Evolution and Systematics of Seymouriamorph Parareptiles

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Abstract—The data on the morphology, systematics, stratigraphy, and ecology of seymouriamorphs (Parareptilia) are revised. Cranial morphology of ten seymouriamorph species belonging to seven genera and three families from the Lower and Upper Permian of European Russia and Central Asia are described. According to the main evolutionary trends characteristic of this group, it is proposed to divide seymouriamorphs into the superfamilies Kotlassioidea and Seymourioidea. The evolution of kotlassioids, which were closely associated with aquatic habitats, predominantly consisted in the specialization of the dental system; the morphological features of this system provided the foundation for the systematics of the lower-rank taxa. The evolutionary development of seymourioids occurred against a background of adaptation to the semiaquatic biotopes.

Key words: Seymouriamorpha, Parareptilia, Early–Late Permian, Eastern Europe, Central Asia, cranial morphology, systematics, evolution, ecology.

INTRODUCTION

Seymouriamorphs are one of the most remarkable groups of Late Paleozoic vertebrates, occupy a key position in the evolution of Paleozoic terrestrial tetrapods, and constantly attract attention. For a long time, this taxon was regarded as possibly the most primitive of known fossil reptiles. Only explicit studies demonstrated its relation to the Anamnia, which, nevertheless, during the Permian gave rise to the wide diversity of parareptiles presented in the Mesozoic and Cenozoic faunas by such widespread and well-adapted animals as turtles and tortoises (Ivakhnenko, 1987). Physiologically, this group is an extremely interesting research object, as it occupies a special place within the orders of modern amphibians which possess a number of key parameters, in particular, the presence of pholidosis, which significantly perplexes cutaneous gas exchange, playing a significant role in the amphibian breathing. The metamorphosis in seymouriamorphs proceeds in a very much evolutive manner and is not accompanied by obvious morphological reorganization, which is much more profound at this boundary in the Anura and Urodela. Only the reduction of external gills, which are sometimes preserved as imprints and traced in a wealth of evidence, as a matter of fact is the only indicator of the larval stage termination. The usage of this indicator, however, is frequently restricted by the state of preservation of the paleontological material.

Seymouriamorphs compose a relatively small group (present paper regards ten valid genera), the stratigraphic distribution of which is restricted to the Permian. This makes possible a detailed description of skeletal parts of the majority of the forms included in the order even within the framework of a small monographic study. The actual diversity of the group was undoubtedly much larger, which is supported by diverse fragmentary material from numerous Late Permian localities, giving an idea of the real range of adaptive radiation. Seymouriamorphs disappeared from the fossil record at the end of the Tatarian Age and did not cross the Permian–Triassic boundary.

As a definite morphotype, seymouriamorphs probably deviated from the anthracosaurian lineage no later than the terminal Carboniferous. All known localities are confined exclusively to the continental facies of the Northern Hemisphere. The Early Permian evolutionary stage of the group has been characterized adequately enough. The major localities of this age in central Europe (Boskovice Furrow and Bromacker), Central Asia (Kurty and Sarytaipan), and North America (West Coffe Creek, Rio Arriba, and San Juan County) yielded extensive material of good preservation, serving as research objects for numerous authors. The Late Permian developmental stage of the order, which was limited according to available data to Eastern Europe, is much less clear and is only partially reconstructed in the present paper. Complex dynamics of the formation of the faunal assemblages of terrestrial vertebrates during this time interval influenced by recurring invasions of Gondwanian elements and repetitive replacement of dominants in the terrestrial, semiaquatic, and aquatic ecotopes (Ivakhnenko, 1990a, 1990b; Golubev, 2000), was one of the reasons for a great adaptive radiation providing high morphological and taxonomic variety of seymouriamorphs. Reconstruction of the natural condition is perplexed by the obvious prevalence of the allochtonous burial type in the overwhelming majority of Late Permian localities in European Russia and, as a consequence, by fragmentation of available material. In the absence of representative sampling this material is not always subject to exact diagnostics or may be used for confident establishment of new taxa. Despite this, such data is of considerable interest, as it presents a number of questions concerning the stratigraphic distribution and morphological variety of seymouriamorphs. In this connection, a number of interesting specimens are mentioned in the open nomenclature in different parts of the monograph.

The taxonomic position of seymouriamorphs occupying an intermediate place between the anthracosauromorph and parareptile lineages is variously treated and in many respects is a matter of preference which are not as important when phylogenetic relationships are already established. The similarity to Carboniferous anthracosauromorph labyrinthodonts is obvious and, considering the set of formal characters, both groups could be assigned to the same taxon, as was proposed earlier by some authors (Romer, 1963, cited after Kuhn, 1972). In the present study, seymouriamorphs are considered according to the opinion of other authors (Olson, 1947; Ivakhnenko, 1987, 2001; Ivakhnenko *et al.*, 1997) as an order of the class Parareptilia chiefly due to realization of one of the basic syndrome of this group, the synpareial pattern of the skull roof; this apparently prevented the formation of the upper temporal fenestra in parareptiles (Ivakhnenko, personal communication). An additional basis for this conclusion is the rather probable origin of procolophonomorphs and nycteroleteromorphs from different groups of seymouriamorph amphibians (Bulanov, 1999). In such case, withdrawal of the Seymouriamorpha from the class would result in the establishment of a polyphyletic taxon requiring further subdivision aimed at the construction of a more vertical system; this would encounter obvious contradictions caused by the morphological similarity of initial groups (Seymourioidea and Kotlassioidea).

The last general revision of seymouriamorphs was undertaken about 15 years ago (Ivakhnenko, 1987). During this time interval, Klembara (1992–1997) significantly revised the Moravian Discosauriscinae in his excellent work. A number of researchers (M. Laurin, D.S. Berman, T. Martens, S.S. Sumida, etc.) specified and presented new data on the morphology and geographical and stratigraphic distribution of seymourids (Laurin, 1996a, 1996b); in addition, important material from the Late Permian localities of Eastern Europe was collected and examined. This provides a better insight into the historical development of the group and relationships among its members. High evolutionary rates and wide geographical distribution make seymouriamorphs appropriate for inter- and intraregional correlation of the continental Permian deposits.

The problems of the basal divergence of parareptiles require reexamination of advanced members of the class and are only briefly considered in the present study. Nor does the monograph cover the large postcranial material requiring extensive work and revision of previously described forms; this is a subject for separate research, which should be performed in the future.

The term *amphibian* often applied in this study to the animals in question means the amphibian evolutionary grade rather than taxonomic attribution. The term *juvenile* is used in the broad sense to designate the animals that have not achieved the definitive state. This is accounted for by the impossibility of determining the threshold of metamorphosis in the majority of forms under study. Wherever possible, more specific terms, such as larval, postlarval, metamorphic, postmetamorphic, etc., are applied to designate the individual age of animals and the period (stage) of their development.

Figures and photos (if the authorship is not stipulated separately) were accomplished by the author. The illustrations of many specimens are reconstructions, in this connection they were often duplicated by photos of original specimens in the text and in the plates allowing completeness and preservation of the material. The taxon diagnoses were created on an alternative principle; for convenience, they are separated from the descriptive part in a particular chapter and, sometimes, as required, are commented on. The descriptions are accompanied by a brief history of their study to facilitate its understanding for foreign authors.

Below is the taxonomic system of seymouriamorph parareptiles accepted in the present study.

CLASS PARAREPTILIA

Order Seymouriamorpha Watson, 1917

Superfamily Kotlassioidea Romer, 1934

Family Utegeniidae Ivachnenko, 1987

Genus *Utegenia* Kuznetzov et Ivachnenko, 1981

***U. shpinari* Kuznetzov et Ivachnenko, 1981**

Family Kotassiidae Romer, 1934

Subfamily Leptorophinae Ivachnenko, 1987

Genus *Biarmica* Ivachnenko, 1987

***B. tchudinovi* Ivachnenko, 1987**

Genus *Leptoropha* Tchudinov, 1955

***L. talonophora* (Tchudinov, 1955)**

Subfamily Kotlassiinae Romer, 1934

Genus *Microphon* Ivachnenko, 1983

(=Raphanodon Ivachnenko, 1987 = Raphaniscus Bulanov, 2000)

***M. exiguus* Ivachnenko, 1983**

***M. gracilis* Bulanov, sp. nov.**

***M. arcanus* Bulanov, sp. nov.**

Genus *Kotlassia* Amalitzky, 1921

***K. prima* Amalitzky, 1921**

Superfamily Seymourioidea Williston, 1911

Family Karpinskiosauridae Sushkin, 1925

Subfamily Discosauriscinae Romer, 1934

Genus *Discosauriscus* Kuhn, 1933

***D. austriacus* (Makowsky, 1876)**

***D. pulcherrimus* (Fritsch, 1879)**

Genus *Ariekanerpeton* Ivachnenko, 1981

***A. sigalovi* (Tatarinov, 1968)**

Subfamily Karpinskiosaurinae Sushkin, 1925

Genus *Karpinskiosaurus* Sushkin, 1925

***K. ultimus* (Tchudinov et Vjuschkov, 1956)**

***K. secundus* (Amalitzky, 1921)**

Family Seymouriidae Williston, 1911

Genus *Seymouria* Broili, 1904

***S. baylorensis* Broili, 1904**

***S. sanjuanensis* Vaugnh, 1966**

***S. grandis* Olson, 1979**

Genus *Rhinosauriscus* Kuhn, 1968

***R. jasykovii* (Fischer von Waldheim, 1847)**

CHAPTER 1. HISTORICAL OVERVIEW

The first veritable seymouriamorph recorded in the literature seems to be *Discosauriscus austriacus*, described by Makowsky (1876) (cited after Ivakhnenko, 1987; Klembara, 1995a) from the Upper Rotliegend of Central Europe (Moravia) as a species of the genus *Archegosaurus*. The new generic name *Discosaurus* proposed for this form by Credner (1883) appeared to be preoccupied and was further replaced by Kuhn (1933) with *Discosauriscus*. At the end of the 19th and during the first half of the 20th century, various authors described and identified numerous forms, i.e., *Branchiosaurus moravicus, Discosaurus moravicus, D. permianus, Melanerpeton spiniceps, M. pulcherrimum, M. falax, M. magnum, M. longicaudatus, M. permeri, M. potamites,* etc. from several European localities. These forms were mainly regarded as batrachomorph labyrinthodonts (branchiosaurs), most of them were later synonymized to various species of the genus *Discosauriscus* (Spinar, 1953; Klembara, 1997). Taking into account the significant amount of European localities, the presence of more than two forms in these regions (e.g., *Discosauriscus austriacus* and *D. pulcherrimus*) seems rather probable, however, currently this is not quite solid due to schematic figures and unsatisfactory preservation of specimens.

In 1904, Broili (1904) described *Seymouria baylorensis* from the Lower Permian of North America using two skulls and postcranial elements and suggested its relationship to the most primitive known reptiles. From this publication on, *Seymouria* was repeatedly reexamined and used as a research and comparison object by numerous authors. Williston (1911) introduced a separate family for this genus. Watson (1917) raised the rank of the group to the order level, and White (1939), based upon already available information, performed a detailed study of the skull and postcranial skeleton of the type species; subsequently, it was revised and supplemented in more recent papers (Sumida *et al.*, 1992; Laurin, 1996a).

The composition of the genus was complemented by several species from a wide stratigraphic interval covering the lower and basal parts of the Upper Permian of North America: *S. sanjuanensis* Vaughn, 1966 (Cutler Formation); *S. grandis* Olson, 1979 (Vale Formation, Leonardian), and *S. agilis* Olson, 1980 (Flowerpot Formation, Guadalupian). The assignment of *S. agilis* described upon vertebral column to the genus *Seymouria* is now challenged in favor of the nycteroleteromorph genus *Macroleter* occurring in the Mezen River localities of northeastern European Russia (Reisz and Laurin, 2001). The taxonomic position of *S. grandis* established on the basis of fragmentary specimens is also doubtful (Sillivan and Reisz, 1999, p. 1264). On the contrary, *S. sanjuanensis* well characterized by complete skeletons from the Lower Permian of North America was recently identified using skulls of juveniles and complete skeletons of adults by Berman and Martens (1993), Berman *et al.* (2000, 2001), and Klembara *et al.* (2001) from the unique locality Bromacker in Central Germany where they were found in association with typical members of the Lower Permian North American fauna: captorhinomorphs (Protorothyrididae), dissorophids, diadectids, synapsids, and bolosaurids. These finds are of great importance for the correlation of continental beds of North America and Europe and probably for their comparisons with the Permian stratotype sections in Russia (Sumida *et al.*, 1996; Eberth *et al.*, 2000).

The composition of the Seymouriamorpha, traditionally placed in the Cotylosauria, was repeatedly changed and specified. Romer's system (1947) was the closest to the modern idea of the general relationships within the group. In addition to the Seymouriidae and Kotlassiidae, he suggested including the European Discosauriscidae in the order, ranked by him as a separate family.

In the same year Olson (1947) proposed the concept of parareptiles, according to which a part of Late Paleozoic tetrapods (cotylosaurs) characterized by anapsid skull structure should belong to a separate lineage which reached the reptile morphological and physiological level of organization independently of other vertebrates and gave rise to a group of extant reptiles comprising turtles and tortoises. The Seymouriamorpha were considered as the most primitive members of parareptiles, the group including the Procolophonia, Diadectomorpha, Pareiasauria, and Chelonia.

Olson's point of view was supported by Ivakhnenko (1987) who regarded the group in the same composition, but elevated its rank to the class level with the inclusion of corresponding orders. Based on the pattern of relationships, Ivakhnenko combined seymouriamorphs and procolophonomorphs in the subclass Batrachosauria, while the Nycteroleteromorpha, Diadectomorpha, and Chelonia were assigned to the subclass Diadectosauria. The basic syndrome of seymouriamorph characters was formulated as a group of angustitabular animals with the synpareial pattern of the attachment of the cheek bones to the skull roof. These features made them very suitable to the role of ancestral taxon for more advanced members of the class.

Ivakhnenko (1987) considerably extended the order, placing in its composition the taxa from the Permian of Eastern Europe previously referred to the other lineages: *Leptoropha*, *Nyctiboetus*, *Enosuchus*, newly described genera *Biarmica* and *Raphanodon*, and discosauriscids described earlier from the Lower Permian of Central Asia, *Utegenia* and *Ariekanerpeton* (Kuznetsov and Ivakhnenko, 1981; Ivakhnenko, 1981). The latter two genera were combined with the Moravian discosauriscids in the same family and considered to be neotenics, which returned to a permanent mode of life. Later, *Nyctiboetus* and *Enosuchus* were excluded from seymouriamorphs again and are currently considered to

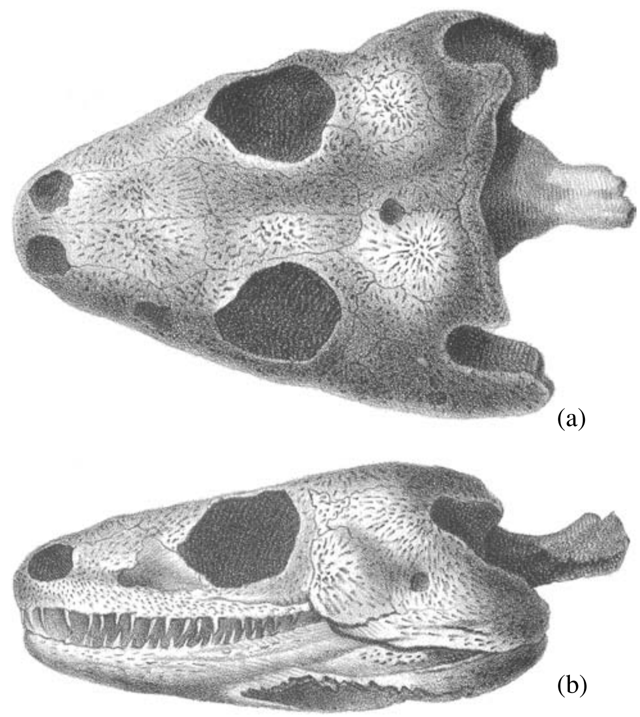


Fig. 1. *Rhinosauriscus jasykovii* (Fischer, 1847), skull, after Fischer von Waldheim (1847): (a) dorsal and (b) lateral views.

be relict gephyrostegid anthracosauromorphs (reptiliomorphs) (Ivakhnenko *et al.*, 1997; Ivakhnenko, 2001).

Central European discosauriscids were revised in a number of papers by Klembara (1992–1997), Klembara and Meszaros (1992), Klembara and Janiga (1993), and Klembara and Bartik (2001) who demonstrated the presence of only two species of the genus *Discosauriscus* (*D. austriacus* and *D. pulcherrimus*) in the localities of the Boskovice Furrow. Based upon extensive material, Klembara proposed that all *Discosauriscus* skeletal parts counted by dozens belonged to the animals that remained at larval and early postlarval stages. These conclusions were later extended to the other species earlier included in the Discosauriscidae, *Ariekanerpeton* and *Utegenia* (Klembara, 1994a, 1995), the burial conditions of which are similar and present accumulations with a high concentration of individuals in their lifetime position and untouched by disarticulation processes. A find of juvenile *Seymouria* (*S. sanjuanensis*) in the Bromacker locality in Germany made possible the comparison of *Discosauriscus* and *Seymouria* of the same size class. This showed morphological distinctions between the genera other than features subject to ontogenetic changes.

The history of studying seymouriamorphs in Russia already totals almost a hundred of years. Possibly, the very first remains of these animals were found in this area long before the discovery of rich Central European localities. In 1847, Fischer von Waldheim (1847) described *Rhinosauriscus jasykovii* based upon a complete skull from the Saratov Region (the generic name *Rhinosaurus* suggested in the original description appeared to be preoccupied and was further replaced). Unfortunately, the type specimen was subsequently lost (Fig. 1). The skull shape and arrangement of exocranial elements in *Rhinosauriscus* is strongly reminiscent of *Seymouria*; therefore, some researchers assigned it to the Seymourida (Konzhukova, 1964; Olson, 1965; Kalandadze *et al.*, 1968). Actually, based upon the figures in Fischer von Waldheim's paper, *Rhinosauriscus* even demonstrates the presence of the characteristic notches at the anterior orbital margins marked in the same position in *Seymouria* (Laurin, 1996a). Unequivocal establishment of the taxonomic position of *Rhinosauriscus* is hindered by complete separation of the lacrimal from the orbital rim; this has never been observed in seymouriamorphs, but is characteristic, for example, of some anthracosauromorph amphibians, such as *Eoherpeton watsoni* and *Eogyrinus atthei* (Panchen, 1972, 1975). However, it is appropriate at this point to recall that, in *Seymouria baylorensis*, the infraorbital process of the lacrimal is extremely weakly developed (Laurin, 1996a). The main argument in favor of the assignment of *Rhinosauriscus* to seymouriamorphs is the presence of deep otic notches, which are atypical of anthracosaurs.

A high probability of the presence of seymourids in the Permian of Russia follows primarily from the relationships between Late Permian faunal assemblages of Eastern Europe with the faunas of North America and Central Europe where this family evolved in the Early Permian.

Two small skeletons found much later at the Kuzminovskoe copper mine (Southern Fore-Urals) and described by Ryabinin (1911) as the only East European species of the genus *Discosauriscus, D. netschajevi* (Fig. 50), may be quite confidently referred to seymouriamorphs. However, this identification based upon insignificant distinctions in the postcranial structure remain doubtful because of poor skull preservation in both specimens and deficient knowledge of the postcranial skeleton of seymouriamorphs in general. Therefore, it is not improbable that these skeletons belong to the other group of the order, in particular, to *Karpinskiosaurus*, especially taking into account recent dating of the locality to the Late Permian (Ivakhnenko *et al.*, 1997), while the Discosauriscinae are limited in their distribution to the Upper Rotliegend (Werneburg and Kiersnowsky, 1996). Nevertheless, the data published by Ryabinin are of great interest: the specimens clearly demonstrate the seymouriamorph characteristics of squamation well imprinted on the marl surface.

The first representative material on East European seymouriamorphs was obtained by Amalitzky as a result of his excavations in 1899 to 1914 at the Malaya Northern Dvina River. Four specimens in total from the locality named Sokolki were found. Amalitzky believed that their similarity to North American *Seymouria* was quite sufficient to relate them to this genus; nevertheless, he established a separate subgenus *Kotlassia*, including two species, *K. prima* and *K. secunda* (Amalitzky, 1921). These species differed in the proportions of the skull, otic notches, pattern of surface ornamentation, and shape of vertebral neural spines.

Sushkin (1925), while restudying the material from the Northern Dvina River, noted different numbers of sacral and presacral vertebrae in these *Kotlassia* species; this, along with the distinctions in the skull structure, substantiated the assignment of *Kotlassia secunda* to a new genus, *Karpinskiosaurus*, ranked as a new family, Karpinskiosauridae. Subsequently, Sushkin (1926) discussed another species of the same genus, *K. neglectus* and its distinctions from *K. secundus*, including somewhat different skull proportions and a different shape and pattern of the postparietal surface ornamentation. However, no formal description was made. The specimen was neither shown in a figure nor numbered, and diagnostic characters listed in the paper seem to be unsatisfactory in the light of modern data for the substantiation of relationships proposed.

Bystrow (1944) erroneously took *Karpinskiosaurus* specimens for a young *Kotlassia prima* and gave a mixed description of both forms, as well as made reconstructions combining *Karpinskiosaurus* and *Kotlassia* characters. This resulted in an erroneous idea of the morphology and taxonomic composition of Northern Dvina seymouriamorphs and complicated the understanding of phylogenetic relationships within the order. Only Watson, who possessed a fragment of *Karpinskiosaurus* skull from the same locality (Watson, 1954, pp. 408–409, text-figs. 31, 32), insisted on the taxonomic independence of this genus. Tatarinov (1972), following Amalitzky, considered *K. secundus* to be a *Kotlassia* species. *Karpinskiosaurus* as a valid taxon was reintroduced into the seymouriamorph system much later, but retained in the same family as *Kotlassia* (Kalandadze *et al.*, 1968; Ivakhnenko, 1987). As shown by the present research, *Kotlassia* is the final unit of the other, kotlassioid, evolutionary lineage of seymouriamorph parareptiles.

