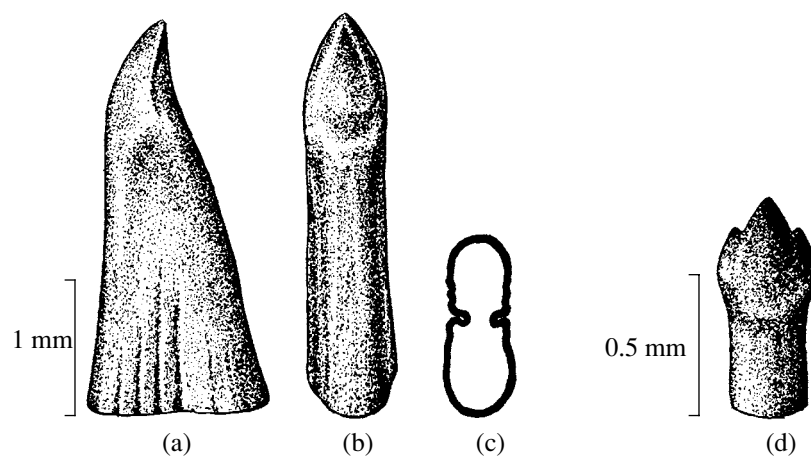


Fig. 4. *Karpinskiosaurus ultimus*; marginal jaw teeth: (a) and (b) maxillary tooth 6 of specimen SGU, no. 104V/2015: (a) lingually and (b) laterally; (c) maxillary tooth of specimen SGU, no. 104V/2011, cross section at the base; and (d) crown of the premaxillary tooth of a juvenile based on specimen SGU, no. 104V/2031, laterally.

to form a single deep, superficial groove directed backwards. Below this groove, the dentary is crosshatched with numerous straight, nonanastomosing creases, the largest of which originate from the foramina in the symphyseal division. The Meckel's cartilage furrow is deep, especially in the anterior part of the dentary, where its lower and upper edges become close to each other. The alveolar canal inside the bone is probably absent. The branches of the mandibular artery pass to the tooth bases through small foramina located at equal intervals on the ventral surface of the dental area. There

are 39 tooth positions in the lower jaw (specimen PIN, no. 4617/158).

The marginal teeth of *K. ultimus* are high, the crowns are small, and the apices are flattened and slightly curved lingually (Figs. 4a and 4b). A larger part of a tooth is occupied by the pulp cavity. In cross section, the thin-walled tooth bases are strongly elongated ovoids, slightly compressed in the middle. There are one or two deep folds strongly embayed inside the pulp cavity on each lateral side of tooth (Fig. 4c).

Large teeth on the palatal surface are only slightly smaller than the marginal teeth and are distinguished by the unfolded pattern of the tooth bases and unflattened conical apices. However, these are also directed inside the mouth cavity. There are five teeth of this type on the palatine (specimen SGU, no. 104V/2032), four of which are located along the posterior edge of the choana and one is placed somewhat posteriorly at the boundary with the maxilla.

Small peglike teeth densely cover the palatine processes of the pterygoids but are almost absent from the palatines and are completely absent from the parasphenoid rostrum.

Variability. The skeletal remains of *Karpinskiosaurus ultimus* from Babintsevo belong to juveniles, the skull of which did not exceed 40 mm of length; some jaws from the Pron'kino locality belonged to considerably larger individuals (specimens PIN, nos. 521/106 and 107).

The smallest available skull of *Karpinskiosaurus ultimus* is approximately 15 mm long (specimen SGU, no. 104V/2033). A more completely preserved specimen SGU, no. 104V/2031 (skull, 17 mm long, Fig. 5) is characterized by rather short and wide nasals and frontals; smaller prefrontals in comparison to the postfrontals; shortened maxillae; and, consequently, by an insignificant elongation of the preorbital skull region.