The position of *Seymouria* in the phylogeny of terrestrial vertebrates was a question widely discussed in the literature for a long time. Broili's suggestion (1904, 1927) of placing this form at the base of the reptile stock was initially supported by a number of researchers (Williston, 1911; Watson, 1917). Other authors challenged this point of view (Sushkin, 1927; Bystrow, 1944), reasonably believing that the primitiveness of *Seymouria* and related genera similar to Carboniferous embolomeres in their skull structure does not give sufficient grounds for this. Sushkin (1927) analyzed the auditory apparatus of *Kotlassia* and *Karpinskiosaurus* and came to the conclusion that none of the modern reptile groups is derivable from seymouriamorphs.

Hartmann-Weinberg (1935) attempted to solve the problem of relationships of the order to one or another class of vertebrates by histological methods. She examined the microstructure of the bony armor from the Sokolki locality that was identified by her as *Kotlassia prima*. Studying thin sections, Hartmann-Weinberg attributed the microstructure of these membrane bones to a special, “seymouriid” type differing from those known in amphibians and reptiles by the preservation of the types of skeletal tissues characteristic of rhipidistians, i.e., vitrodentin, cosmine, and isopedin. Based on this information and other distinctive characters discovered by other researchers, she proposed to exclude seymouriamorphs from cotylosaurs and establish a separate taxon, Proreptilia.

Bystrow (1940) revised her results and showed this interpretation to be groundless, since membrane bones of *Kotlassia* are identical structurally to those of typical labyrinthodonts. In the study devoted to *Kotlassia prima*, Bystrow (1944) assigned this form to amphibians, nevertheless, specifying a number of its cranial features characteristic of reptiles. In addition, subsequent study of the composition of East European tetrapod faunas revealed the erroneous assignment of dermal bone armor rather common in the Tatarian to seymouriamorphs. These fossils actually belong to chroniosuchids, a group of relict anthracosauromorphs that dominated in the aquatic communities of terrestrial tetrapods of Eastern Europe in this time interval. In particular, the armor attributed by Hartmann-Weinberg and, later, by Bystrow (1944) to *Kotlassia prima* from the Sokolki locality in actual fact belongs to *Chroniosuchus licharevi* (Golubev, 2000).

Efremov (1946) proposed to assign tetrapods combining the features of amphibians and reptiles to a special subclass, Batrachosauria, intermediate between the two classes. This taxon included the most controversial genera, such as *Seymouria*, *Kotlassia*, and the new genus *Lanthanosuchus* from the Isheevo locality (Russia, Lower Tatarian Substage). The place of batrachosaurs within the system of vertebrates suggested an origin no later than the Middle Carboniferous, i.e., before the emergence of the first apparent cotylosaur reptiles. Efremov explained the rare occurrence and relatively late geological age of known batrachosaurs by their relict nature and dwelling within specific biotopes, which allowed them to avoid the direct competitive pressure of more advanced groups. The general diagnosis of the subclass, as might be expected, was not precise enough and the subclass composition was treated in a very wide sense without preservation of its original semantic content (Heaton, 1980; Holmes, 1984; Ivakhnenko, 1987; Laurin and Reisz, 1995).

Remarkable finds of discosauriscs in Moravia, demonstrating imprints of external branchiomeres in the cervical division, which unequivocally indicated the transition through the larval stage (Spinar, 1953), played a key role in elucidation of the question of the position of seymouriamorphs with reference to their physiology. The dispute on this matter based on the analysis of osteological data lasted over half a century without any success. Later, the imprints of external gills were discovered in a closely related Central Asian genus, *Ariekanerpeton* (Tatarinov, 1964; Ivakhnenko, 1981, 1993), in which, along with some other Eurasian genera (*Utegenia*, *Biarmica*, and *Microphon* (=*Raphanodon*)), the skull roof surface demonstrated the presence of seismosensory system grooves (Kuznetsov and Ivakhnenko, 1981; Ivakhnenko, 1987).

Currently, the presence of the seismosensory system or its rudiments has been demonstrated in the majority of members of this order (Ivakhnenko, 1987; Klembara, 1996; Bulanov, 1999), including *Discosauriscus austriacus*, the dermatocranial surface of which additionally has pitted structures interpreted as electrically sensitive organs, later noticed in the same position in *Microphon* (Bulanov, 2000) and *Utegenia* (Malachov, 2000a).

On the strength of the above facts, the amphibian level of seymouriamorph organization may now be regarded as proved. The main discussion is currently focused on certain special questions, such as the degree of terrestrial or aquatic adaptations of particular forms (*Seymouria* and *Discosauriscus*), the degree of fetalization, and the establishment of more precise relationships between the taxa within the order; this encounter insufficient understanding of Late Permian seymouriamorphs, which perplexes elaboration of the general concept of evolution in this group. The present study is based on the analysis of cranial morphology in Late Permian seymouriamorphs of Eastern Europe and aimed at filling the gaps in the knowledge and reconstructing a more complete picture of evolutionary development of the group.

CHAPTER 2. MATERIALS AND METHODS

The material examined in the present study is stored at the Paleontological Institute of the Russian Academy of Sciences (PIN) and Saratov State University (SGU). It was collected by a large number of researchers over the past 100 years. *Utegenia shpinari* (from the Kurty locality, collected by I.I. Radchenko and E.G. Novikov in 1958 and by N.N. Kalandadze in 1975), *Ariekanerpeton sigalovi* (Sarytaipan locality; collected by L.P. Tatarinov and N.N. Kalandadze in 1962), and *Microphon exiguus* (Donguz 6 locality; collected by D.L. Sumin) are represented by an especially large series of specimens. The remainder of the material was collected by V.P. Amalitzky, B.P. Vjuschkov, P.K. Tchudinov, Yu.M. Gubin, V.K. Golubev, and V.L. Mashin. Terrestrial tetrapods from a number of Upper Permian localities of the southern Fore-Urals, which were collected by research fellows from Saratov State University and the Research Institute of Geology of this university were transferred to the PIN by G.I. Tverdokhlebova. Some of the material was collected by the author of this study in 1994 to 2001 during expeditions and individual official journeys to the localities of the Vologda, Arkhangelsk, and Orenburg regions.

Below is the list of cranial material examined in the present study.

LIST OF SPECIMENS UNDER STUDY

Utegenia shpinari Kuznetzov et Ivachnenko, 1981

Collection PIN, no. 2078; Kurty locality: Kazakhstan, Almaty Region, Kaskelenskii District, Kurty–Utegen interfluve; Lower Permian (Upper Carboniferous?), Kugaly Formation; collected by I.I. Radchenko and E.G. Novikov in 1958 and by N.N. Kalandadze in 1975.

A total of about 400 skeletons of various individual ages compose the collection. The casts of the following specimens were used in the present study: nos. 100, 103, 106, 112, 115, 130, 147, 157, 212, 219, 286, 300, 330, 337, 351–354, 357–362, 364, 366, 369–373, 374, 376–378, 380–384, 387, 388, 394, and 399.

Biarmica tchudinovi Ivachnenko, 1987

Collection PIN, no. 1581; Vyshka locality: Russia, Perm Region, Perm; Upper Permian, Lower Kazanian Substage, Baitugan Beds, *Parabradysaurus silantjevi* Zone; collected by N.M. Shomysov in 1937.

Incomplete skulls, nos. 1 (holotype) and 2.

Leptoropha talonophora (Tchudinov, 1955)

Collection PIN, no. 161; Shikhovo-Chirki locality: Russia, Kirov Region, Slobodskoi District; Upper Permian, Upper Kazanian Substage, Pechishchi Beds, *Parabradysaurus silantjevi* Zone; collected by M.N. Mikhailov in 1937.

Incomplete skull, holotype no. 72; fragmentary skull roofs, nos. 67 and 105; fragmentary lower jaw, no. 69; maxilla, no. 75; and dentaries, nos. 68 and 106.

Leptorophinae gen. indet.

Collection PIN, no. 4805; Sukhaya Loshchina locality: Russia, Orenburg Region; data on the stratigraphic position of the locality are not available.

Tooth, no. 1.

Microphon exiguus Ivachnenko, 1983

Collection PIN, no. 3585; Donguz 6 locality: Russia, Orenburg Region, Orenburgskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone, Malaya Kinel Formation; collected by N.N. Kalandadze and M.F. Ivakhnenko in 1972 and by D.L. Sumin in 1995.

Juvenile skulls, nos. 25 (holotype *Raphanodon tverdochlebovae*), 89, 92, 107–111, 113, 114, 140, 203, and 207; squamosals, nos. 28 and 103; maxillae, nos. 26, 31 (holotype), 101, 142, and 204; dentaries, nos. 24, 129, and 141; and teeth, nos. 130–132, 144–164, 166, 168–183.

Collection PIN, no. 4547; Poteryakha 1 locality: Russia, Vologda Region, Nyuksenskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone, Poldarsa Formation; collected by V.K. Golubev in 1993.

Maxillae, nos. 2, 3, and 5; and ectopterygoid, no. 4.

Collection PIN, no. 3713; Poteryakha 2 locality: Russia, Vologda Region, Nyuksenskii District; Upper Permian, Upper Tatarian Substage, *Proelginia permiana* Zone, Poldarsa Formation; collected by V.K. Golubev in 1993 and by V.V. Bulanov in 1995.

Skull roof fragments, nos. 48, 53, 60, 61, and 75; nasal, no. 86; squamosal, no. 49; maxillae, nos. 45–47, and 72; dentaries, nos. 50, 52, and 59; and teeth, nos. 66–71, 73, 76–85, 171–180.

Collection PIN, no. 4723; Kochevala 2 locality: Russia, Vologda Region, Nyuksenskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone, Poldarsa Formation; collected by V.L. Mashin in 1994.

Premaxilla, no. 2; and dentary, no. 1.

Collection PIN, no. 3709; Navoloki locality: Russia, Vologda Region, Nyuksenskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone, Poldarsa Formation; collected by V.K. Golubev in 1993.

Squamosal, no. 30; and teeth, nos. 24–29.

Collection PIN, no. 4548; Ust'e Strelny locality: Russia, Vologda Region, Velikoustyugskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone; collected by V.K. Golubev in 1993 and by D.L. Sumin in 1994.

Squamosal, no. 18; maxilla, no. 17; dentary, no. 2; and teeth, nos. 19–27.

Microphon gracilis Bulanov, sp. nov.

Collection PIN, no. 4617; Babintsevo locality: Russia, Orenburg Region, Grachevskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone; collected by G.I. Tverdokhlebova in 1976.

Juvenile skulls, nos. 109, 110 (holotype), 170, 185, 189, and 190; squamosals, nos. 119-121; maxillae, nos. 111–114, 175, 182, and 191; lower jaw, no. 180; dentaries, nos. 164 and 183; and pterygoid, no. 115.

Collection SGU, no. 104B; Babintsevo locality: Russia, Orenburg Region, Grachevskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone; collected by G.I. Tverdokhlebova in 1976.

Juvenile skulls, nos. 2010 and 2024.

Microphon arcanus Bulanov, sp. nov.

Collection PIN, no. 3711; Mutovino locality: Russia, Vologda Region, Velikoustyugskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone, Poldarsa Formation, Kichuga Member; collector and date of collecting are not known.

Maxilla, no. 1 (holotype).

Microphon sp.

Collection PIN, no. 523; Gorki 1 locality: Russia, Nizhni Novgorod Region, Nizhegorodskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; collected by B.P. Vjuschkov in 1949.

Squamosal, no. 111; maxilla, no. 3; and dentary, no. 112.

Collection PIN, no. 4540; Koptyazhevo locality: Russia, Orenburg Region, Buguruslanskii District; Upper Permian, Upper Tatarian Substage; collector and date of collecting are not known.

Premaxilla, no. 1.

Collection PIN, no. 2648; Vomba-Kassy locality: Russia, Chuvash Republic, Morgaushskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; collected by Yu.M. Gubin in 1980.

Squamosal, no. 9.

Collection PIN, no. 4645; Preobrazhenka locality: Russia, Orenburg Region, Buzulukskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone; collector and date of collecting are not known.

Pterygoid, no. 21.

Collection PIN, no. 4545; Titova Gora locality: Russia, Vologda Region, Babushkinskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; collected by V.K. Golubev in 1993.

Postparietal, no. 19.

Collection PIN, no. 3712; Mikulino locality: Russia, Vologda Region, Velikoustyugskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone; collected by V.K. Golubev in 1993.

Dentary, no. 2.

Collection PIN, no. 4620; Ust'-Elva locality: Komi Republic, Udorskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Deltavjatia vjatkensis* Zone; collected by D.L. Sumin and V.V. Bulanov in 1994.

Fragmentary skull roof, no. 1.

Kotlassia prima Amalitzky, 1921

Collection PIN, no. 2005; Sokolki locality: Russia, Arkhangelsk Region, Kotlasskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; collected by V.P. Amalitzky from 1899 to 1914.

Skeleton with skull, no. 74 (holotype); incomplete skull, no. 75; and tooth no. 2689.

Collection PIN, no. 4818, Gorokhovets locality: Russia, Vladimir Region, Vyaznikovskii District, town of Gorokhovets; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; collected by A.G. Sennikov in 1999 and 2000.

Squamosal, no. 881; ectopterygoid, no. 614; dentary, no. 615; and teeth, nos. 2–25, 857–863.

Kotlassiidae gen. indet.

Collection PIN, no. 4549; Klimovo 1 locality: Russia, Vologda Region, Velikoustyugskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone, Salarevo Formation; collected by Yu.M. Gubin in 1999.

Tooth, no. 10.

Ariekanerpeton sigalovi (Tatarinov, 1968)

Collection PIN, no. 2079; Sarytaipan locality: Tajikistan, Leninabadskii District; Lower Permian; collected by L.P. Tatarinov and N.N. Kalandadze in 1962 and by N.N. Kalandadze and M.F. Ivakhnenko in 1975.

A total of more than 800 complete and fragmentary skeletons of various individual ages compose the collection; the following specimens were used in the present study:

Skeleton, no. 1 (holotype); larval skeletons in host rock, nos. 254, 325, and 617.

Casts of specimen nos. 21, 35, 128, 133, 199, 218, 242, 247, 253, 309, 324, 332, 337, 347, 373, 394, 396, 398, 431, 434, 436, 478, 500, 510, 600, 608, 638, 641, 686, 704, 764, 800, 823, 830, and 866.

Karpinskiosaurus ultimus
(Tchudinov et Vjuschkov, 1956)

Collection PIN, no. 521; Pron'kino locality: Russia, Orenburg Region, Sorochinskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; collected by B.P. Vjuschkov in 1948 and 1949.

Tabular, no. 84; maxillae, nos. 114–116, 147–150; and dentaries, nos. 54, 104 (holotype), 106–113, 140–146.

Collection SGU, no. 104B; Babintsevo locality: Russia, Orenburg Region, Grachevskii District; Upper Permian, Upper Tatarian Substage, *Proelginia permiana* Zone, Malaya Kinel Formation; collected by G.I. Tverdokhlebova in 1976.

Incomplete skulls, nos. 2008, 2009, 2031–2035; squamosal, no. 2036; maxillae, nos. 2011–2016; and dentaries, nos. 2017–2019, 2024, 2025, and 2037.

Collection PIN, no. 4617; Babintsevo locality: Russia, Orenburg Region, Grachevskii District; Upper Permian, Upper Tatarian Substage, *Proelginia permiana* Zone, Malaya Kinel Formation; collected by V.V. Bulanov in 1997.

Skulls, nos. 158, 188; maxilla, no. 186; dentaries, nos. 172–174 and 187; and tooth, no. 181.

Collection SGU, no. 104B; Vyazovka 1 locality: Russia, Orenburg Region, Orenburgskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone, Kutuluk Formation; collected by researchers from SGU, collector and date of collecting are not known.

Dentary, no. 530.

Karpinskiosaurus cf. *ultimus*

Collection SGU, no. 104B; Sambullak locality: Russia, Orenburg Region, Saraktashskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Archosaurus rossicus* Zone, Malaya Kinel Formation; collected by G.I. Tverdokhlebova in 1976.

Fragmentary skull, no. 165 (holotype *Kotlassia grandis*).

Collection PIN, no. 3582; Aristovo locality: Russia, Vologda Region, Velikoustyugskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; collected by Yu.M. Gubin in 1999.

Maxilla, no. 77.

Karpinskiosaurus secundus (Amalitzky, 1921)

Collection PIN, no. 2005; Sokolki locality: Russia, Arkhangelsk Region, Kotlasskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone, Salarevo Formation, Komaritsy Member; collected by V.P. Amalitzky from 1899 to 1914.

Skeleton with skull, no. 81 (holotype); and skull, no. 82.

Collection SGU, no. 104B; Adamovka locality: Russia, Orenburg Region, Perevolotskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone, Kutuluk Formation; collected by G.I. Tverdokhlebova in 1976.

Squamosal, no. 1075; maxillae, nos. 301, 314–319, 320–323; and dentaries, nos. 302, 303, 305, 307, 309–313.

Collection PIN, no. 2896; Blumental 3 locality: Russia, Orenburg Region, Belyaevskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone, Kutuluk Formation; collected by SGU; collector and date of collecting are not known.

Dentary, no. 5.

Collection PIN, no. 4818, Gorokhovets locality: Russia, Vladimir Region, Vyaznikovskii District, town of Gorokhovets; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; collected by A.G. Sennikov in 1999 and 2000.

Postparietal, no. 882; and teeth, nos. 851–856.

Karpinskiosaurus sp.

Collection PIN, no. 4538, Vozdvizhenka locality: Russia, Orenburg Region, Grachevskii District; Upper Permian, Upper Tatarian Substage, *Ulemosaurus svijagensis* Zone; collected by V.V. Bulanov in 1998.

Tabular, no. 4; jugal, no. 5; frontal, no. 6; and dentary, no. 2.

Collection PIN, no. 1100; Vyazniki 2 locality: Russia, Vladimir Region, Vyaznikovskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Archosaurus rossicus* Zone; collected by B.P. Vjuschkov in 1955 and 1956.

Jugal, no. 145.

Collection PIN, no. 1534; Strizhenskaya Gora locality: Russia, Vologda Region, Babushkinskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone, Salarevo Formation; collected by V.K. Golubev in 1993.

Parietal, no. 18.

Karpinskiosaurinae gen. indet.

Collection PIN, no. 4416; Ust'-Koin locality: Komi Republic, Knyazhpogostskii District; Upper Permian, Lower Kazanian Substage, *Parabradysaurus silantjevi* Zone; collected by P.K. Tchudinov in 1975.

Dentary, no. 14; and marginal tooth, no. 43.

Almost every specimen under study was treated mechanically and chemically to examine the morphology in detail. In laboratory conditions, large preparatory work was needed for the examination of specimens from the Poteryakha 2, Donguz 6, Babintsevo, Pron'kino, and Adamovka localities. In some cases, isolated teeth were found by washing the rock of the bone beds (Gorokhovets) or dissolution of rock blocks using acetic acid of low concentration (Poteryakha 1, Poteryakha 2; Donguz 6, Navoloki, Klimovo 1, etc.). Microphotographs were taken with the aid of a scanning microscope CemScan 4 (PIN); prior to taking photos of macrofossils, they were usually sprayed with the ammonium chloride. Some pictures were obtained by scanning objects with subsequent tone correction of the digitized images (squamation and imprints of external gills of *Ariekanerpeton*).

The state of specimens of *Utegenia shpinari* and *Ariekanerpeton sigalovi* recommends the use of plastic contact copies of imprints in the host rock for the examination of cranial structures. Regarding the first species, this is associated with the characteristics of the host rock (laminated siliceous schist), which allow no mechanical treatment of the enclosing rock and bone specimens (where bony tissue is replaced by calcium carbonate). In the second case, the use of this technique is due to disintegration of the bone tissue by a thermal effect on the rocks of the intrusive stock (Kuznetsov and Ivakhnenko, 1981; Ivakhnenko, 1981).

As the plastic models of *Ariekanerpeton* were produced, fossil bone tissue burnt to the powder state was removed from the hard siltstone matrix; subsequently, they were used as a mold for plastic copies. Of particular value are models of larval *Ariekanerpeton* from claystone interbeds, which occasionally show certain morphological features rarely observed in fossils, such as squamation and imprints of branchiomeres.

Latex models of *Utegenia* were produced after treatment by hydrochloric acid, which etched off the calcite replacing the bone tissue. This technique allows one to obtain contact copies of imprints of as high a quality as well-preserved original specimens and reveals even the tiniest structural details (e.g., narrow ridges on the tooth crowns of animals the skulls of which are 30 mm long or even shorter). In the type locality, skeletons of *Utegenia* occurred in several schist interbeds (Kuznetsov and Ivakhnenko, 1981); only some rock blocks were split in plates containing bone fossils. In this case, the rock enclosing a skeleton was mechanically removed on one side; this allowed for special treatment and examination of the counterpart of natural imprints. In the case where bones were exposed in cross breaks of the host rock, chemical treatment alternated with the removal of rock from one side of the cavities formed by etching. Prior to the production of plastic models, an imprint in the rock was impregnated with a butyral solution. We failed to study the skeletons enclosed in rock with the aid of x-ray analysis.

THE FOLLOWING ABBREVIATIONS ARE USED IN THE FIGURES AND PLATES

(*An*) angular;

(*ap*) groove of the postchoanal anastomosis of the palatine and infraorbital arteries;

(*cicp*) intercapsular crest of the endocranial print;

(*cot*) orbitotemporal crest of the endocranial print;

(*ctr*) transverse crest;

(*D*) dentary;

(*Ect*) ectopterygoid;

(*Ep*) epipterygoid;

(*Ex*) exoccipital;

(*F*) frontal;

(*faia*) anterior foramen for the infraorbital artery;

(*faip*) posterior foramen for the infraorbital artery;

(*fl.*) any articular area for a certain bone (e.g., *fl.Mx* is an articular area for the maxilla);

(*fpa*) articular fossa for the preorbital process;

(*fpq*) paraquadrate foramen;

(*It*) intertemporal;

(*L*) lacrimal;

(*Mx*) maxilla;

(*P*) parietal;

(*Par*) parasphenoid;

(*Pmx*) premaxilla;

(*poct*) occipital process of the tabular;

(*Por*) postorbital;

(*Pp*) postparietal;

(*ppt*) paroccipital process of the tabular;

(*Pra*) prearticular;

(*Psf*) postfrontal;

(*Qj*) quadratojugal;

(*sio*) infraorbital groove of the seismosensory system;

(*Smx*) septomaxilla;

(*Sq*) squamosal;

(*St*) supratemporal;

(*T*) tabular;

(*tsin*) bones of the intercapsular roof.

CHAPTER 3. SYSTEMATICS OF THE ORDER SEYMOURIAMORPHA

In the present study, I follow the taxonomic system of the higher taxa of the class Parareptilia proposed by Ivakhnenko (1987); the main changes in the order Seymouriamorpha concern the taxa of family rank.

On the basis of cranial morphology, the Seymouriamorpha are divided into two superfamilies, Kotlassioidea and Seymourioidea, showing the main evolutionary trends of the group. Seymouriamorphs were initially divided into superfamilies by Tatarinov (1972); however, the volume and composition of the superfamilies were different. In particular, it is worthwhile to raise the rank of the Utegeniidae and oppose them to other discosauriscids (*Discosauriscus* and *Ariekanerpeton*); this agrees well with the data accumulated in recent studies. On the basis of the relationships of *Discosauriscus* and *Ariekanerpeton* with Late Permian karpinskiosaurs from Eastern Europe, they are combined in the family Karpinskiosauridae Sushkin, 1925 (composed of the subfamilies Discosauriscinae and Karpinskiosaurinae, respectively). The genus *Urumqia* is considered to be a junior synonym of *Utegenia*. Certain distinctions seen in the figures accompanying the original description of *Urumqia* (Zhang *et al.*, 1984, text-fig. 1) are most likely of species rank; thus, this Chinese form is probably a species closely related to *Utegenia shpinari* rather than a separate genus.

The genus *Raphanodon* Ivachnenko 1987 (= *Raphaniscus* Bulanov, 2000) is considered to be a junior synonym of *Microphon* Ivachnenko, 1983 (Bulanov, 2000; 2002). Two new species of this genus, *Microphon gracilis* sp. nov. and *M. arcanus* sp. nov., are described in this study. New data allow for the conclusion that *Microphon* and other leptorophids are similar to *Kotlassia prima* from the Northern Dvina. Therefore, the family name Leptorophidae should be replaced by the Kotlassiidae (nomen introduced by Romer as early as 1934); this family is divided into the subfamilies Leptorophinae and Kotlassiinae. *Kotlassia grandis* established on the basis of poorly preserved specimens from the Sambullak locality (Tverdokhlebova and Ivakhnenko, 1984) is a karpinskiosaurine that is formally indistinguishable using key cranial characters from *Karpinskiosaurus ultimus*.

In the earlier studies, *Nyctiboetus liteus* and aberrant *Enosuchus breviceps* were excluded from the order Seymouriamorpha (Ivakhnenko *et al.*, 1997; Ivakhnenko, 2001). The first was transferred to gephirostegid anthracosaurs mainly on the basis of the apopareial pattern of the skull roof and the presence of the adsymphysial plate in the lower jaw. The second is characterized by the absence of intertemporal, the beamlike pattern of surface sculpturing, extraordinarily thickened and stout cranial bones, and an unusual endocranial imprint; therefore, it is currently assigned to a separate reptiliomorph family.

The family Seymouriidae, in addition to the type genus, includes *Rhinosauriscus* Kuhn, 1968 characterized on the basis of published data only.

The diagnoses and comparisons of the species from the genera *Seymouria* and *Discosauriscus* are omitted; these genera were recently revised by Laurin (1995, 1996a) and Klembara (1997).

CLASS PARAREPTILIA

Order Seymouriamorpha

Diagnosis. Separate intertemporal, postparietal, and tabular retained in skull roof. Two splenials and three toothed coronoids present in lower jaw. Postorbital skull region extended. Prefrontals and postfrontals coming in wide contact above orbit. Ascending lamina of maxilla undeveloped or relatively weakly developed. Premaxillae lacking palatine processes. Parasphenoid with long cultriform process. Marginal teeth with plicate bases. Medial and posterior to choana, palate with large teeth, comparable in size to marginal teeth. Shagreen teeth on palatal surface not arranged in specialized rows.

Comparison. The Seymouriamorpha differ from the Procolophonomorpha and Nycteroleteromorpha by the presence of well-developed intertemporals, postparietals, and tabulars; the presence of two splenials and three toothed coronoids in the lower jaw; a relatively longer postorbital skull region; the presence of contact between the prefrontal and the postfrontal; the absence or weak development of the ascending lamina of the maxilla; the absence of palatine processes of the premaxillae; extended ensiform process of the parasphenoid; plicate bases of marginal teeth; the presence of large palatal teeth medial and posterior to the choana; and the absence of specialized rows of shagreen teeth on the palatine surface.

In addition, seymouriamorphs differ from the Procolophonomorpha by their smaller orbits and the absence of notches between the quadratojugal and the jugal; they differ from the Nycteroleteromorpha by the nonpitted pattern of surface ornamentation on the skull roof.

Composition. Two superfamilies, Kotlassioidea Romer, 1934 and Seymourioidea Williston, 1911.

Occurrence. Lower Permian of Western Europe, Central Asia, China, and North America; Upper Permian of European Russia.

Superfamily Kotlassioidea Romer, 1934

Diagnosis. Anterior edges of otic notches located in line with midlength of supratemporals. On dorsal surface of skull roof, postparietals larger than tabulars. Parafenestral wings of parasphenoid short. Rostrum of parasphenoid and bases of quadrate rami of pterygoids covered by shagreen teeth.

Composition. Two families, Utegeniidae Ivachnenko, 1987 and Kotlassiidae Romer, 1934.

Occurrence. Lower Permian of Central Asia and China; Upper Permian of European Russia.

Family Utegeniidae Ivachnenko, 1987

Diagnosis. Skull at most 50 mm long. Parietal foramen large. In adults, maxilla with more than 30 teeth and dentary with more than 40 teeth. Marginal teeth retaining unicuspid pattern at all ontogenetic stages. In anterior region of upper jaw, teeth strongly differentiated by size. Vomer and palatine with at most three large teeth each. Endocranium nonossified.

Generic composition. Type genus.

Occurrence. Lower Permian of Central Asia and China.

Genus *Utegenia* Kuznetzov et Ivachnenko, 1981

Pelosaurus: Konzhukova, 1963, p. 104.

Utegenia: Kuznetsov and Ivakhnenko, 1981, p. 104; Ivakhnenko, 1987, p. 21; Laurin, 1996b, p. 374.

Urumqia: Zhang *et al.*, 1984, p. 304; Li and Cheng, 1995, p. 35.

Type species. *Utegenia shpinari* Kuznetzov et Ivachnenko, 1981.

Diagnosis. Genus of a monotypic family.

Species composition. Type species.

Remarks. Following Ivakhnenko (1987), the genus *Urumqia* is considered here to be a junior synonym of *Utegenia*. Certain distinctions discovered on the basis of figures accompanying the original description of *Urumqia* (Zhang *et al.*, 1984, text-fig. 1), in particular, shorter frontals, elongated nasals, and expanded otic flank of the squamosal, are most likely attributable to erroneous reconstruction or age differences. It is likely that China was inhabited by a species closely related to *Utegenia shpinari*, the validity of which necessitates a special substantiation.

Utegenia shpinari Kuznetzov et Ivachnenko, 1981

Pelosaurus laticeps: Konzhukova, 1963, p. 104.

Utegenia shpinari: Kuznetsov and Ivakhnenko, 1981, p. 105; Ivakhnenko, 1987, p. 21; Laurin, 1996b, p. 374.

?Urumqia liudaowanensis: Zhang *et al.*, 1984, p. 304.

Holotype. PIN, no. 2078/1, skeleton; Lower Permian, Kugaly Formation; Kazakhstan, Almaty Region, Kaskelenskii District, Kurty locality.

Diagnosis. Species of a monotypic genus.

Occurrence. Type locality.

Family Kotlassiidae Romer, 1934

Diagnosis. Definitive skull more than 50 mm long. Parietal foramen small. Maxilla with at most 25 teeth and dentary with at most 30 teeth. In adults, marginal tooth crowns with supplementary denticles. Large palatal teeth arranged in mediochoanal and postchoanal rows. Teeth in premaxilla and anterior region of maxilla only weakly differentiated. Endocranium ossified at definitive stage.

Composition. Two subfamilies, Leptorophinae Ivachnenko, 1987 and Kotlassiinae Romer, 1934.

Comparison. The Kotlassiidae differ from the Utegeniidae by their larger size; small parietal foramen; a smaller number of marginal teeth, the presence of supplementary denticles at late ontogenetic stages; the absence of clear size differentiation of teeth in the anterior region of the upper jaw; ossified endocranium and a larger number of large palatal teeth arranged in specialized rows.

Remarks. The presence of denticulate crowns of marginal teeth is characteristic of the majority of kotlassiidae. The unicuspid crowns of *Kotlassia prima* are a result of secondary simplification.

Occurrence. Upper Permian, Kazanian and Tatarian stages; European Russia.

Subfamily Leptorophinae Ivachnenko, 1987

Type genus. *Leptoropha* Tchudinov, 1955.

Diagnosis. Supratemporal widely connected to postorbital. At definitive stage, bone surfaces predominantly covered by radial ridged ornamentation. Squamosal small.

Generic composition. Two genera, *Biarmica* Ivachnenko, 1987 and *Leptoropha* Tchudinov, 1955.

Occurrence. Upper Permian, Kazanian Stage; European Russia.

Genus *Biarmica* Ivachnenko, 1987

Biarmica: Ivakhnenko, 1987, p. 43; 2001, p. 44; Ivakhnenko *et al.*, 1997, p. 15.

Type species. *Biarmica tchudinovi* Ivachnenko, 1987.

Diagnosis. Ascending lamina of maxilla undeveloped. Otic flank of squamosal shaped into wide plate. Orbitotemporal crests of endocranial imprint widely diverge anteriorly. Dentary relatively low. Coronoid process of lower jaw extremely weakly developed. Maxilla with approximately 25 teeth and dentary with approximately 30 teeth. Marginal teeth with only weakly thickened crowns, at most two small supplementary denticles present on each side of apex.

Species composition. Type species.

Occurrence. Upper Permian, Lower Kazanian Substage; European Russia.

Biarmica tchudinovi Ivachnenko, 1987

Biarmica tchudinovi: Ivakhnenko, 1987, p. 43; 2001, p. 44; Ivakhnenko *et al.*, 1997, p. 15.

Holotype. PIN, no. 1581/1, incomplete skull; Upper Permian, Lower Kazanian Substage, Baitugan Beds, *Parabradysaurus silantjevi* Zone; European Russia, Perm Region, Perm, Vyshka locality.

Diagnosis. Species of a monotypic genus.

Occurrence. Type locality.

Genus *Leptoropha* Tchudinov, 1955

Rhipaeosaurus: Tchudinov, 1955, p. 913 (partim); 1957, p. 39 (partim); Efremov and Vjuschkov, 1955, p. 17 (partim); Kalandadze *et al.*, 1968, p. 82 (partim).

Rhipeosaurus, err.: Olson, 1965, p. 302.

Leptoropha: Tchudinov, 1955, p. 914; 1957, p. 59; Efremov and Vjuschkov, 1955, p. 17; Kalandadze *et al.*, 1968, p. 82; Ivakhnenko, 1987, p. 39; 2001, p. 44; Ivakhnenko *et al.*, 1997, p. 14.

Type species. *Rhipaeosaurus talonophorus* Tchudinov, 1955.

Diagnosis. Maxilla with well-developed ascending lamina. Otic flank of squamosal narrow. Orbitotemporal crests of endocranial imprint fusing anterior to parietal foramen and forming wide ventrally projecting area within surface of frontals and nasals. Dentary high. Lower jaw with well-pronounced coronoid process. Maxilla and dentary containing up to 20 and 22 teeth, respectively. Crowns of marginal teeth strongly thickened at bases, each side of central apex with three or four large lateral denticles.

Species composition. Type species.

Comparison. *Leptoropha* differs from the genus *Biarmica* by a well-developed ascending lamina of the maxilla; a narrower otic flank of the squamosal; anteriorly converging orbitotemporal crests of the endocranial imprint, which form a wide ventrally projecting area on the frontals and nasals; a higher dentary; the presence of well-pronounced coronoid process of the lower jaw; a smaller number of marginal teeth, relatively thicker crowns; and by a larger number of larger supplementary denticles.

Occurrence. Upper Permian, Upper Kazanian Substage; European Russia.

Leptoropha talonophora (Tchudinov, 1955)

Rhipaeosaurus talonophorus: Tchudinov, 1955, p. 913; 1957, p. 55; Kalandadze *et al.*, 1968, p. 82.

Rhipaeosaurus thalanophorus, err: Efremov and Vjuschkov, 1955, p. 17.

Leptoropha novojilovi: Tchudinov, 1955, p. 914; 1957, p. 60; Efremov and Vjuschkov, 1955, p. 17; Kalandadze *et al.*, p. 82.

Leptoropha talonophora: Ivakhnenko, 1987, p. 39; 2001, p. 44; Ivakhnenko *et al.*, 1997, p. 14.

Holotype. PIN, no. 161/72, incomplete skull; Upper Permian, Upper Kazanian Substage, Pechishchi Beds, *Parabradysaurus silantjevi* Zone; European Russia, Kirov Region, Slobodskoi District, Shikhovo-Chirki locality.

Diagnosis. Species of a monotypic genus.

Occurrence. Type locality.

Subfamily Kotlassiinae Romer, 1934

Type genus. *Kotlassia* Amalitzky, 1921.

Diagnosis. Contact between supratemporal and postorbital broken by intertemporal and squamosal widely connected with each other. At definitive stage, bone surfaces predominantly covered by tuberculate, joint tuberculate, and cellular ornamentation. Squamosal very large.

Generic composition. Two genera: *Microphon* Ivachnenko, 1983 and *Kotlassia* Amalitzky, 1921.

Comparison. The subfamily differs from the Leptorophinae by the prevalence of different patterns of surface ornamentation at the late stages of ontogenetic development, the absence of contact between the postorbital and supratemporal, and a larger squamosal.

Occurrence. Upper Permian, Upper Tatarian Substage, Northern Dvina and Vyatka horizons; European Russia.

Genus *Microphon* Ivachnenko, 1983

Microphon: Ivakhnenko, 1983, p. 131; 1987, p. 52; 2001, p. 45; Ivakhnenko *et al.*, 1997, p. 16.

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

Raphaniscus: Bulanov, 2000, p. 82.

Type species. *Microphon exiguus* Ivachnenko, 1983.

Diagnosis. At definitive stage, crowns of marginal teeth moderately thickened. Tooth base near crown only slightly compressed. Lateral denticles on cutting edge not fused to form stout crests.

Species composition. Type species.

Occurrence. Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon; European Russia, Orenburg and Vologda regions and Komi Republic.

Microphon exiguus Ivachnenko, 1983

Microphon exiguus: Ivakhnenko, 1983, p. 131; 1987, p. 53; 2001, p. 45; Ivakhnenko *et al.*, 1997, p. 16.

Raphanodon tverdohlebovae: Ivakhnenko, 1987, p. 43; Ivakhnenko *et al.*, 1997, p. 15.

Raphaniscus tverdohlebovae: Bulanov, 2000, p. 83.

Holotype. PIN, no. 3585/31, juvenile maxilla; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon; Orenburg Region, Orenburgskii District, Donguz 6 locality.

Diagnosis. In skulls shorter than 30 mm in length, maxilla with at most 18 teeth and premaxilla with six teeth; crowns of marginal teeth only weakly thickened, with relatively low central apex and at most one supplementary denticle on each side of tooth apex; maxilla extended and lacking high postnasal process; quadratojugals weakly projecting ventrally; on ventral surface of squamosal, crest bordering ascending region of palatoquadrate cartilage extending along anterior edge of otic notch.

Occurrence. Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone; European Russia, Vologda and Orenburg regions: Donguz 6, Kochevala 1, Kochevala 2, Mikulino, Navoloki, Poteryakha 1, Poteryakha 2, and Ust'e Strel'ny localities.

Microphon gracilis Bulanov, sp. nov.

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

Etymology. From the Latin *gracilis* (slender).

Holotype. PIN, no. 4617/110, juvenile skull; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon; Orenburg Region, Grachevskii District, Babintsevo locality.

Diagnosis. In skulls less than 28 mm in length, maxilla with at most 13 teeth and premaxilla with seven teeth; crowns of marginal teeth substantially thickened, with high central apex and up to three supplementary denticles on each side of cutting edge; maxilla short and having well-pronounced postnasal process; quadratojugal strongly projecting ventrally relative to jugal; on ventral surface of squamosal, transverse crest bordering ascending region of palatoquadrate cartilage projecting far anterior with reference to anterior edge of otic notch.

Comparison. The new species differs from *M. exiguus* of the same size class by a smaller number of maxillary teeth and a larger number of premaxillary teeth; more thickened crown bases, a higher central apex, and a larger number of supplementary denticles on the cutting edge; a shorter maxilla; the presence of extended postnasal process on the anterior edge of the maxilla; a greater ventral projection of the quadratojugal; and a more anterior position of the transverse crest on the ventral side of the squamosal.

Occurrence. Type locality.

Microphon arcanus Bulanov, sp. nov.

Etymology. From the Latin *arcanus* (keeping secret).

Holotype. PIN, no. 3713/1, right maxilla; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon, *Proelginia permiana* Zone; Vologda Region, Velikoustyugskii District, Mutovino locality.

Diagnosis. Crowns of marginal teeth expanded proximally, club-shaped; near-crown part of tooth bases abruptly compressed laterally. Lateral denticles on cutting edge fused into broad and stout crests.

Comparison. The new species differs from *M. exiguus* and *M. gracilis* by a thicker proximal part of the tooth crowns, a greater compression of the tooth bases, and fusion of supplementary denticles into stout lateral crests. In addition, it differs from *M. gracilis* by the absence of postnasal process of the maxilla.

Occurrence. Type locality.

Genus *Kotlassia* Amalitzky, 1921

Seymouria (*Kotlassia*): Amalitzky, 1921, p. 1 (partim).

Kotlassia: Sushkin, 1925, p. 179; Bystrow, 1944, p. 380 (partim); Efremov, 1946, p. 630 (partim); Watson, 1954, p. 407; Efremov and Vjuschkov, 1955, p. 18 (partim); Olson, 1965, p. 296 (partim); Kalandadze *et al.*, 1968, p. 79; Tatarinov, 1972, p. 71 (partim); Ivakhnenko, 1987, p. 35; 2001, p. 45; Ivakhnenko *et al.*, 1997, p. 15 (partim).

Type species. *Kotlassia prima* Amalitzky, 1921.

Diagnosis. Preorbital skull region extended. Jaw condyles located anterior somewhat to occipital condyle. Crowns of marginal teeth nonexpanded and lacking supplementary denticles on cutting edge and ridges on lingual side.

Species composition. Type species.

Comparison. *Kotlassia* differs from the genus *Microphon* by the nonexpanded crowns of marginal teeth at the definitive stage and by the absence of supplementary denticles on the cutting edge and ridges on the lingual side of the tooth crowns.

In addition, it differs from, at least, some *Microphon* species by a more posterior position of the jaw joints and the prevalence of cellular surface sculpturing on the skull roof.

Kotlassia prima Amalitzky, 1921

Kotlassia prima: Amalitzky, 1921, p. 13; Bystrow, 1944, p. 380 (partim); Efremov and Vjuschkov, 1955, p. 18 (partim); Kalandadze *et al.*, 1968, p. 79; Tatarinov, 1972, p. 71; Ivakhnenko, 1987, p. 36; 2001, p. 45; Ivakhnenko *et al.*, 1997, p. 15.

Holotype. PIN, no. 2005/74, skeleton; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; European Russia, Vologda Region, Sokolki locality.

Diagnosis. Species of a monotypic genus.

Occurrence. Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; European Russia, Vologda and Vladimir regions, Sokolki and Gorokhovets localities.

Superfamily Seymourioidea Williston, 1911

Diagnosis. Otic notches deep, reaching line of anterior edge of supratemporals. On dorsal surface of skull roof, tabulars larger than postparietals. Parasphenoid with narrow and widely spaced parafenestral wings. Rostrum of parasphenoid and bases of quadrate rami of pterygoids lacking shagreen teeth.

Composition. Two families, Karpinskiosauridae Sushkin, 1925 and Seymouriidae Williston, 1911.

Comparison. The Seymourioidea differ from the Kotlassioidea by deeper otic notches; relatively large dorsal flanks of the tabulars, as compared to the postparietals; the presence of narrow and widely spaced parafenestral wings of the parasphenoid; and by the absence of shagreen teeth on the rostrum of the parasphenoid.

Occurrence. Lower Permian of North America, Western Europe, and Central Asia; Upper Permian of European Russia.

Family Karpinskiosauridae Sushkin, 1925

Diagnosis. Preorbital skull region relatively short (nasals substantially shorter than frontals). Orbital rim lacking notches in anteroventral part. Lateral regions of supratemporals and tabulars lacking massive ventral projections for articulation with zygomatic regions. Splenial not contributing to formation of symphysial surface.

Composition. Two subfamilies, Discosauriscinae Romer, 1947 and Karpinskiosaurinae Sushkin, 1925.

Occurrence. Lower Permian of central Europe (Czech Republic) and Central Asia (Tajikistan); Upper Permian of European Russia.