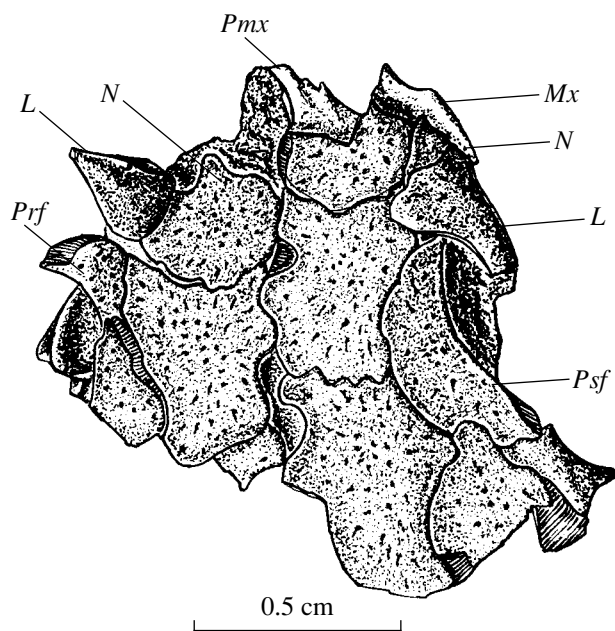


Fig. 5. *Karpinskiosaurus ultimus*; specimen SGU, no. 104V/2031, skull of a juvenile, dorsally. Designations: (L) lacrimal, (Mx) maxilla, (N) nasal, (Pmx) premaxilla, (Prf) prefrontal, and (Psf) postfrontal.

The parasphenoid rostrum is long and lacks shagreen teeth. The parafenestral wings are narrow and directed posterolaterally. The maxilla of specimen SGU, no. 104V/2033 bears 22 tooth positions. The tooth crowns are clearly tricuspid, as the cutting edge consists of the central cone and one large triangular cone on each lateral side (Fig. 4d).

The external surface of the skull roof bones is smooth; it bears hardly visible depressions located at the sites of emergence of nutritive vessels. The seismosensory grooves cannot be traced, which may be due to the absence of ornament on the surface of the skull roof at this developmental stage.

Sculpturing develops at an early stages. Skulls ranging from 30 to 40 mm in length (specimens SGU, no. 104V/2009 and PIN, no. 4617/158) are already ornamented with deep cells, which become elongated at the bone periphery. This is especially well pronounced on the frontals and the nasals, which become longer and narrower in the course of growth. Dentigerous bones, as well as the lachrymals, prefrontals, and surangulars remain unsculptured or poorly sculptured. The prefrontals become larger and exceed the postfrontals in size. The maxillae elongate, and the amount of tooth positions they bear increases from 22 to 30. The crowns of the marginal teeth lose lateral cones and become monocuspid; the bases become folded.

Folding develops in *K. ultimus* at relatively late ontogenetic stages and is observed in the teeth of the largest known specimens (or isolated jaw bones of appropriate size). Deep folds in the middle of the lateral side of the tooth base are formed first; further on, folds of the second order arise close to them.

Comparison. *K. ultimus* differs from *K. secundus* (Amalitzky, 1921) by the larger size of intertemporals, the absence of ascending lamina of the maxilla, and the smaller lingual curvature of the marginal tooth apices.

Occurrence. East of European Russia, Orenburg Region, Upper Permian, Upper Tatarian Substage, North Dviniian and Vyatkian Regional Stages.

Material. The present study is based upon collections of the Paleontological Institute of the Russian Academy of Sciences (specimen numbers PIN) and the Saratov State University (specimen numbers SGU).

Babintsevo locality yielded incomplete skulls: specimens SGU, nos. 104V/2008, 2009, 2031–2035; specimen PIN, no. 4617/158; dentaries: specimens SGU, nos. 104V/2017–2019, 2024, 2025, and 2037; maxillae: specimens SGU, nos. 104V/2011–2016; and squamosal, specimen SGU, no. 104V/2036.

Isolated jaws from the Pron'kino locality are dentaries: holotype PIN, no. 521/104, specimens nos. 521/54, 106, 107–113, and 140–146; maxillae: specimens PIN, nos. 521/114–116 and 147–149.

DISCUSSION

The general structural pattern of the *Karpinskiosaurus* skull only slightly differs from that of the Early Permian Discosauriscinae (*Discosauriscus* and *Ariekanerpeton*). The reduction of seismosensory systems at the early developmental stages, the presence of long dorsal processes of the premaxillae and the retention of fontanels between them, the dissimilar folding pattern of the marginal tooth bases, the stronger expansion of the jugal behind the orbit, the large size (based upon the size of *K. secundus* and fragmentary karpinskiosaurids from a number of localities: Pron'kino, Sambullak, Blumenthal 3, Vyazniki 2, etc.), and the completely ossified endocranium at the adult stage are the basic characters that make possible the placement of this genus within the separate subfamily Karpinskiosaurinae in the same family together with the Discosauriscinae.