Subfamily Discosauriscinae Romer, 1947

Type genus. *Discosauriscus* Kuhn, 1933.

Diagnosis. Skull at most 65 mm long. Grooves of lateral line system on surface of skull roof well developed. At definitive stage, ossified endocranial elements presented by only occipital ring (exoccipitals and basioccipital) and basisphenoid. Dorsal processes of premaxillae short and premaxillary fontanel absent. Bases of marginal teeth round in cross section and having intense plicate structure. Jugal with small postorbital segment.

Generic composition. Two genera, *Discosauriscus* Kuhn, 1933 and *Ariekanerpeton* Ivachnenko, 1981.

Occurrence. Lower Permian of Central Europe (Czech Republic) and Central Asia (Tajikistan).

Genus *Ariekanerpeton* Ivachnenko, 1981

Letoverpeton: Tatarinov, 1964, p. 139.

Discosauriscus: Tatarinov, in Kalandadze *et al.*, 1968, p. 79; Tatarinov, 1972, p. 70 (partim); Kuhn, 1972, p. 32 (partim).

Ariekanerpeton: Ivakhnenko, 1981, p. 118; 1987, p. 26; Laurin, 1996c, p. 654.

Type species. *Discosauriscus sigalovi* Tatarinov, 1968.

Diagnosis. In anterior region of upper jaw, teeth clearly differentiated in size. At definitive stage, radial ridged and tuberculate ornamentation prevailing on external surface of skull roof.

Species composition. Type species.

Occurrence. Lower Permian of Tajikistan.

Ariekanerpeton sigalovi (Tatarinov, 1968)

Discosauriscus sigalovi: Kalandadze *et al.*, 1968, p. 79; Tatarinov, 1972, p. 70.

Ariekanerpeton sigalovi: Ivakhnenko, 1981, p. 118; 1987, p. 26; Laurin, 1996c, p. 654

Holotype. PIN, no. 2079/1, skeleton; Lower Permian; Tajikistan, Leninabad Region, Sarytaipan locality.

Diagnosis. Species of a monotypic genus.

Occurrence. Type locality.

Genus *Discosauriscus* Kuhn, 1933

Discosaurus: Credner, 1883, p. 294.

Discosauriscus: Shpinar, 1953, p. 26; Watson, 1954, p. 419; Kuhn, 1972, p. 32 (partim); Kalandadze *et al.*, 1968, p. 79 (partim); Ivakhnenko, 1987, p. 31; Klembara, 1997, p. 258.

Letoverpeton: Shpinar, 1953, p. 67; Kuhn, 1972, p. 32

Phaiherpeton: Romer, 1947, p. 292; Watson, 1954, p. 414.

(For detailed synonymy, see Klembara, 1997.)

Type species. *Archegosaurus austriacus* Makowsky, 1876.

Diagnosis. In anterior region of upper jaw, teeth only slightly differentiated in size. At definitive stage, cellular ornamentation prevailing on external surface of skull roof.

Species composition. Two species, *D. austriacus* (Makowsky, 1876) and *D. pulcherrimus* (Fritsch, 1879).

Comparison. *Discosauriscus* differs from *Ariekanerpeton* by insignificant size differentiation of marginal teeth in the anterior region of the upper jaw and cellular ornamentation at late ontogenetic stages.

Remarks. The taxonomic position of *Discosauriscus netschajevi* (Riabinin, 1911) from the Kuzminovskii Mine locality is uncertain; this species is apt to be a karpinskiosaurine.

Occurrence. Lower Permian, Upper Rotliegend of Czech Republic (and, probably, Germany and Poland).

Subfamily Karpinskiosaurinae Sushkin, 1925

Type genus. *Karpinskiosaurus* Sushkin, 1925.

Diagnosis. In adults, skull more than 65 mm long, canals of seismosensory system absent, and endocranium well ossified (periotic region, occipital ring, basisphenoid, and stapes). Dorsal processes of premaxillae high, fontanel preserved between them at definitive stage. Bases of marginal teeth extended and weakly plicate. Postorbital region of jugal enlarged.

Generic composition. Type genus.

Comparison. The Karpinskiosaurinae differ from the Discosauriscinae by their larger size, the reduction of canals of the seismosensory system at early ontogenetic stages, a more profound ossification of endocranial elements, the presence of long dorsal processes of the premaxillae, preservation of the premaxillary fontanel at the definitive stage, a longitudinally extended and different pattern of plication of the bases of marginal teeth, and a greater expansion of the jugal behind the orbit.

Occurrence. Upper Permian, Kazanian and Tatarian stages; European Russia.

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); Konzhukova, 1964, p. 141 (partim); Tatarinov, 1972, p. 71 (partim).

Karpinskiosaurus: Sushkin, 1925, p. 179; Watson, 1954, p. 407; Kalandadze *et al.*, 1968, p. 81 (partim); Ivakhnenko, 1987, p. 33; 2001, p. 43; Ivakhnenko *et al.*, 1997, p. 15.

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

Type species. *Kotlassia secunda* Amalitzky, 1921.

Diagnosis. Genus of a monotypic subfamily.

Species composition. Two species, *K. secundus* Amalitzky, 1921 and *K. ultimus* (Tchudinov et Vjuschkov, 1956).

Occurrence. Upper Permian, Upper Tatarian Substage, Northern Dvina and Vyatka horizons; European Russia, Arkhangelsk and Vologda 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).

?Kotlassia grandis: Tverdokhlebova and Ivakhnenko, 1994, p. 124.

Karpinskiosaurus ultimus: Ivakhnenko, 2001, p. 43; Bulanov, 2002, p. 79.

Holotype. PIN, no. 521/104, dentary; Upper Permian, Upper Tatarian Substage, Vyatka Horizon; European Russia, Orenburg Region, Sorochinskii District, Pron'kino locality.

Diagnosis. Anterior edge of otic notches in line with anterior edge of strongly extended supratemporal. Ascending lamina of maxilla undeveloped. Apices of marginal teeth only weakly curved lingually.

Occurrence. Upper Permian, Upper Tatarian Substage, Northern Dvina and Vyatka horizons, *Proelginia permiana* and *Scutosaurus karpinskii* zones; European Russia, Orenburg Region, Pron'kino, Babintsevo, and (?) Sambullak localities.

Karpinskiosaurus secundus (Amalitzky, 1921)

Kotlassia secunda: Amalitzky, 1921, p. 13; Tatarinov, 1972, p. 72.

Karpinskiosaurus secundus: Sushkin, 1925, p. 79; Watson, 1954, p. 408; Kalandadze *et al.*, 1968, p. 79; Ivakhnenko, 1987, p. 33; 2001, p. 43; Ivakhnenko *et al.*, 1997, p. 15.

Karpinskiosaurus neglectus: Sushkin, 1926, p. 339.

Kotlassia prima: Bystrow, 1944, p. 380 (partim); Efremov and Vjuschkov, 1955, p. 18 (partim).

Holotype. PIN, no. 2005/81, skeleton; Upper Permian, Upper Tatarian Substage, Vyatka Horizon, *Scutosaurus karpinskii* Zone; European Russia, Arkhangelsk Region, Kotlasskii District, Sokolki locality.

Diagnosis. Anterior edge of otic notches terminating short of reaching anterior edge of intertemporal. Intertemporal relatively small. Maxilla with ascending lamina. Apices of marginal teeth strongly curved inside mouth cavity.

Comparison. *K. secundus* differs from *K. ultimus* by a lesser depth of the otic notch, smaller intertemporal, better developed ascending lamina of the maxilla, and by a greater lingual curvature of the apices of marginal teeth.

Occurrence. Upper Permian, Upper Tatarian Substage, Northern Dvina and Vyatka horizons; European Russia, Arkhangelsk and Orenburg regions, Sokolki and Adamovka localities.

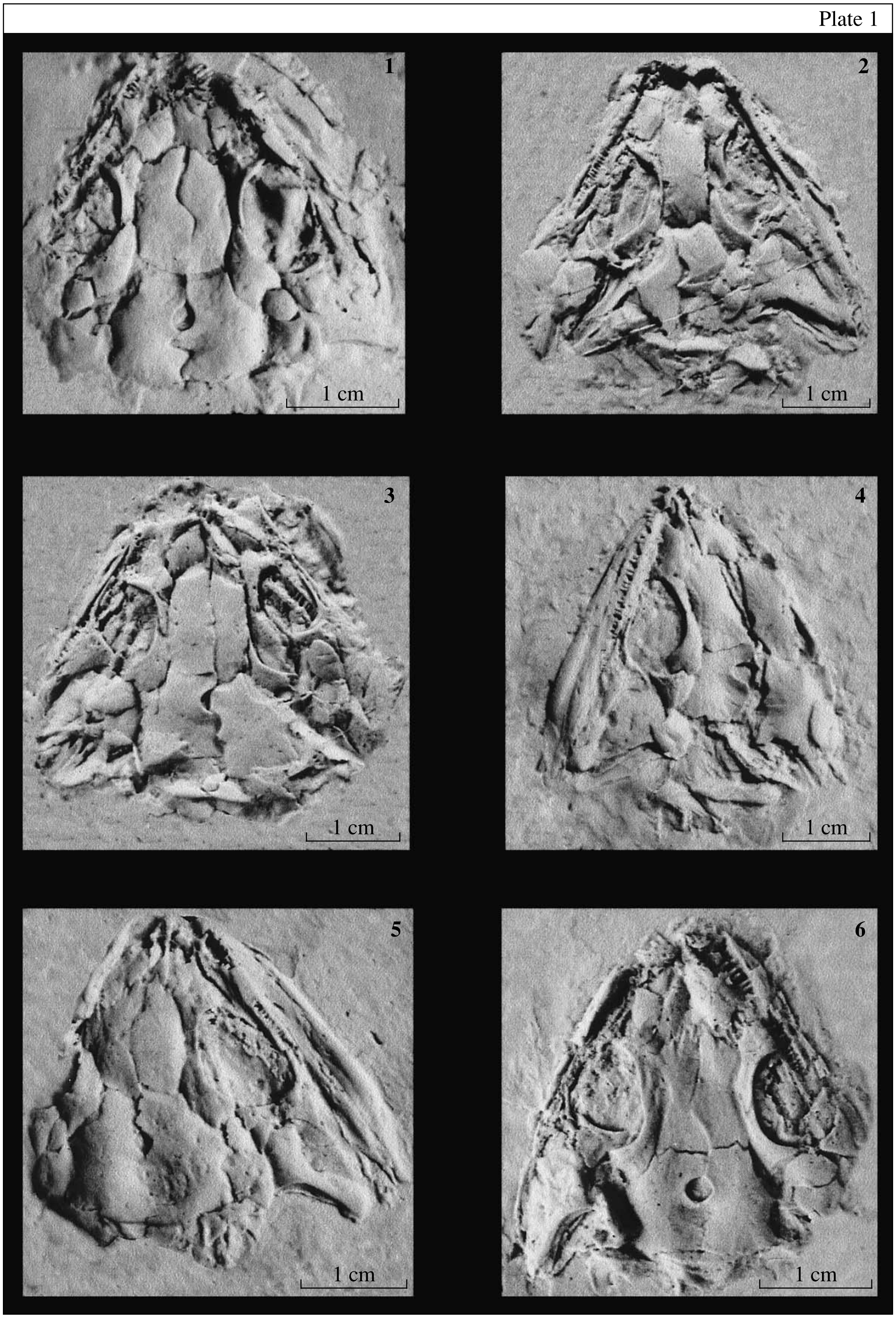
Family Seymouriidae Williston, 1911

Type genus. *Seymouria* Broili, 1904.

Diagnosis. Preorbital skull region as long as postorbital region (frontals shorter than nasals). Anterior orbital margins with wide anteriorly directed notches. Lateral areas of parietal shield forming stout and ventrally projecting crests, either side of which enveloped by expansions of squamosal. Splenial contributing to formation of symphysial surface.

Generic composition. Two genera: *Seymouria* Broili, 1904 and *Rhinosauriscus* (Fischer von Waldheim, 1847) Kuhn, 1968.

Plate 1



Comparison. The Seymouriidae differ from the Karpinskiosauridae by a relatively larger preorbital skull region, the presence of wide notches in the anterior orbital margins, a different pattern of articulation between the jugal region and the parietal shield, and the participation of the splenial in the formation of the symphysial surface.

Explanation of Plate 1

Utegenia shpinari Kuznetzov et Ivachnenko, 1981; skull casts, dorsal view; Kurty locality (Kazakhstan, Almaty Region, Kaskelenskii District; Lower Permian).

Fig. 1. Specimen PIN, no. 2078/369.
Fig. 2. Specimen PIN, no. 2078/380.
Fig. 3. Specimen PIN, no. 2078/374.
Fig. 4. Specimen PIN, no. 2078/382.
Fig. 5. Specimen PIN, no. 2078/300.
Fig. 6. Specimen PIN, no. 2078/376.

Occurrence. Lower Permian of North America and Western Europe (Germany) and Permian of Eastern Europe (Saratov Region).

Genus *Seymouria* Broili, 1904

Type species. *Seymouria baylorensis* Broili, 1904.

Diagnosis. Lacrimal reaching orbital rim.

Species composition. Three species: *S. baylorensis* Broili, 1904; *S. sanjuanensis* Vaughn, 1966; and *S. grandis* Olson, 1979.

Remarks. *Seymouria agilis* described by Olson (1980) on the basis of a postcranial skeleton has been excluded from this genus and transferred to the East European genus *Macroleter* (Reisz and Laurin, 2001).

Occurrence. Lower Permian of North America and Western Europe (Germany).

Genus *Rhinosauriscus* Kuhn, 1968

Rhinosaurus: Fischer von Waldheim, 1847, p. 363; Konzhukova, 1963, p. 140; Kalandadze *et al.*, 1968, p. 79.

Rhinosauriscus: Kuhn, 1968, p. 515; Tatarinov, 1972, p. 73.

Type species. *Rhinosaurus jasykovii* Fischer von Waldheim, 1847.

Diagnosis. Lacrimal terminating short of reaching orbital rim.

Species composition. Type species.

Comparison. *Rhinosauriscus* differs from *Seymouria* by the lacrimal terminating short of reaching the orbital rim.

Rhinosauriscus jasykovii (Fischer von Waldheim, 1847)

Rhinosaurus jasykovii: Fischer von Waldheim, 1847, p. 366; Konzhukova, 1963, p. 140; Kalandadze *et al.*, 1968, p. 79.

Rhinosauriscus jasykovii: Kuhn, 1968, p. 515; Tatarinov, 1972, p. 73.

Holotype. Lost, Permian of Saratov Region.

Diagnosis. Species of a monotypic genus.

Occurrence. Permian of Eastern Europe.

CHAPTER 4. CRANIAL MORPHOLOGY

This chapter describes in detail the cranial morphology of seymouriamorph species presented in the collections under study. The descriptions are arranged taxonomically. Each description considers the following characteristics: a brief history of its study, general characteristics, skull roof, palatal complex, lower jaw, dentition, surface ornamentation, grooves of the seismosensory system, and endocranium.

Order Seymouriamorpha Watson, 1917

Superfamily Kotlassioidea Romer, 1934

Family Utegeniidae Ivachnenko, 1987

Genus *Utegenia* Kuznetzov et Ivachnenko, 1981

Utegenia shpinari Kuznetzov et Ivachnenko, 1981

The material on *Utegenia shpinari* comes only from the type locality (Kurty, Kazakhstan) and comprises many complete skeletons belonging to various age stages. These animals were first identified by Konzhukova (1963) as branchiosaurs of the genus *Pelosaurus* (*P. laticeps*). The use of a new technique for reexamination of the first specimens collected in 1958 and extensive material obtained by a special expedition (1975) has shown that the animal from the Kurty locality belongs to a new genus and species of seymouriamorph amphibians, *Utegenia shpinari* (Kuznetsov and Ivakhnenko, 1981). In the original description, *Utegenia* was assigned to the family Discosauriscidae. In the subsequent revision of seymouriamorphs, Ivakhnenko (1987) retained the same taxonomic position of this genus. However, it was assigned to a separate subfamily and considered to be a senior synonym of *Urumqia* from China. Laurin (1996b) partially reexamined the material from the Kurty locality and considered the Discosauriscidae to be a paraphyletic group; in essence, he proposed to exclude *Utegenia* from the family. Additional data on the distribution of seismosensory structures on the skull roof of *Utegenia* were provided by Malachov (2000a).

The collection stored at the PIN contains about 400 specimens, the examination of which is far from being accomplished (for the technique, see section *Material* and *Methods*). The description given below is based on only a small part of available specimens.

General characteristics. The skull is extended triangular in plan and has a relatively narrow preorbital region. It was undoubtedly high, as indicated by the curved transverse contour of the parietals (e.g., specimen PIN, no. 2078/369; Pl. 1, fig. 1); this shows the gently sloping position of the entire parietal shield and the basically steep position of the zygomatic regions (Fig. 2a). The state of the majority of specimens is

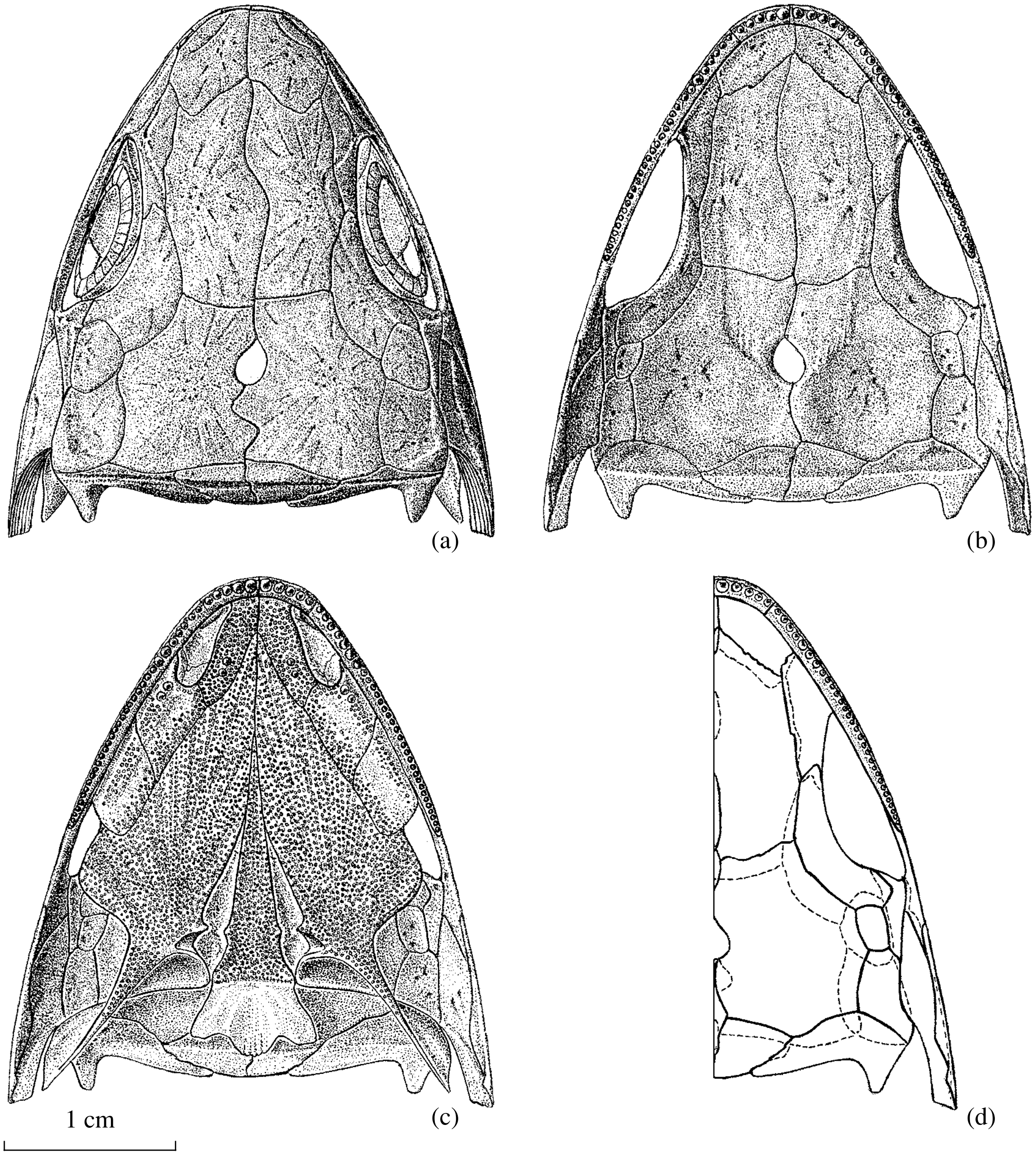


Fig. 2. *Utegenia shpinari*, skull, reconstruction based on specimens PIN, nos. 2078/369, 376, and 388: (a, b) skull roof: (a) dorsal and (b) ventral views; (c) palatal complex, ventral view; and (d) relative positions of dorsal and ventral boundaries of the bones of the skull roof.

indicative of such a cranial structure, since the bones are usually disarticulated in the temporal region of the dermatocranium; in a number of cases, paired bones of the axial region, i.e., the parietals, frontals, and (or) nasals, partially or completely overlie each other as a result of a dorsoventral compression in the burial (e.g., specimens PIN, nos. 2078/374, 380; Pl. 1, figs. 2, 3).

The skull of the largest *Utegenia* examined in this study is 30 mm long (PIN, no. 2078/378); however, Malachov (2000a) has indicated that, occasionally, it is larger and reaches 40 mm in length.

The occipital edge of the parietal shield is straight or, occasionally, slightly curves posteriorly. The orbits are large, widened posteriorly, and narrowed somewhat in the anterior region (Pl. 1; fig. 4). The otic notches are very shallow, their anterior walls are in line with the anterior boundary of the posterior one-third of the supratemporal (specimen PIN, no. 2078/300; Pl. 1, fig. 5); however, it is not improbable that, in certain large animals, the notches extended to the midlength of the supratemporal (specimen PIN, no. 2078/361). At the definitive ontogenetic stage, the jaw condyles are located posterior to the occiput. Although the preorbital region is narrow, the nares faced mainly anteriorly, as indicated by the notches in the nasals (specimens PIN, nos. 2078/369, 374, etc.)

Skull roof. The parietals are short; anterolaterally, they have large notches for the postfrontals. The parietal foramen is large and, usually, irregularly teardrop-shaped. Posterior to the foramen, the medial suture is usually zigzag (Pl. 1, fig. 1). The frontals are substantially longer than the parietals, their maximum width is in line with the orbital center. The boundary between the frontals is usually shaped into a broad zigzag. A distinctive feature is that, in all specimens, the frontals enter the preorbital region and strongly wedge in between the nasals along the medial suture; as a result, the nasals are extended rhombic. The anterior ends of the nasals form narrow flanks for the attachment of the dorsal processes of the premaxillae.

The prefrontal is usually shorter than the postfrontal; however, the opposite situation is occasionally observed (specimens PIN, nos. 2078/212, 376; Pl. 1, fig. 6). These bones come into relatively narrow contact with one another. The postorbital is extended triangular and has a strongly extended caudal process connected posteriorly to the supratemporal. In the majority of satisfactorily preserved specimens, the presence of this articulation is evident (e.g., specimens PIN, nos. 2078/300, 369; Pl. 1, figs. 1, 5); however, in the case where the intertemporal is large, it can be reduced to a point (specimen PIN, no. 2078/361; Pl. 2, fig. 3) or broken (specimen PIN, no. 2078/388). The intertemporal widely varies in size independently of the size variation of the skull. The supratemporal is larger than the intertemporal; in some cases, the intertemporal is very small (e.g., specimen PIN, no. 2078/300; Pl. 1, fig. 5). In specimens PIN, nos. 2078/362 and 383 (Pl. 2, figs. 1, 2), the intertemporal is large, almost equal in size to the supratemporal. Within the available material, the left and right intertemporals of the same skull are similar in size.

The postorbital region of the jugal is strongly developed and extends far posteriorly along the suture between the quadratojugal and the squamosal. Anteriorly, the jugal closely approaches the anterior orbital rim (specimens PIN, nos. 2078/366, 380, 381) where a significant area of this bone is covered by a long infraorbital process of the lacrimal (specimen PIN, no. 2078/351). In the postnasal region, the lacrimal strongly expands dorsally; the high distal wall of the naris is formed exclusively by this element. The canal of the nasolacrimal duct passes along the boundary between the lacrimal and the maxilla. In specimen PIN, no. 2078/380, the right lateral wall of the canal is underossified in the area adjoining the orbit (Pl. 1, fig. 2). The septomaxilla freely lies in the nasal cavity and looks like a weakly curving plate. The septomaxillary foramen remains unclosed (specimens PIN, nos. 2078/378, 380).

The bones forming the occipital edge are strongly reduced dorsally. The tabulars are narrow bands terminating short of reaching the otic notches and limited laterally by the characteristic protrusions of the supratemporals. The paroccipital processes are narrow and long and extend posteriorly and somewhat medially (Pl. 1, figs. 1). Their ends are positioned closer to the horizontal than the occipital plates and isolated from the latter by deep notches. Even in the largest animals, the postparietals are very short, only slightly wedge in the posterior region of the parietals, and the only a little larger than the tabulars. At the boundary between the parietals and postparietals of specimen PIN, no. 2078/374, there is a separate additional membrane bone; it is pentagonal and has a well-pronounced anterior plate spreading under the parietals (Pl. 1; fig. 3).

The otic flank of the squamosal is shaped into a narrow plate framing the otic notch anteriorly. The squamosal is isolated from the orbital rim by the postorbital and jugal coming into a broad contact with each other. The posterior edge of the squamosal is located posterior to the occiput. The quadratojugal only slightly projects ventrally with reference to the jugal and, expanding dorsally, covers the posterior edge and, in some specimens, a part of the dorsal edge of the jugal (specimens PIN, nos. 2078/380, 382). Anteriorly, the bone most likely terminates short of reaching the level of the posterior orbital rim.

Fragmentary sclerotic rings are preserved in the orbits of many specimens. A complete ring consists of 22 rectangular elements approximately equal in size (specimen PIN, no. 2078/382; Pl. 1, fig. 4).

The premaxillae have narrow and very short dorsal processes closely adjoining each other so that there is no room for the premaxillary fontanel. The fontanel are probably present in only specimen PIN, no. 2078/378, since the anterior edges of its nasals are isolated from each other at the medial suture and the medial flanks of the processes of the premaxillae are weakly concave.

The palatine processes are absent. The bone is connected to the maxilla at the midlength of the nares. The premaxilla of *Utegenia* usually contains five teeth (specimens PIN, nos. 2078/376, 382, 383); exceptionally, four (specimen PIN, no. 2078/381) or six premaxillary teeth are observed (specimen PIN, no. 2078/370).

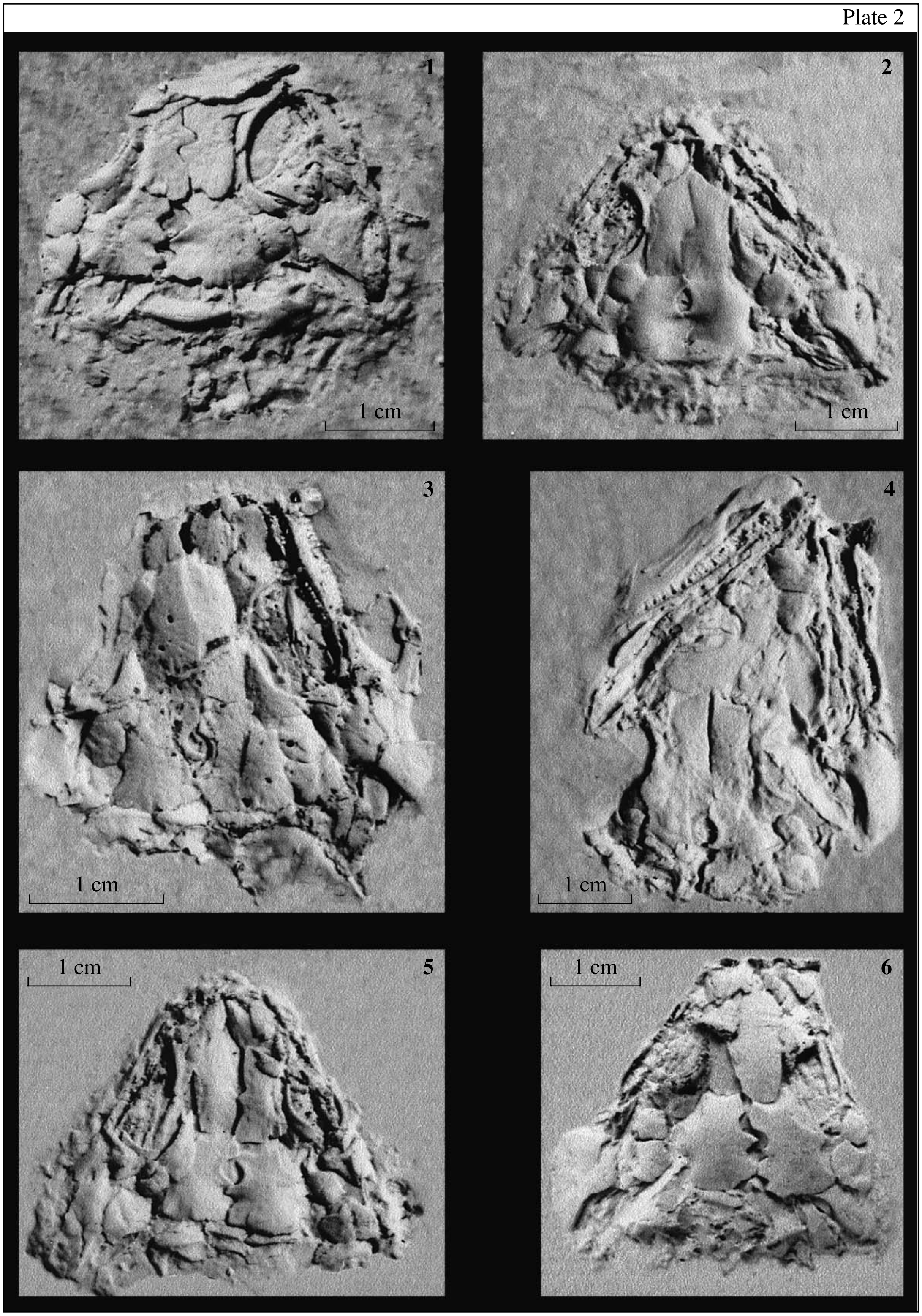
The maxilla is low and terminates short of reaching the posterior wall of the orbit and far from the quadratojugal so that it never contacts this bone. The anterior region of the bone is pierced labially by numerous small foramina; in the posterior part of the maxilla, the foramina are usually arranged in a row and accompanied by furrows extending posteriorly.

The maxilla contains up to 32 teeth (specimen PIN, no. 2078/388).

The presence of a large number of more or less disarticulated skulls allows one to examine in detail the relative positions of the boundaries between dermatocranial bones on the ventral and dorsal surfaces (Fig. 2d) and discover the features of the endocranial imprint (Fig. 2c).

In the axial region, the anterior bones successively overlap the bones located posteriorly, i.e., the nasals overlie the frontals and the frontals overlie the parietals,

Plate 2



which spread under all neighboring bones, except for the postparietals and tabulars positioned posteriorly. The intertemporal is in the external position and overlies all adjacent bones so that only its central part containing foramina for nerves and blood vessels is exposed on the ventral surface. The medial plate of the squamosal articulated with the parietal shield is relatively narrow; however, it extends along the entire medial flank of the bone. The bones contributing to the formation of the orbital rim slightly overlap each other; only the postfrontal substantially narrows on the ventral side and expands on the ventral surface of the orbital

Explanation of Plate 2

Utegenia shpinari Kuznetzov et Ivachnenko, 1981; skull casts, dorsal view; Kurty locality (Kazakhstan, Almaty Region, Kaskelenskii District; Lower Permian).

Fig. 1. Specimen PIN, no. 2078/362.

Fig. 2. Specimen PIN, no. 2078/383.

Fig. 3. Specimen PIN, no. 2078/361.

Fig. 4. Specimen PIN, no. 2078/212.

Fig. 5. Specimen PIN, no. 2078/381.

Fig. 6. Specimen PIN, no. 2078/387.

rim to a greater extent than on the dorsal surface. The quadratojugal forms a wide plate spreading under the external flank of the squamosal. The lacrimal is high and strongly overlaps the prefrontal and its infraorbital process overlies the anterior region of the jugal.

The orbitotemporal crests on the ventral side of the parietals originate from the posterior edge of the parietal foramen and widely diverge laterally. Short of the anterior boundary of the parietals, they abruptly curve and extend almost in parallel to each other to the ossification centers of the frontals; further anteriorly, they become indiscernible. A wide intercapsular crest divides a concave roof of the parietals into two. In the anterior part of the tabular, there is an oblong depression.

Palate. The choanae are extended and weakly narrowed in the anterior part (Fig. 2b). The vomers are connected to each other by weakly expanded anterior regions; posteriorly, they are drawn apart by the anterior rami of the pterygoids deeply wedging in between the vomers. The laterochoanal process of the palatine is well developed (specimens PIN, nos. 2078/359, 369). The vomer adjoins the palatine at the posterior edge of the choana. The ectopterygoid is approximately equal in size to the palatine; however, it is somewhat narrower. The medial edges of the vomer, palatine, and ectopterygoid are aligned; none of these bones wedge in the pterygoids to a greater extent than the others (specimens PIN, nos. 2078/147, 380; Pl. 3, figs. 1, 2).

The pterygoid flanges strongly project in the adductor cavities and curve ventrally (specimen PIN, no. 2078/369; Pl. 1, fig. 1). The angle between the flanges and the quadrate rami is approximately 90°. The parasphenoid has a wide rostrum, the anterior region of which is bounded by the palatine rami of the pterygoids, adjoining each other within an extended interval between the rostrum and the vomers. A prominent boundary isolates the toothed anterior region of the bone from the posterior region lacking teeth. In a number of specimens, the bone is deformed in this area by compression (it is pressed in ventrally, see specimens PIN, nos. 2078/359, 366; Pl. 3, figs. 3, 4), probably attributable to the presence of a cartilage bone, sellae turcica, on the dorsal side.

The parafenestral wings are clearly defined; however, they are short and oriented posterolaterally (Pl. 3, fig. 5). The parasphenoid of *Utegenia* widely varies in width. Occasionally, the bone edges are weakly concave in the area of the basipterygoid articulation (specimens PIN, nos. 2078/359, 382; Pl. 3, fig. 3).

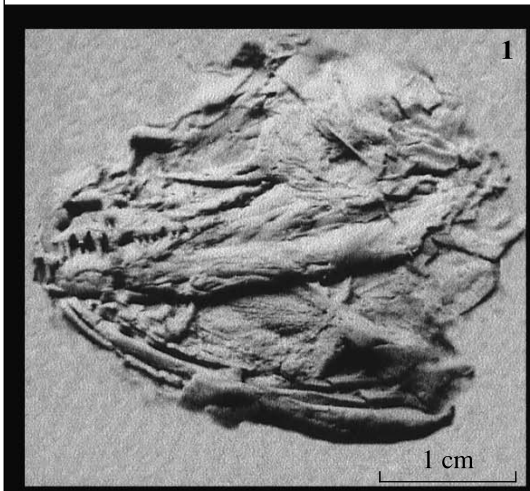
Lower jaw. The dentary is three times as long as the postdentary region of the lower jaw (Fig. 4e). The coronoid process is undeveloped. The lower margin of the angular is broad and round in cross section and the angular crest is absent. The internal wall of the adductor cavity of the lower jaw lowers posteriorly and the minimum depth is observed near the articulation. The upper edge of the prearticular gently curves medially anterior to the condyle. The splenial terminates short of reaching the symphysis and widely spreads under the postsplenial, which is twice as long and forms a large expansion underlying the angular. The posterior edge of the postsplenial is located opposite the end of the tooth row. Both bones occupy ventral positions and virtually lack expansion on the external side of the jaw. Using available material, it is impossible to discover the boundaries between the coronoids and determine with certainty the relative positions of the prearticular, splenial, and dentary.

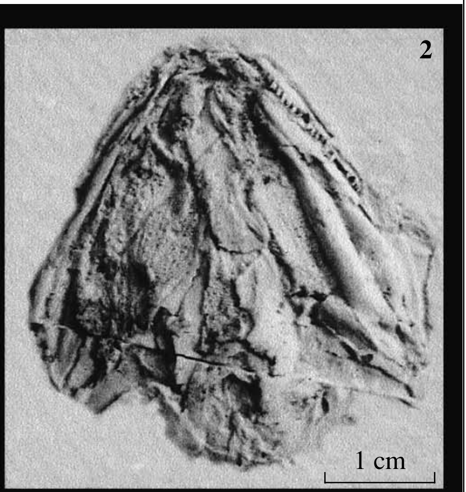
The posterior region of the dentary is long and pointed and extends far posteriorly above the surangular. The posterior margin of the latter bone contains a foramen facing posteriorly (specimens PIN, nos. 2078/300, 380). The labial side of the symphysial region is strongly perforated; in the posterior region of the bone, the foramina are smaller in number and accompanied by dichotomizing furrows directed mainly posteriorly. The main foramen for the mandibular artery enclosed in the Meckel's groove opens opposite the fifteenth most posterior mandibular tooth (specimen PIN, no. 2078/354). The lower jaw of *Utegenia* contains up to 44 teeth (specimen PIN, no. 2078/354).

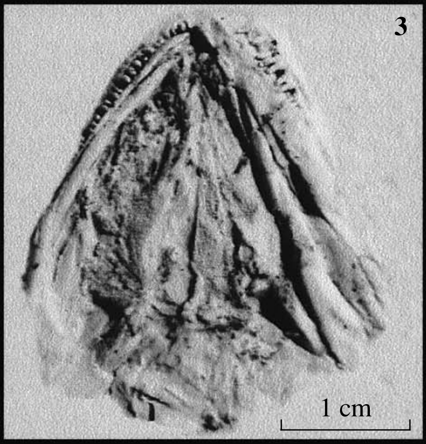
Dentition. At the level of attachment to the bone, the bases of the marginal teeth are round in cross section (Fig. 3). Plication is usually observed in only the proximal region of the teeth; however, in large teeth from the preorbital region of the upper jaw, the folds closely approach the crowns. The folds observed over the perimeter of the tooth base are small in number. The great depth of the external grooves is probably associated with the penetration of the folds deep into the pulp cavity.

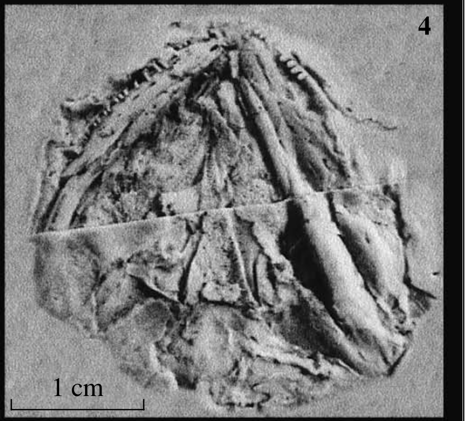
The high unicuspid crowns are covered by prominent ridges on both the lingual and labial sides (in the plastic models, the ends of these ridges are considered to be an indicator of the boundary of the enamel-like

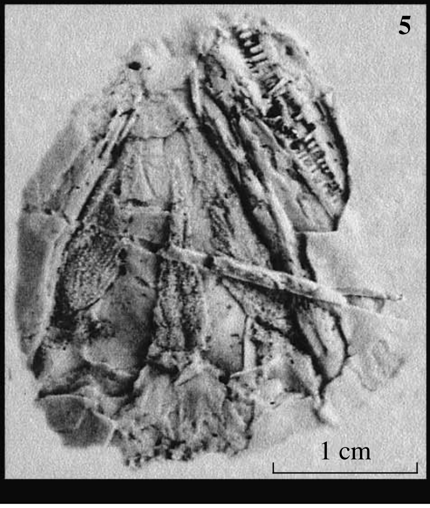
Plate 3

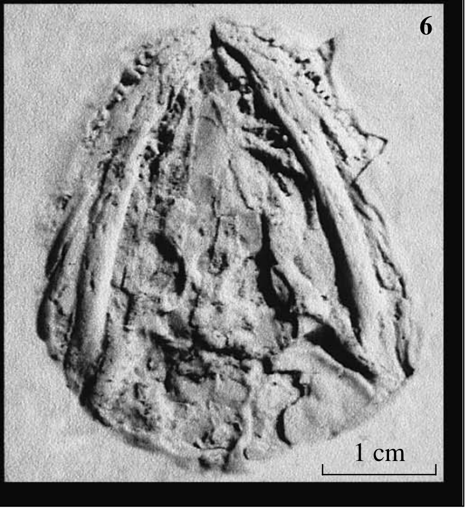












cover) (specimens PIN, nos. 2078/376, 361). The apices of the anterior teeth are flattened and weakly inclined lingually, whereas the crowns of the posterior teeth are conical.

Two proximal premaxillary teeth and maxillary teeth 5–7 are substantially larger than the neighboring teeth.

Within the palatal complex, only the vomers and palatines have large teeth (specimen PIN, no. 2078/372;

Explanation of Plate 3

Utegenia shpinari Kuznetzov et Ivachnenko, 1981; skull casts, ventral view; Kurty locality (Kazakhstan, Almaty Region, Kaskelenskii District; Lower Permian).

Fig. 1. Specimen PIN, no. 2078/147.

Fig. 2. Specimen PIN, no. 2078/380.

Fig. 3. Specimen PIN, no. 2078/359.

Fig. 4. Specimen PIN, no. 2078/366.

Fig. 5. Specimen PIN, no. 2078/357.

Fig. 6. Specimen PIN, no. 2078/372.

Pl. 3, fig. 6). Their bases are regularly folded and round in cross section. The crowns are conical and covered by ridges on the labial and lingual sides. In the majority of cases, each bone has two teeth; however, the number of vomerine teeth ranges from one to three (specimens PIN, nos. 2078/380 and 372, respectively). The rest of the vomerine surface is covered by randomly arranged shagreen teeth (Pl. 3, fig. 2).

On the palatine and ectopterygoid, small teeth form two longitudinally extended fields separated from each other by an area lacking teeth. The lateral field composed of somewhat larger teeth extends along the boundary of the maxilla and curves inward near the posterior end of the ectopterygoid. The teeth of the medial field continue the rows of shagreen located on the pterygoids (specimens PIN, nos. 2078/359, 380). In some specimens, the medial flank of the ectopterygoid lacks teeth (specimen PIN, no. 2078/147, 369); when they are present, the two shagreen fields join in the posterior region of the bone.

Numerous rows of small teeth cover the anterior part of the parasphenoid and the entire surface of the palatine rami of the pterygoids, including the pterygoid flanges (Pl. 3, fig. 1). Only the anterior end of the pterygoids, which apparently spread above the vomers, lack teeth. Toothed fields cover the bases of the quadrate rami and, occasionally, expand posteriorly almost to the quadrate–articular articulation (specimens PIN, nos. 2078/219, 370, etc.). The coronoids are covered by small teeth smaller than, or equal to, the shagreen teeth located on the pterygoids.

Surface ornamentation. In the majority of specimens under study, including the largest animals (specimen PIN, no. 2078/373, 30.5-mm-long skull), the external surface of the skull roof is even and covered by a few furrows diverging radially from the ossification centers. The smallest sculptured skulls are 22.5–23.5 mm long (specimens PIN, nos. 2078/384, 366, 360); in specimen PIN, no. 2078/384 (22.5-mm-long skull), a prominent surface relief is observed on the majority of bones of the axial and zygomatic regions. The primary relief composed of flat ridges alternating with furrows occurs at the grooves for blood vessels in the zone around the ossification center. This zone is slightly elevated because of the intensive growth of bone tissue; together with the development of surface ornamentation, the elevation increases. Subsequently, the external surface becomes somewhat tuberculate (specimen PIN, no. 2078/382; Pl. 3, fig. 4); later, tubercles also appear in the central part of the bones where surface relief is absent up to this time. In the marginal areas of bones, the largest tubercles appear on the primary ridges at the foramina for blood vessels.