Karpinskiosaurus ultimus ontogenetic information also demonstrates the earlier development of cellular ornament in comparison with the Discosauriscinae. This was obviously characteristic of all karpinskiosaurids, which possessed better developed sculpturing of this type at the late developmental stages. A good distinctive feature of *Karpinskiosaurus* is an unusual pattern of vascular grooves on the external surface of the dentary (see *Description*). This allows for the identification of fragmentary remains of the Karpinskiosaurinae from numerous localities characterized by allochthonous burial type.

The distinctions of *Karpinskiosaurus* from *Utegenia shpinari* and Kazanian leptorophids (*Leptorophia* and *Biarmica*) are more significant and, in addition to those mentioned above, include a different depth of the otic notches, the absence of contact between the postorbital and supratemporal, the presence of well-developed parafenestral wings, and nondenticulated rostrum of the parasphenoid, increased size of the tabulars (Laurin (1996a) incorrectly represented rather large tabulars in the *Utegenia* reconstruction). In all specified characters, *Utegenia* seems to be closer to leptorophids (*Leptorophia* and *Biarmica*) than to the Discosauriscinae, and for this reason, probably deserves attribution to a separate family.

The position of the North American and European genus *Seymouria* in the seymouriamorph taxonomic system is not quite clear. This Early Permian genus includes three species, two of which, *S. baylorensis* and *S. sanjuanensis*, are well characterized by cranial material and were subject to prolonged study. The assignment of *S. agilis* described by E. Olson (1980) based upon a vertebral column to the genus *Seymouria* is presently doubted (Laurin, 1996b).

Recent revising papers (Laurin, 1995, 1996a, 1996b) demonstrated the affinity of *Seymouria* (especially, less specialized *S. sanjuanensis*) to the genus *Ariekanerpeton*. A large part of characters separating them (size, degree of endocranial ossification, and the

presence of seismosensory canals) were explained by Laurin by their positions at different ontogenetic stages.

Seymouria seems to be related to the Discosauriscinae in its origin; this inference follows from the general skull pattern distinguishing it from *Utegenia*, *Leptoropha*, and *Biarmica*. However, the conclusion concerning a larger distance of *Ariekanerpeton* from *Discosauriscus* than from *Seymouria* was not well grounded. In actual fact, the first two genera demonstrate only little divergence in skull structure, and they are assigned to different genera based mainly upon differences in the postcranial skeleton. In particular, *Ariekanerpeton* is characterized by reduced phalangeal formula of the forelimb and the loss of the squamous cover at the late ontogenetic stages (Ivakhnenko, 1987; Laurin, 1996b). In addition, paleontological material does not support the idea concerning the attribution of all currently known discosauriscine specimens to premetamorphic and early juvenile individuals (Klembara, 1997). Taking into account the large number of known localities, prolonged period of studying, and the abundant skeletal remains, the absence of adult Discosauriscinae is surprising, especially as the reproduction of these animals should be closely connected to the aquatic environment, even if the trophic adaptation was not.

A number of features in the skull structure of *Seymouria* sets this genus apart from other seymouriamorphs. The most essential difference is the more complicated pattern of articulation between the parietal shield and the jugal region. This was shown by Watson (1954; text-fig. 30); namely, at the attachment, the ventral surface of the parietal shield has a massive ventrally directed longitudinal crest, which is laterally and medially enclosed by the squamosal. In other seymouriamorphs, this articulation is formed by a lamellar process of the squamosal spreading under the bones of the temporal region (Fig. 2a; Klembara, 1997, text-fig. 5; Bulanov, 2000, text-fig. 1b; pl. 11, fig. 4a).

Other distinctive characters of *Seymouria* are the stronger development of the preorbital growth zone (the nasals are longer than the frontals; the orbits are located at the skull midlength), the presence of a wide anteriorly facing notches at the anteroventral edges of the orbits, and the participation of the splenial in the formation of the symphyseal surface of the lower jaw.

Within the order, *Karpinskiosaurus* shares the largest number of characters with *Seymouria*. The former genus, on the one hand, shares major structural features of the discosauriscine skull and, on the other, has attained large size; possesses well ossified endocranium at the adult stage and posteriorly closed posttemporal fossae (*K. secundus*); and lacks seismosensory grooves at the late developmental stages. Nevertheless, *Seymouria* cannot be regarded as an ancestor of the *Karpinskiosaurinae*, since it has a specialized articulation between the parietal shield and the jugal region. In its turn, *Karpinskiosaurus*, occupying an intermediate position between *Seymouria* and the Discosauriscinae

with reference to many characters, is known only from Upper Tatarian deposits. A similarity between these genera might be best explained by common ancestry (Discosauriscinae) and developmental parallelisms, partly caused by its adaptation to a more terrestrial mode of life.

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