In animals with well-developed surface ornamentation (specimens PIN, nos. 2078/212, 361, 384, skulls 29.5, 30, and 22.5 mm long, respectively), it is especially prominent on the frontals; on the other membrane bones of the skull roof, it is somewhat weaker and developed to approximately the same extent on the majority of bones, except for the nasals, lacrimals, and, probably, quadratojugals where the surface relief is smoothened (Pl. 3, figs. 3, 4). The lower jaw lacks surface sculpturing.

Seismosensory system. The supraorbital seismosensory canal undoubtedly originated from the premaxilla where it does not leave clear traces on a background of a strongly perforated external surface. On the nasals, the seismosensory groove is usually absent as well; however, the position of the canal is often marked by a narrow furrow for the superficial ophthalmic nerve (of the facial nerve, VII), passing along the upper wall of the naris. Laterally, this furrow gradually curves toward the ossification center; it extends beyond the nasal and terminates as a large foramen in the anterior part of the prefrontal where the groove for the seismosensory canal is always distinctly seen. As the seismo-

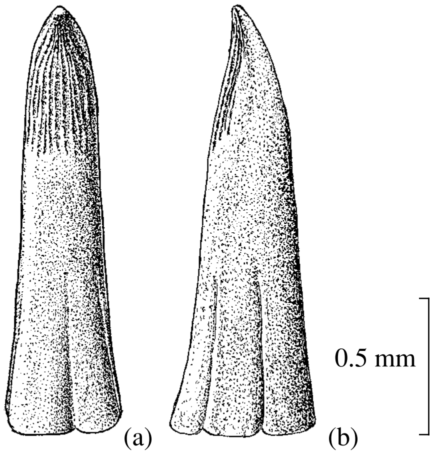


Fig. 3. *Utegenia shpinari*, maxillary tooth 7, specimen PIN, no. 2078/388: (a) lingual and (b) labial views.

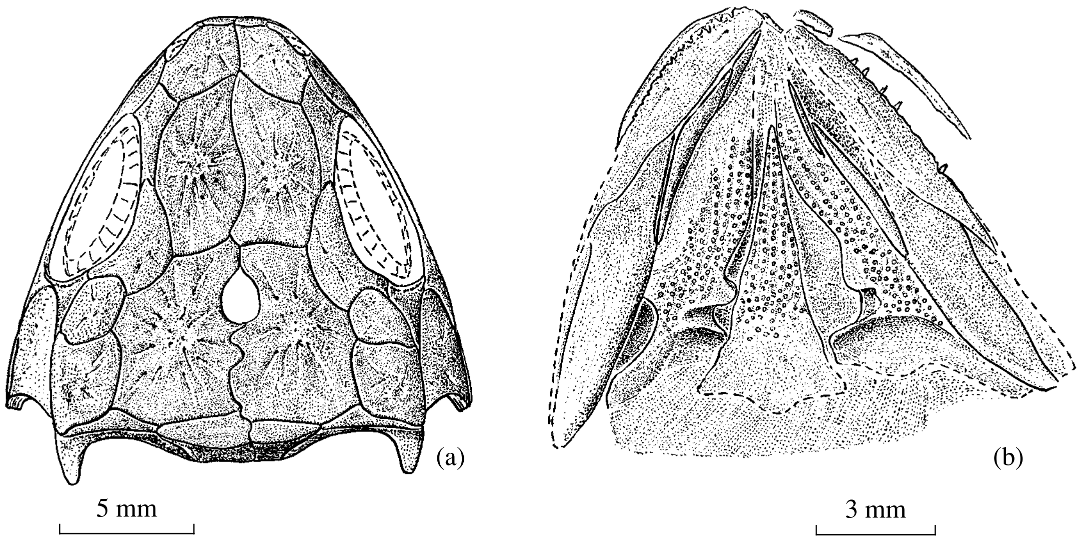


Fig. 4. *Utegenia shpinari*, juvenile skull: (a) reconstruction based on specimens PIN, nos. 2078/100, 112, and 286, dorsal view; and (b) PIN, no. 2078/330, ventral view.

sensory canal passed onto the prefrontal, it overlapped a small adjacent area of the lacrimal. The flexure formed by this groove is relatively small because the preorbital skull region is narrow.

More posteriorly, the supraorbital groove passes onto the frontal where it rather strongly deviates medially and extends along the lateral flank of this bone, forming a relatively long segment; subsequently, it passes onto the postfrontal. Some skulls (specimens PIN, nos. 2078/212, 359, 376, 377, 387, 370) show a shallow additional groove that extends along the orbital rim and is probably related to the sensory structures (Pl. 1, fig. 6; Pl. 2, fig. 6). It emerges on the prefrontal and most likely merges into the main ramus at the point where it passes onto the postfrontal (specimens PIN, nos. 2078/359, 376) or within the postorbital (specimens PIN, nos. 2078/376, 387). The presence of an additional seismosensory canal in some animals is evidenced by the positions of deep furrows for blood vessels and nerves on the postorbital, since they are oriented along the orbital rim rather than according to the orientation of the main branch of the canal. Nevertheless, the majority of skulls, including those with well-pronounced surface ornamentation (except for specimen PIN, no. 2078/212), lack additional grooves. It is not improbable that the presence of these grooves is a form (although a rather common form) of individual variation in the differentiation of seismosensory placodes. It should be pointed out that the main canal often passes close to the orbit and, consequently, leaves too little space for an additional branch.

As the supraorbital groove passes onto the intertemporal, it always bypasses the parietal. The temporal branch branches off on the intertemporal (specimen PIN, no. 2078/361) or, more often, on the postorbital (e.g., in specimens PIN, nos. 2078/369, 377). In the latter case, the position of this groove is variable; when passing onto the supratemporal, it either overlaps the intertemporal or bypasses this bone and extends laterally along the caudal process of the postorbital (specimen PIN, no. 2078/369).

Within the supratemporal, the seismosensory canal passes posteromedially, gradually deviating from the edge of the otic notch. Such an orientation of the groove is associated with the position of the tabular that terminates short of reaching the lateral edge of the parietal shield and is often exposed dorsally only in the angle between the parietal and the supratemporal. The seismosensory groove on the supratemporal always passes through a large pit distinctly seen in many specimens and most likely containing electrically sensitive organs (see specimens PIN, nos. 2078/369, 382; Pl. 1, figs. 1, 4); a similar depression slightly smaller in size is occasionally marked on the intertemporal (specimens PIN, nos. 2078/361, 384). It was impossible to discover any segments of the occipital commissure because the tabulars and postparietals are weakly developed.

The infraorbital groove is traced from the posterior part of the lacrimal where one or two relatively large foramina are located at its lower edge. In the majority of specimens, this bone is strongly deformed and often damaged because the external wall of the nasolacrimal duct is broken. On the infraorbital part of the jugal, this groove is continued by a series of deep lacunae; as they are overgrown by bone tissue, several large foramina are observed on the bone surface. The postorbital commissure branches off in the upper part of the postorbital region of the jugal; further posteriorly, the groove comes onto the squamosal and, bypassing the ossification center, extends toward the quadrate–articular articulation along the edge of the otic notch. The groove surface often has narrow furrows for the nerve responsible

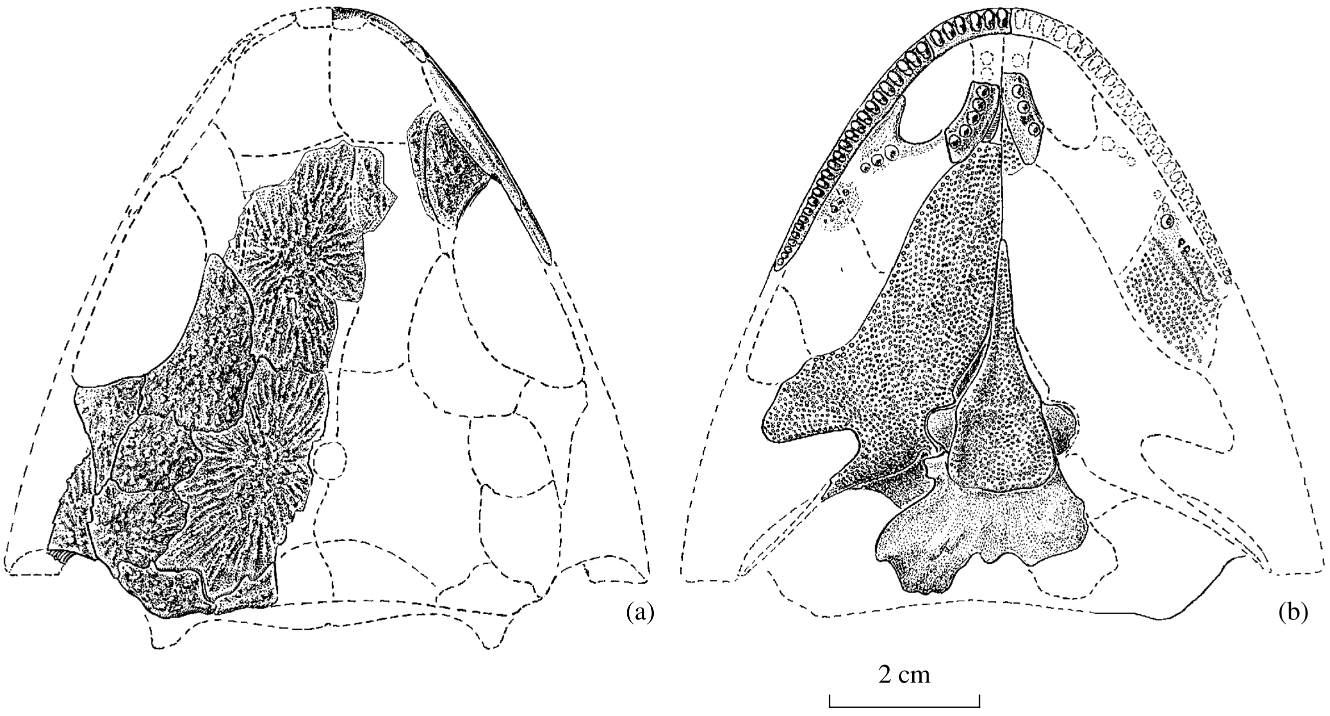


Fig. 5. *Biarmica tchudinovi*, skull, reconstruction based on holotype PIN, no. 1581/1: (a) dorsal and (b) ventral views.

for innervation of this part of the infraorbital seismosensory canal.

No trace of the mandibular branch of the seismosensory system on membrane bones of the lower jaw has been discovered.

Larval skull. The smallest *Utegenia* skull of which plastic models were produced is 14 mm long (specimens PIN, nos. 2078/100, 330, 399) and belongs to the larval stage (Fig. 4). The main difference from adults is that the jaw articulations are positioned anterior to the occipital skull edge, whereas in a 18-mm-long skull (specimen PIN, no. 2078/286), the jaw condyles are already displaced posteriorly and reach the plane of the occipital condyles. The parietal foramen is very large and its anterior part enters the interorbital region. The frontals are equal in length to the parietals and wedge in between the nasals along the medial suture. The postparietals project posteriorly with reference to the tabulars (specimen PIN, no. 2078/394). The paroccipital processes of the latter bone have developed to the same extent as those of adults. The contact between the supratemporal and the postorbital is evident.

The palatal complex of skulls of the size class under consideration includes a broad parasphenoid, the rostral region of which is covered by large shagreen teeth arranged in rows (specimen PIN, no. 2078/330; Fig. 4b). At this ontogenetic stage, the pterygoids have already come into contact with the parasphenoid, and the interpterygoid vacuity is almost completely closed (specimens PIN, nos. 2078/112). The posterior region of the bone has short parafenestral projections. The tooth rows are well developed on the medial flanges of the pterygoids. The features of dentition on the lateral regions of the pterygoids and on the other palatal bones remain obscure. The maxilla contains at least 17 teeth (specimen PIN, no. 2078/330). In 18–20-mm-long skulls (specimens PIN, nos. 2078/286, 399), the number of teeth increases to 23–26.

Family Kotlassiidae Romer, 1934

Subfamily Leptorophinae Ivachnenko, 1987

Genus *Biarmica* Ivachnenko, 1987

Biarmica tchudinovi Ivachnenko, 1987

Biarmica tchudinovi is only known from the Vyshka locality discovered by Shomysov in 1937 within the area of Perm (Shomysov, 1954). Shomysov collected the first specimens of this species in the bone beds composed of medium-grained sandstones. The material was collected repeatedly and transferred for study to A.P. Hartmann-Weinberg who participated in field work in this locality in 1938. Not counting postcranial bones, at least three skulls were found there; two were referred to as a “batrachomorph labyrinthodont” and a “seymouriamorph reptile.” The study of this material was not accomplished; during World War II, some specimens were lost (Shomysov, 1954), whereas the others are currently stored at the PIN; they are determined as *Biarmica tchudinovi* and probably belong to two individuals of approximately the same size (Ivakhnenko, 1987). The holotype (PIN, no. 1681/1) is an incomplete skull with partially preserved skull roof, palatal complex, and the right ramus of the lower jaw. The second specimen (PIN, no. 1681/2) is small isolated cranial fragments providing no additional information.

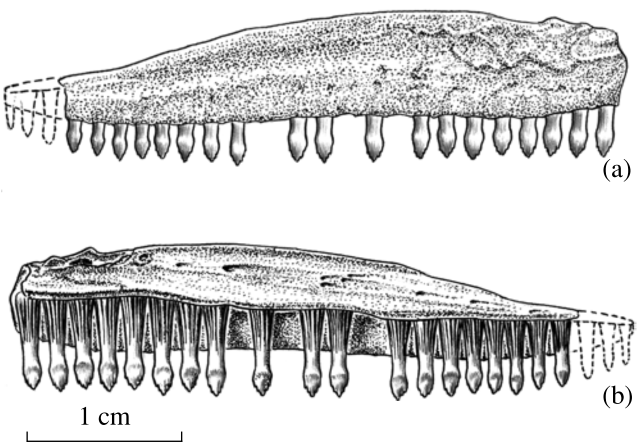


Fig. 6. *Biarmica tchudinovi*, right maxilla, reconstruction based on holotype PIN, no. 1581/1: (a) labial and (b) lingual views.

General characteristics. Available material gives no way to estimate the skull proportions. *Biarmica* most likely had a narrow and relatively long preorbital region (similar to that of *Utegenia*). Presumably, the skull of the holotype was approximately 75 mm long. The occipital edge of the parietal shield is slightly concave. The orbits are large and most likely expanded posteriorly. The anterior edge of the otic notches is in line with the boundary between the supratemporal and the tabular. The jaw condyles are positioned anterior to, or, less probably, in line with, the occiput (Fig. 5a).

Skull roof. The parietals are extended and weakly widened posteriorly, their anterior edges strongly wedge in the interorbital region. The ossification centers are located close to the midlength of the bone posterior to the posterior orbital rim. The parietal foramen was located approximately at the same level, i.e., far from the edge of the frontals; this inference follows from the position of the orbitotemporal crest on the ventral surface of the skull roof. The frontals most likely entered the preorbital region.

The postfrontal is extended; a fragmentary prefrontal is preserved on only the right side; therefore, it is impossible to compare the sizes of these elements and determine the pattern of contact between them. The postorbital is extended; its long caudal process comes into a wide contact with the supratemporal and isolates the squamosal from the intertemporal. The latter bone is weakly elongated lateromedially and only slightly smaller than the supratemporal, which narrows posteriorly.

The lacrimal is high and has a short infraorbital process. Its lower surface expands and overlies the maxilla, the dorsal surface of which has a special attachment area slightly inclined ventromedially. The canal of the nasolacrimal duct originates as a small foramen in the anteroinferior corner of the orbit and opens in the anteroventral margin of the lacrimal.

Of the membrane bones composing the occipital edge of the skull, the holotype retains the right tabular. This bone is small and terminates short of reaching the lateral edge of the parietal shield, being isolated from the otic notch by a projection of the supratemporal. The paroccipital and occipital processes of the tabular are not preserved. The postparietal is incompletely preserved.

The squamosal was not large, to judge from the fragment preserved in the specimen. Its occipital flank looks like a wide plate.

The premaxilla forms the greater part of the lower wall of the external naris and contains six teeth. The dorsal process of the only preserved premaxilla of the holotype is broken off; therefore, it is impossible to judge the height of this process and determine whether or not the premaxillary fontanel is retained in this species.

The maxilla lacks a well-developed ascending lamina and remains low over its entire extent (Figs. 6a, 6b). On the lateral side, at the posterior edge of the naris, the anterior region of the bone has an attachment area for the septomaxilla. Immediately posterior to this area, the dorsal surface bears a longitudinal depression (with a large foramen for blood vessels) for a weakly lowered anterior margin of the lacrimal.

The main foramen for the infraorbital artery is located opposite the eighth maxillary tooth. A groove extending from this tooth along the attachment area for the lacrimal contains seven or eight unevenly distributed additional foramina facing posteriorly and providing passage for the arteries inside the bone. Their arrangement suggests the absence of an accomplished alveolar canal inside the maxilla. A well-pronounced fossa for the antorbital process of the olfactory capsule is absent.

The anterior region of the maxilla is strongly perforated externally. The upper labial foramina face ventrally and form a row extending at the midheight of the bone. A wide groove formed by external expansion of the dorsal border of the maxilla stretches above this row along almost the entire extent of the bone. There is a good probability that it belongs to the seismosensory system of grooves that, in the majority of seymouriamorphs, bypasses the maxilla and extends above this level along the lacrimal where *Biarmica* has a groove in the standard position.

The maxilla contains at most 25 teeth, since an almost complete maxilla of the holotype contains 22 teeth.

Palate. The vomer is narrow and comes into a contact with the palatine at the posterior edge of the bony choana. The anterior region of the bone is lost. On the upper side, the external wing of the vomer expands dorsally to form a high flange extending along the margin of the choana. Within the preserved fragment of the right side, there are five large palatal teeth arranged in a regular row extending along the choanal margin; the posterior part of the left vomer retains three large teeth and one empty alveolus (Fig. 5b).

The palatine has a long laterochoanal protrusion, the anterior end of which is located opposite the main foramen for the infraorbital artery in the maxilla. The anterior edge of the bone holds three large teeth arranged in a line and decreasing in size posteriorly.

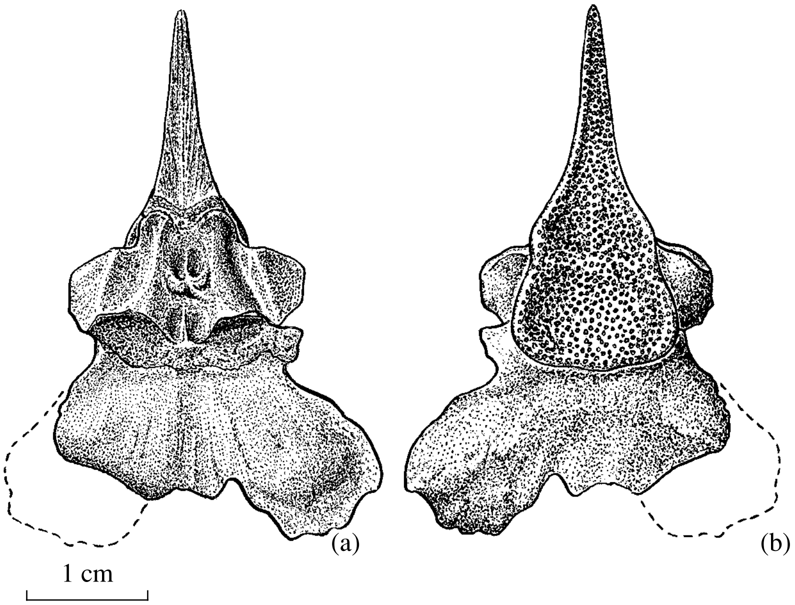


Fig. 7. *Biarmica tchudinovi*, parabasisphenoid, based on holotype PIN, no. 1581/1: (a) dorsal and (b) ventral views.

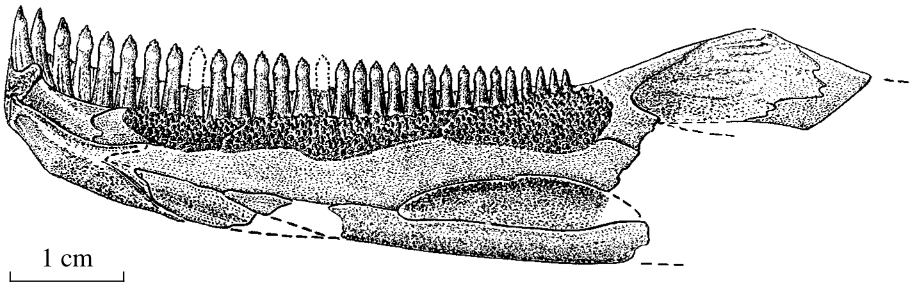


Fig. 8. *Biarmica tchudinovi*, right ramus of the lower jaw, reconstruction based on holotype PIN, no. 1581/1, lingual view.

The pterygoid flanges project deep into the adductor cavities and are positioned at an angle of 30° to the quadrate rami. The palatine rami of the pterygoids are narrow; on the dorsal side, they have a wide longitudinal depression for the anterior part of the palatoquadrate. A perichondral facet opposite the basipterygoid articulation apparently marks the attachment area for the epipterygoid.

The parasphenoid has a short rostrum, the dorsal side of which forms the base for the sphenethmoid and is covered by longitudinal ridges. The toothed region of the bone extends posteriorly beyond the basipterygoid articulation and is isolated from the parafenestral region lacking the teeth by a high projection. The wide and rounded parafenestral wings weakly curve ventrally and are isolated from each other by a wide notch in the posterior edge of the bone (Fig. 7).

Lower jaw. In the holotype, only the right ramus of the lower jaw is preserved (Fig. 8); its adductor region is lost and the external surface is strongly damaged. The splenial and angular are lost, the postsplenial is preserved as a fragment of the internal plate only.

The coronoid process is low and only slightly projects above the tooth row. Judging from the preserved fragment of the surangular, the internal wall of the adductor cavity decreases in height toward the jaw joint. The jaw retains the entire set of three coronoids, in the smallest of which, precoronoideum, the anterior edge lacks teeth and rests on the perisymphysial expansion of the dental area. The anterior edge of the middle coronoid is in line with mandibular tooth 10; the posterior edge is probably in line with mandibular tooth 20, at the point where the field of shagreen teeth narrows. The lower flanks of the coronoids lack teeth and are covered by the prearticular.

A large extended oval Meckel's foramen is located immediately anterior to the adductor region between the prearticular and angular. The splenial did not contribute to the formation of the symphysis, to judge from the attachment facet for this bone on the dentary. The

Fig. 9. *Biarmica tchudinovi*, rudimentary crown of maxillary tooth 11 of holotype PIN, no. 1581/1, lingual view.

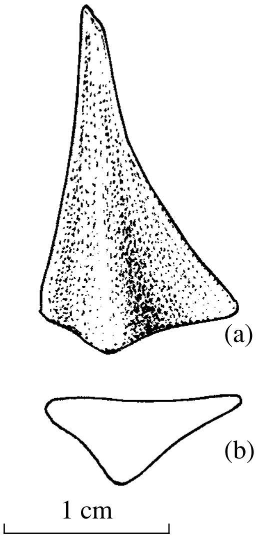


Fig. 10. *Biarmica tchudinovi*, right epipterygoid, based on holotype PIN, no. 1581/1: (a) lingual view and (b) outlines of the bone base.

symphysial surface is enlarged by medial expansion of the anterior face of the dental area.

Externally, the dentary is pierced by many foramina, especially numerous in the perisymphysial region. The lower jaw of the holotype contains 30 teeth.

Dentition. The bases of the marginal teeth are regularly plicate; in the anterior region of the jaws, they are longitudinally extended, strongly compressed laterally, and elongated ovals in cross section. The folds project deep into the pulp cavity at the middle of the lateral sides of the tooth bases; therefore, the cavity is often almost completely divided into two. Other folds are shallower and, in fully developed teeth, their lateral sides closely adjoin each other to thicken the dentin walls. The folded pattern of the walls is clearly seen in the teeth broken transversely. On the external side of the tooth bases, the grooves extend approximately to the middle of the tooth height and terminate short of reaching the lower boundary of the enamel cover.

The crowns of all marginal teeth of the holotype were damaged in the course of primary preparation. However, some empty alveoli of the maxilla contain rudimentary replacement teeth. A completely developed crown from the eleventh alveolus is clearly thickened at the base and has a flattened apex slightly inclined internally; on either side of the apex, the cutting edge has a pair of well-developed lateral denticles (Fig. 9). In addition, the anterior side of the edge has a supplementary pair of rudimentary denticles which look like small tubercles slightly projecting above the tooth edge. On the lingual side, a short ridge extends from the main tooth apex and each lateral denticle.

A rudimentary tooth from the fourteenth alveolus is relatively small, weakly thickened in the near-basal region, and has only two large lateral denticles. A similar structure is observed in the crown of the eleventh mandibular tooth.

Large palatal teeth are round and regularly plicate in cross section at the tooth base and have weakly flattened conical crowns. In the palatal complex, shagreen teeth arranged in closely spaced rows cover the anterior rami of the pterygoids and expand far posterior onto the quadrate rami. The lateral and medial fields of small teeth, covering the lateral palatal elements, fuse within the ectopterygoids.

Surface ornamentation. The surface sculpture on the skull roof of the holotype is strongly damaged. The surface relief on the parietal is composed of radial ridges; around the ossification center, the ridges are divided by furrows into individual tubercles. The squamosal shows a similar ornamentation pattern. The caudal process of the postorbital is also covered by ridges. On the frontal, the tuberculate relief prevails over the ridged radial ornament, the elements of which occur in the marginal area of the bone. The tuberculate relief also dominates on relatively small membrane bones, i.e., the intertemporal, supratemporal, prefrontal, postfrontal, and tabular. The lacrimal virtually lacks surface sculpturing, its surface is covered in places by low tubercles and short obscure ridges.

Seismosensory system. Since the surface of the skull roof is strongly damaged, the distribution of grooves of the seismosensory system in *Biarmica* is mainly uncertain. An imprint of the infraorbital canal is clearly seen within the lacrimal and the mandibular groove is distinct in the perisymphysial region of the dentary.

Endocranium. The auditory capsules of *Biarmica* ossified; however, they are poorly preserved. The thin-walled bones (prootici) indicate an early stage of the replacement of the cartilaginous tissue.

The basipterygoid processes of the basisphenoid are stout and have rounded triangular facets facing anterolaterally and slightly ventrally (Fig. 7b). The hypophysial fossa is small and divided into two by a longitudinal medial septum. Anteriorly, the dorsal side of the basisphenoid contains a pair of closely located foramina of the canals of the internal carotid arteries entering the bone at the posterior margin of the basipterygoid processes. The dorsum sellae is low.

The epipterygoids are columnar; their base is compressed laterally, extended lateromedially, and widened somewhat in the central part (Figs. 10a, 10b). The sphenethmoids clearly ossified. They look like short plates slightly S-shaped in cross section with thickened upper and lower edges (Fig. 11). The sphenoids lack well-pronounced foramina; however, the notches in the posterior edge of the bones are in the same position as the foramina for the optic and oculomotor nerves in Recent urodelans (Lebedkina, 1979).

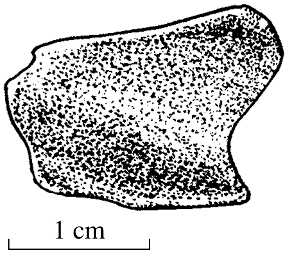


Fig. 11. *Biarmica tchudinovi*, left sphenethmoid, based on holotype PIN, no. 1581/1, lateral view.

Genus *Leptoropha* Tchudinov, 1955

Leptoropha talonophora (Tchudinov, 1955)

The material on *Leptoropha talonophora* is limited to a small number of specimens from the type locality (Shikhovo-Chirki), which is presently inaccessible for excavation. Originally, Tchudinov (1955) assigned the majority of these specimens to a new species of the genus *Rhipaeosaurus* Efremov, 1940 (Pareiasauroidea), *Rhipaeosaurus talonophorus*. The other specimens were described in the same publication under the name *Leptoropha novojilovi* and also referred to rhipaeosauroids mainly on the basis of the structure of their marginal teeth which resemble the typical pareiasaurian teeth in split crowns.

Ivakhnenko (1987) has shown that *Rhipaeosaurus talonophorus* and *Leptoropha novojilovi* belong to the same species and, on the basis of the cranial structure, should be referred to as seymouriamorph amphibians. According to the International Code of Zoological Nomenclature, the new name of this species is *Leptoropha* talonophora. *Leptoropha* substantially differs from the majority of typical and well-known genera of the order Seymouriamorpha (*Seymouria*, *Discosauriscus*, *Ariekanerpeton*, and *Utegenia*); therefore, the seymouriamorph suborder Leptorophida was established. The latter includes the genera *Biarmica* Ivachnenko, 1987 and *Raphanodon* Ivachnenko, 1987, which are also characterized by polycuspid teeth, and *Enosuchus breviceps* Konzhukova, 1955 of uncertain taxonomic position, which is ranked as a separate family.

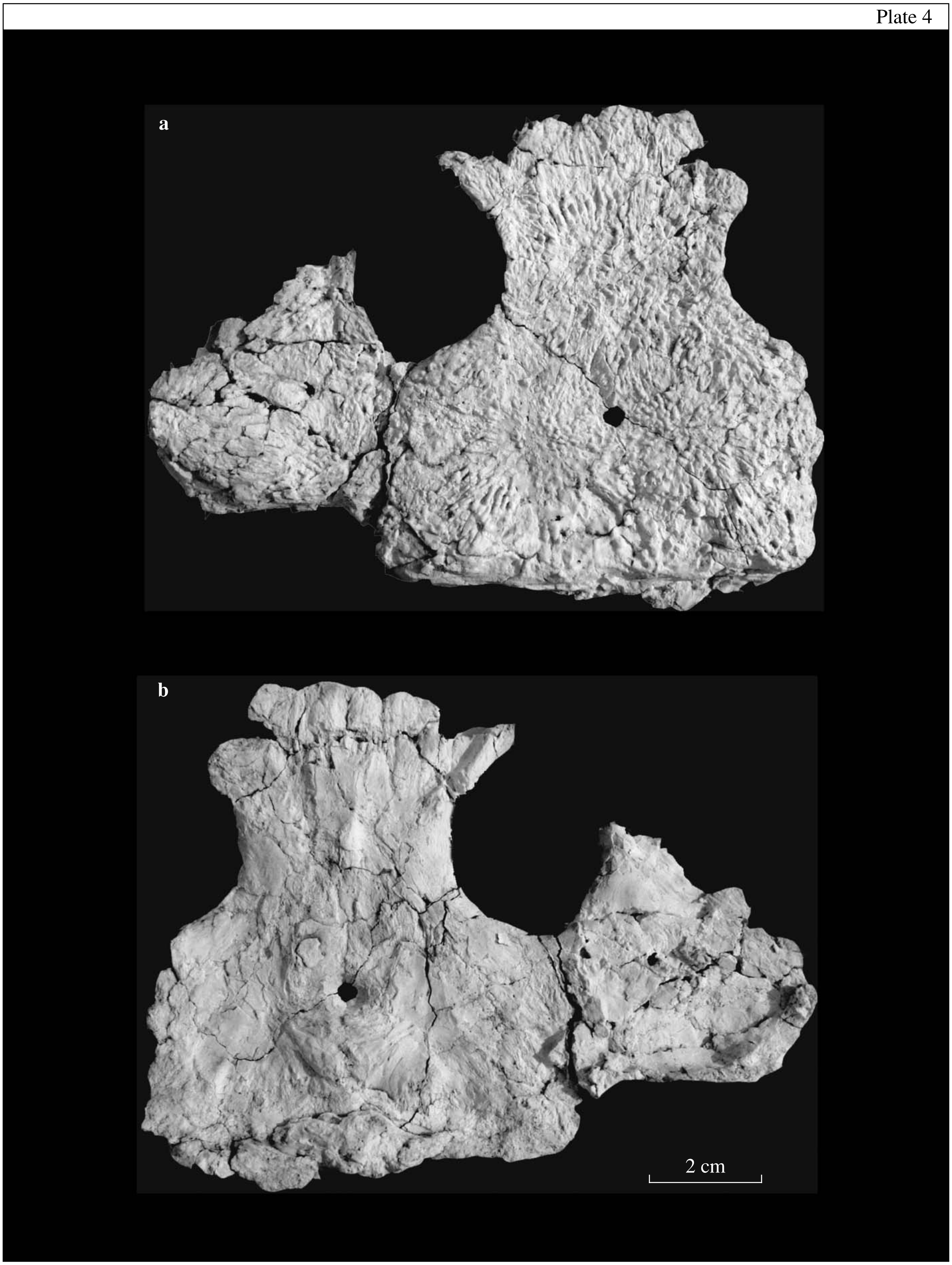
The holotype of *Leptoropha talonophora* (PIN, no. 161/72) is an incomplete skull, including a large part of the dermatocranium, a maxilla, poorly preserved membrane bones of the palatal complex, and the auditory capsule. In addition, the collection contains two small fragments of the skull roof of larger individuals (specimens PIN, nos. 161/67, 105), isolated jaws, and jaw fragments.

General characteristics. Because of dorsoventral compression in the burial, the skull roof of the holotype is entirely flat (Pl. 4, figs. 1a, 1b); however, the presence of relatively narrow pterygoids is evidence that the zygomatic regions of *Leptoropha* abruptly curved relative to the parietal shield. The orbits are located mainly in the anterior part of the skull; they are round and large, 40% as long as the skull (estimated skull length is approximately 105 mm). The occipital edge of the parietal shield is straight, the lateral edges strongly curve ventrally. A small round parietal foramen is located in the anterior third of the parietals posterior somewhat to the posterior orbital margins. The otic notches are broad, their anterior edge is located posterior to the ossification center of the supratemporal. The jaw condyles are displaced anteriorly with reference to the occiput.

Skull roof. The parietals are large, their anterior ends enter the interorbital region (Fig. 12a; Pl. 4, figs. 1a, 1b; Pl. 5, fig. 1). Posteriorly, they abruptly expand and come into a wide contact with the tabulars. The ossification centers are located in the anterior region of the parietals only slightly posterior to the parietal foramen. The frontals are narrow and only weakly project in the preorbital region. The nasals of *Leptoropha* are substantially wider than the frontals and protrude deep into the latter along the medial suture, entering the interorbital region; this is atypical of other seymouriamorphs. Only the posterior regions of the nasals are preserved in the holotype; however, the position of the ossification centers of these bones allows one to estimate the actual length of these elements. The postparietals only slightly jut out into the parietals. On different sides of the skull, they are unequal in size; the right postparietal is almost twice as large as the left postparietal.

The prefrontal and postfrontal are of approximately the same size and come into wide contact above the orbit. The postorbital is extended and undoubtedly connected to the supratemporal on either side of the skull. Laterally, it is bounded by the jugal, which strongly expands in the postorbital region, and displaces the squamosal far from the orbit. The right and left supratemporals of the holotype considerably differ in size; on the right side, the supratemporal is substantially smaller than the intertemporal, whereas on the left side, it is substantially larger. Specimen PIN,

Plate 4



Explanation of Plate 4

Leptoropha talonophora (Tchudinov, 1955); Shikhovo-Chirki locality (Kirov Region, Slobodskoi District; Upper Permian, Upper Kazanian Substage).

Fig. 1. Holotype PIN, no. 161/72, skull roof: (a) dorsal and (b) ventral views.

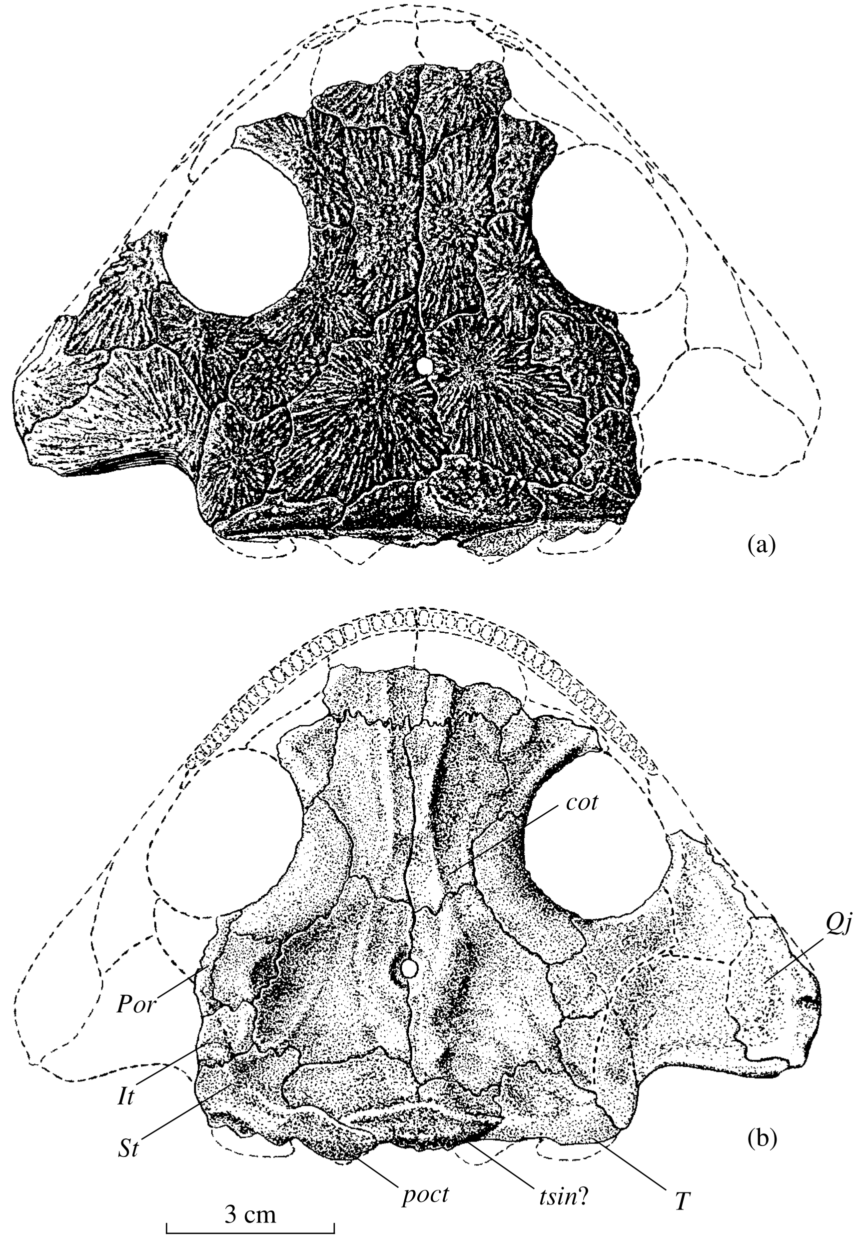


Fig. 12. *Leptoropha talonophora*, holotype PIN, no. 161/72, skull: (a) dorsal and (b) ventral views.

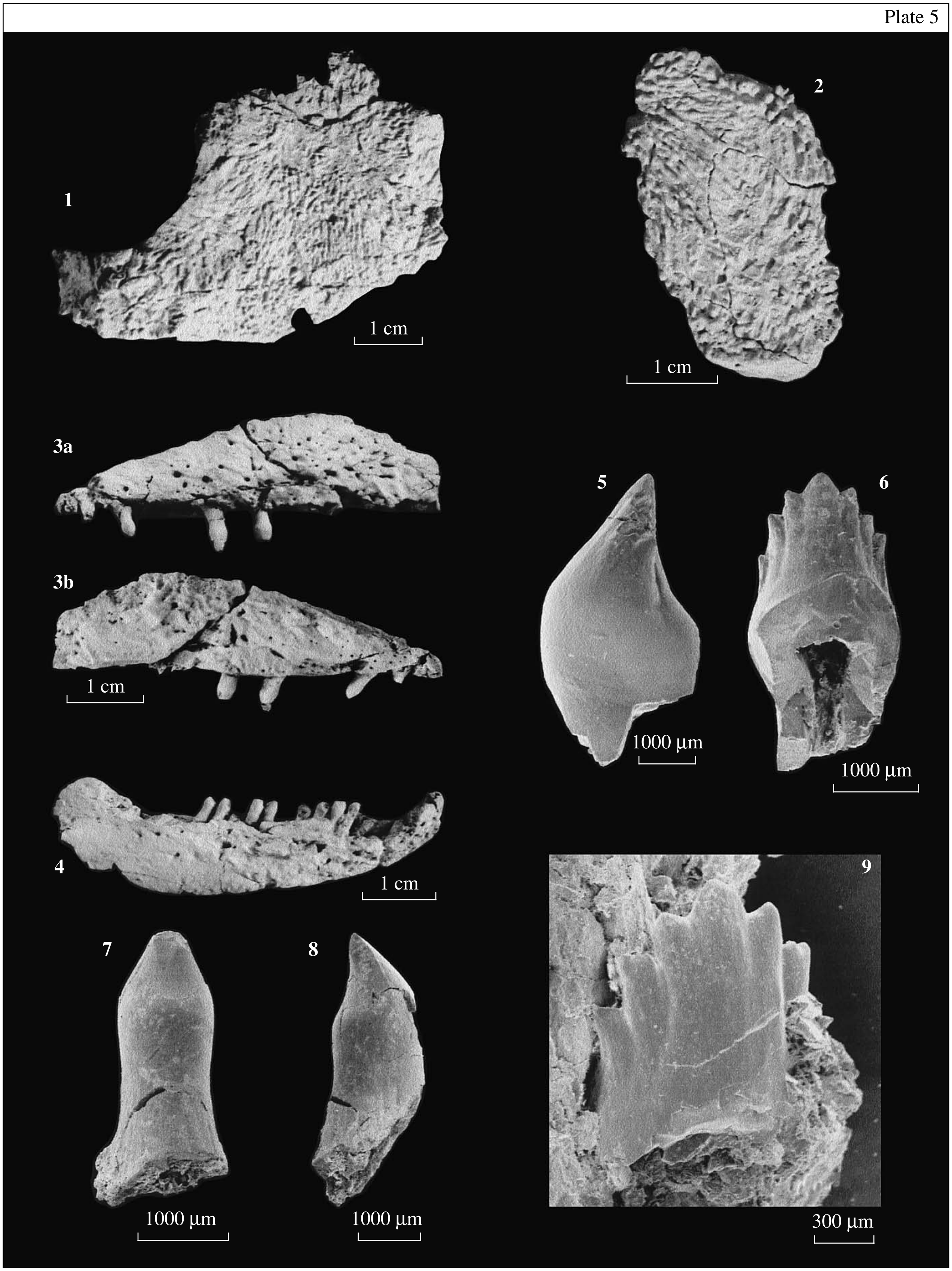
no. 161/105 (fragmentary parietal shield) shows the same relations of these bones (Pl. 5, fig. 2); thus, this should be regarded as a normal state.

The dorsal flanks of the tabulars are weakly developed; laterally, they taper and only their ends reach the edge of the otic notches. The paroccipital processes of the tabulars are broken off at the base; between them and the occipital processes, there are gaps, indicating that the posttemporal fossae were open.

The squamosal is small. Its occipital flank looks like a narrow plate and largely contributes to the formation of the otic notch. The extraordinarily expanded quadratojugal forms a large part of the zygomatic region and covers posteriorly and partially dorsally a pointed end of the jugal (Fig. 12c).

The structure of the premaxillae of *Leptoropha* is not known. The maxilla has a well-pronounced ascending lamina with a broad attachment area for the lacrimal on the lingual side (Figs. 13a, 13b; Pl. 5, figs. 3a, 3b). Posterior to the nares, the anterior edge of the internal side of the lamina has a depression, a trace of articulation with the anterior end of the lacrimal, which reaches the nares, notwithstanding the fact that the ascending lamina is well developed. Specimen PIN, no. 161/75 lacks ascending lamina of the maxilla.

Plate 5


1
1 cm
2
1 cm
3a
3b
1 cm
4
1 cm
5
1000 µm
6
1000 µm
7
1000 µm
8
1000 µm
9
300 µm

Explanation of Plate 5

Leptoropha talonophora (Tchudinov, 1955); Shikhovo-Chirki locality (Kirov Region, Slobodskoi District; Upper Permian, Upper Kazanian Substage).

Fig. 1. Specimen PIN, no. 161/67 fragments of skull roof, dorsal view.

Fig. 2. Specimen PIN, no. 161/105, fragment of the parietal shield, dorsal view.

Fig. 3. Right maxilla of the holotype (PIN, no. 161/72): (3a) labial and (3b) lingual views.

Fig. 4. Specimen PIN, no. 161/68, right dentary, labial view.

Figs. 5 and 6. Mandibular tooth, specimen PIN, no. 161/68: (5) lateral view and (6) lingual view; crown damaged, pulp cavity exposed.

Figs. 7 and 8. Palatal tooth of the holotype (PIN, no. 161/72): (7) lateral and (8) lingual views.

Fig. 9. Rudimentary mandibular tooth, specimen PIN, no. 161/68, labial view.

A small foramen for the infraorbital artery is located in the standard position, i.e., in the anterior part of the bone above the articular fossa for the antorbital process of the olfactory capsule; the latter is positioned in the area of the maximum expansion of the ascending lamina. The other foramina providing passage into the maxilla for the branches of the artery and accompanying nerve are arranged in a random manner in the central region of the bone. Externally, the maxilla is pierced by a large number of foramina, which are especially numerous in the postnasal region; in the posterior part, there is a row of relatively large foramina located along the alveolar margin and accompanied by the grooves oriented posteriorly and ventrally. The relatively completely preserved right maxilla of the holotype contains 19 teeth (there could be 20, since the anterior end of the bone is broken off).

The internal surface of the skull roof of the holotype allows for the study of the structural features of the endocranial imprint and relative positions of the boundaries between membrane bones on the ventral and dorsal surfaces.

On the ventral side, the parietal foramen is located in the center of a funnel-shaped depression bordered laterally and posteriorly by the orbitotemporal crests and the crista mediocapsularis (a stout expansion formed by the fusion of the orbitotemporal crests), respectively (Fig. 12b; Pl. 4, fig. 1b). On either side of the crista mediocapsularis, the parietals are concave. Immediately anterior to the parietal foramen, the orbitotemporal crests converge; in the anterior part of the skull, they fuse to form a wide ventrally projecting area passing from the frontals onto the nasals. In addition, each parietal has a crest extending from the boundary of the tabular to the ossification center. Along the occipital edge of the parietal shield, the tabulars and postparietals form a shelflike projection with attachment facets for the auditory capsules and the occipital ring.

Palate. The data on the structure of the palatal complex are extremely scarce; in the holotype, only the right pterygoid and an anterior fragment of the parasphenoid rostrum with a field of small teeth are preserved. The quadrate ramus of the pterygoid is broken off at the base and the palatine ramus is narrow (Fig. 14a). The anterior part of the medial flange of the

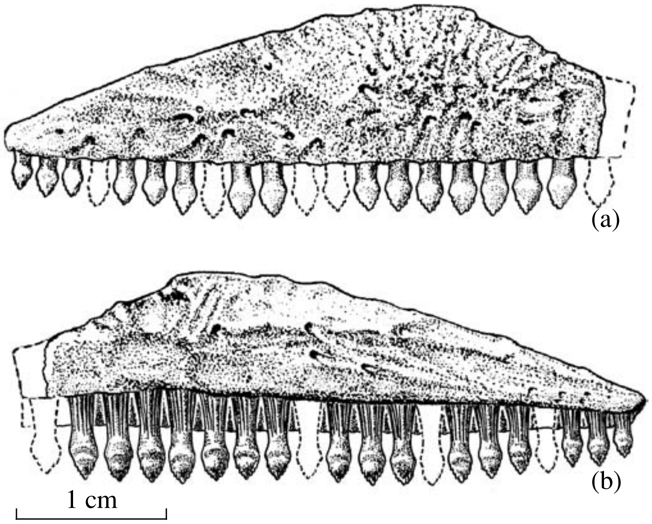


Fig. 13. *Leptoropha talonophora*, right maxilla, reconstruction based on holotype PIN, no. 161/72: (a) labial and (b) lingual views.

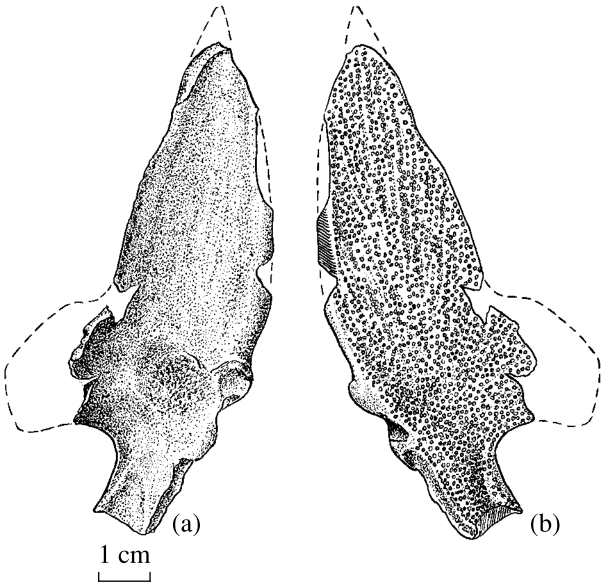


Fig. 14. *Leptoropha talonophora*, palatine ramus of pterygoid, based on holotype PIN, no. 161/72: (a) ventral and (b) dorsal views.

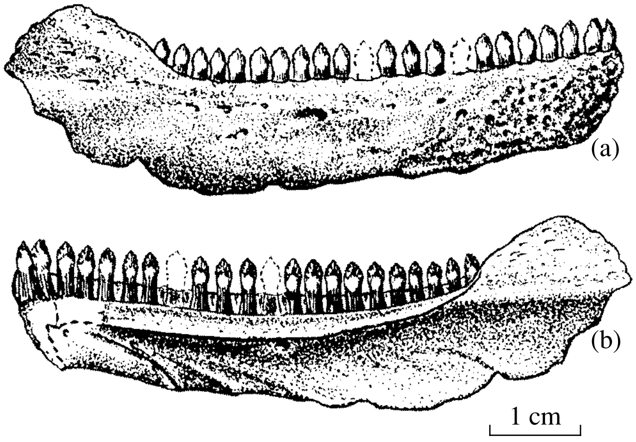


Fig. 15. *Leptoropha talonophora*, right dentary, reconstruction based on specimen PIN, no. 161/68: (a) labial and (b) lingual views.

pterygoid has a well-pronounced attachment facet for the parasphenoid, this facet dorsally overlies the latter bone. By all appearances, the interpterygoid vacuity opened ventrally within a short segment anterior to the basipterygoid articulation. A comparison of the small width of the pterygoids with the cranial measurements and the width of the zygomatic regions suggests that *Leptoropha* possessed a parasphenoid that was widened in the basipterygoid region.

The pterygoid flange is positioned at an angle of about 90° to the quadrate lamina. A fossa for the basipterygoid process is narrow and extended and has an articular facet facing anterolaterally and slightly ventrally. Immediately anterior to the fossa, the dorsal surface of the bone has a trace of contact with the epipterygoid (Fig. 14b). Judging from the structure of the dorsal surface, the anterior region of the palatoquadrate was resorbed at the definitive stage, since a rough surface indicating the presence of cartilage laterally envelopes the articular fossa, passes onto the base of the quadrate ramus, and does not extend anteriorly and further.

Lower jaw. The dentary is the only mandibular bone preserved in *Leptoropha* (specimen PIN, no. 161/68; Figs. 15a, 15b; Pl. 5, fig. 4). It is short, high, and forms a platelike dorsal projection at the posterior end, which indicates the presence of a well-developed coronoid process. The main foramen for the mandibular artery is located opposite marginal tooth 12. At the point where the bone was broken off transversely, it is seen that, as the artery entered the bone, it gave rise to a stout labial branch that came on the external surface through a posteriorly facing foramen in the central part of the dentary.

The anterior region of the Meckel's groove contains two foramina; the first is near the symphysis and the second, accompanied by a posteroventrally extending groove, is in a more posterior position above the articular facet for the splenial.

The anterior region of the bone is pierced by numerous canals; the posterior region, on the contrary, almost lacks foramina for blood vessels. In specimen PIN, no. 161/69 (a poorly preserved fragmentary lower jaw), the Meckel's groove contains bony tissue replacing cartilage. The lower jaw contains 22 teeth (specimen PIN, no. 161/68).

Dentition. The bases of the marginal teeth are strongly folded; strongly compressed laterally, especially in the near-crown region; and long and narrow ovoid in cross section. The crowns are symmetrical and denticulate; on either side of the medium-sized central apex, the cutting edge has three or four large supplementary denticles; the middle denticle is usually the largest. Occasionally, the lingual side of the teeth bears short ridges extending from the lateral denticles (specimen PIN, no. 161/69); however, more often, this side of the crown is smooth.

The basal region of the tooth crowns is club-shaped and forms a wide shelflike projection posterior to the central apex (Pl. 5, fig. 5). The pulp cavity extends into this projection and forms an expansion even in completely developed teeth (Pl. 5, fig. 6). The apical part of the crown is flattened and usually strongly curved lingually (at an angle up to 45° to the vertical).

The holotype has two large palatal teeth most likely coming from the postchoanal row (Pl. 5, figs. 7, 8). Their crowns are substantially thickened, however, to a lesser degree than those of the marginal teeth. The lateral denticles are absent; one tooth has a well-pronounced blunt cutting border (Pl. 5, fig. 7). The bases are strongly folded and compressed somewhat laterally.

Small palatal teeth cover the parasphenoid rostrum and occupy a wide extended area on the base of the quadrate ramus of the pterygoid; at the border of the vomer, the shagreen teeth become somewhat larger (holotype PIN, no. 191/72).

Surface ornamentation. The surface of the skull roof is strongly damaged in all specimens. At the definitive stage, the relief composed of high extended ridges replaced in the ossification centers by separate tubercles prevails (Pl. 4, fig. 1a; Pl. 5, figs. 1, 2). The radial ridged pattern is well developed on large bones of the axial and zygomatic regions, i.e., the parietals, frontals, nasals, squamosals, quadratojugals, and the postorbital part of the jugals. The ridges are sometimes connected to each other by cross bonds, have a tuberculate surface, and can be divided by furrows into short ridges and tubercles, covering almost completely relatively small bones of the occipital margin and the temporal region (tabulars, postparietals, intertemporals, and supratemporals). The same ornamentation prevails on the prefrontals and postfrontals; in the marginal regions of these bones, the fragments of partially broken ridges are retained. At the ossification centers, adjacent pectens are often fused in a random manner; as a result, short ridges of irregular shape are formed (e.g., on the intertemporal of specimen PIN, no. 161/105; Pl. 5, fig. 2). A similar relief develops near the symphysis of the dentaries; this is most likely associated with the fact that this region is strongly perforated, whereas the greater part of the labial surface of the dentary remains smooth. The maxillae are only weakly ornamented.

Seismosensory system. The external surface of membrane bones of the skull roof is strongly damaged; therefore, it is rather difficult to recognize with certainty the positions of the lateral line grooves. This is also hindered by the development of surface ornamentation (also damaged) in areas where the primary grooves occur. An example is the supratemporal of specimen PIN, no. 161/105 where the position of the temporal branch of the supraorbital canal on the lateral flank of bone is marked by numerous foramina for nerves and blood vessels (Pl. 5, fig. 2). At the posterior end of the bone, a zone rich in foramina passes onto the tabular and extends along the occipital edge of the skull.

In the holotype, the groove segments on the prefrontals are especially clearly defined; their position indicates that, when passing onto the nasals, the supraorbital seismosensory canal bypassed the lacrimal. In specimen PIN, no. 161/67, the right postorbital has a distinct groove of the postorbital commissure passing onto the intertemporal. A fragmentary right jugal, most likely belonging to the same specimen, shows a well-pronounced segment of the infraorbital groove. In addition, the anterior region of the mandibular canal of the lateral line organs is observed against the background of the surface relief in the symphysial region of the dentary of specimen PIN, no. 161/68.

Endocranium. The endocranium of *Leptoropha* is undoubtedly well ossified, as evidenced by the presence of ossified regions of the Meckel's cartilage in specimen PIN, no. 161/69 and cartilage bones of auditory capsules and presumable tectum synoticum in the holotype. These bones are strongly damaged and virtually unsuitable for examination.

Subfamily Kotlassiinae Romer, 1934

Genus *Microphon* Ivachnenko, 1983

Microphon exiguus Ivachnenko, 1983

Microphon exiguus is known from several localities of the Late Tatarian Age. The first specimens from the type section of the Donguz 6 locality (complete and fragmentary maxillae, Fig. 16) were assigned to a new form of primitive procolophons of the subfamily Spondylolestinae (Ivakhnenko, 1983); until recently, they were considered to belong to this group under the above name. Subsequently, isolated cranial bones widely varying in size and an almost complete skull of a juvenile were found and described as a species of the genus *Raphanodon, R. tverdochlebovae*, and assigned to seymouriamorph parareptiles (Ivakhnenko, 1987). Correct identification of the type series of the two taxa was impeded by the poor preservation of specimens of *M. exiguus.*

The abandonment of the genus *Raphanodon* (caused by the transfer of the holotype of the type species *R. ultimus* to the genus *Karpinskiosaurus*) necessitated the introduction of a new generic name for the form from Donguz; therefore, Bulanov (2000) gave this animal the accordant name *Raphaniscus*. To date, thorough examination of all type specimens and new representative material from the type locality has shown with confidence that *Raphanodon* (Raphaniscus) *tverdochlebovae* and *Microphon exiguus* are synonyms (Bulanov, 2002); according to the principle of priority, only the second name should be used.

Due to the great collecting activity of D.L. Sumin, the material on seymouriamorphs from Donguz 6 has been substantially enlarged and currently includes more than ten juvenile skulls. They provide the basis for the analysis of the early ontogenetic stages of this form. Adults are rather scarce in the type locality and presented by isolated jaws and bones from the skull roof.

Other material on *M. exiguus* comes from a number of geographically remote localities in the basin of the Sukhona River (Poteryakha 1, Poteryakha 2; Kochevala 1, Kochevala 2; and Ust'e Strel'ny) and includes only poorly preserved specimens; nevertheless, they are confidently identified with the form from Donguz. An indirect argument in support of this identification is the fact that *M. exiguus* co-occurs with the chroniosuchid *Chroniosaurus dongusensis* in all sections listed above. The material from the Poteryakha 2 locality is most valuable with reference to both the number of specimens and their preservation; therefore, it provided the basis for the reconstruction of the late development stages of *M. exiguus* (Bulanov, 2000).

General characteristics. Available juvenile skulls from the type locality range from 23 (specimens PIN, nos. 3585/25, 109, 110, 203) to 35 mm in length (specimen PIN, no. 3585/314).

The preorbital region is relatively wide (Fig. 16a). The orbits are regularly oval and displaced anteriorly from the central position; their posterior edges are located approximately at the midlength of the skull. The occipital edge is straight or, occasionally, weakly concave (specimens PIN, nos. 3585/89, 140). The nares face almost anteriorly, being only slightly turned laterally. The anterior edges of the otic notches are located opposite the ossification centers of the supratemporals or a little posterior to this position. The jaw condyles are strongly displaced anteriorly with reference to the occiput, especially in the smallest juveniles (e.g., specimen PIN, no. 3585/203; Pl. 6, fig. 1).

Skull roof. The parietals are large and weakly narrowed anteriorly. The small parietal foramen is round. The frontals are short, shorter than, or equal to, the orbital length. The nasals are somewhat wider and

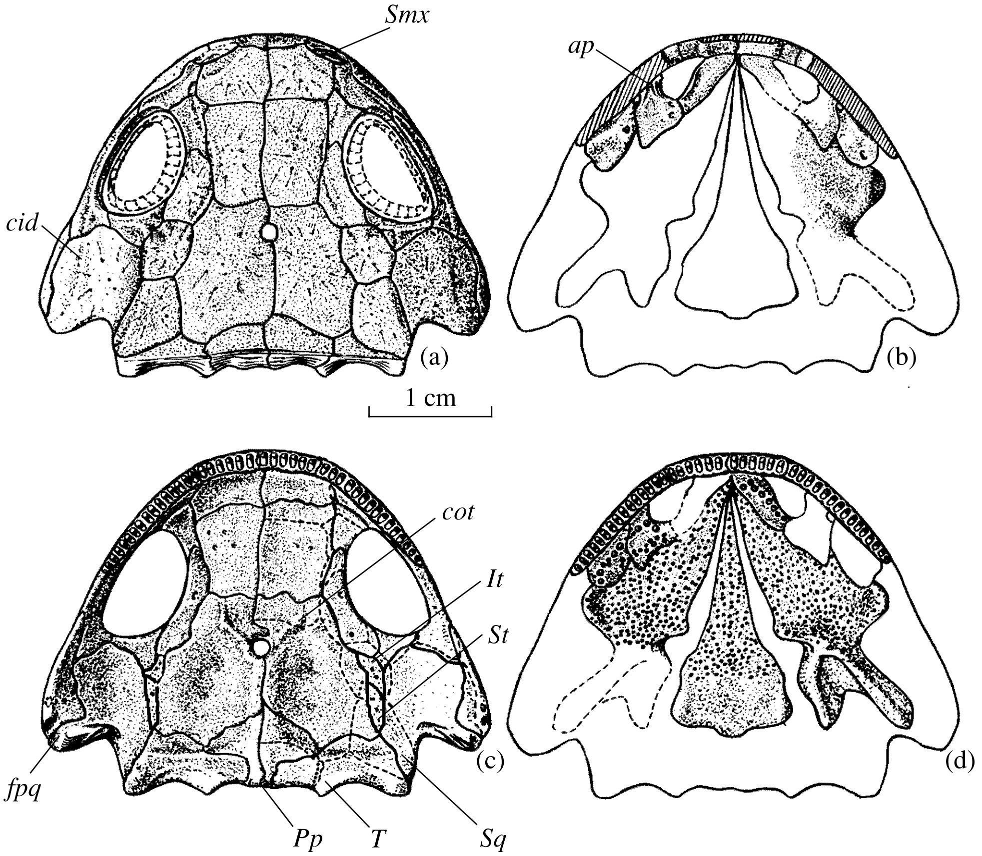


Fig. 16. *Microphon exiguus*, reconstructed juvenile skull: (a) dorsal view (based mainly on specimen PIN, no. 3585/92); (b) skull roof, ventral view (based on specimens PIN, nos. 3585/28, 89, 92, 109, 113, 114); on the right, the dotted line shows bone boundaries on the dorsal side; (c) palatal complex, ventral view (based on specimens PIN, nos. 3585/25, 107, 114); and (d) palatal complex, ventral view (based on specimen PIN, no. 3585/107).

approximately half as long as the frontals. The prefrontal is always smaller than the postfrontal; these bones come into wide contact above the orbit. Since the caudal process is weakly developed, the postorbital is located far from the supratemporal. The pointed posterior region of the jugal only slightly wedges in the suture between the quadratojugal and the squamosal; in some specimens (PIN, nos. 3585/89, 109; Pl. 4, fig. 2), the postorbital region of the jugal is widened. Contact with the lacrimal is very short and located close to the anterior orbital margin; thus, the lower wall of the orbit is formed mainly by the jugal. The lacrimal is short and low; the nasolacrimal duct is not enclosed in this bone. The septomaxilla looks like a U-shaped plate. The septomaxillary foramen is not closed.

The intertemporal is relatively small and usually isometric (occasionally, weakly extended hexagonal) and comes into wide contact with the squamosal. In one skull (specimen PIN, no. 3585/92), the right intertemporal is absent and its place is occupied by the laterally expanded parietal (Pl. 4, fig. 3). In this case, the ossification center of the parietal is displaced laterally to the position where the boundary between these elements is normally observed.

Explanation of Plate 6

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Microphon exiguus Ivachnenko, 1983; juvenile skulls, dorsal view (Fig. 5, lateral view); Donguz 6 locality (Orenburg Region, Orenburg District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon).

Fig. 1. Specimen PIN, no. 3585/203.

Fig. 2. Specimen PIN, no. 3585/109.

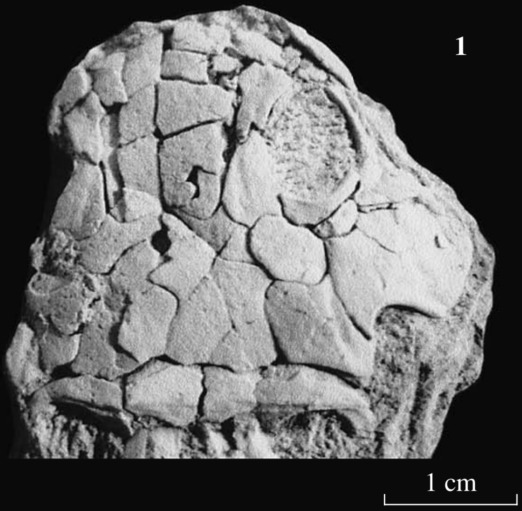
Fig. 3. Specimen PIN, no. 3585/92.

Fig. 4. Specimen PIN, no. 3585/89.

Fig. 5. Specimen PIN, no. 3585/108.

Fig. 6. Specimen PIN, no. 3585/114.

Plate 6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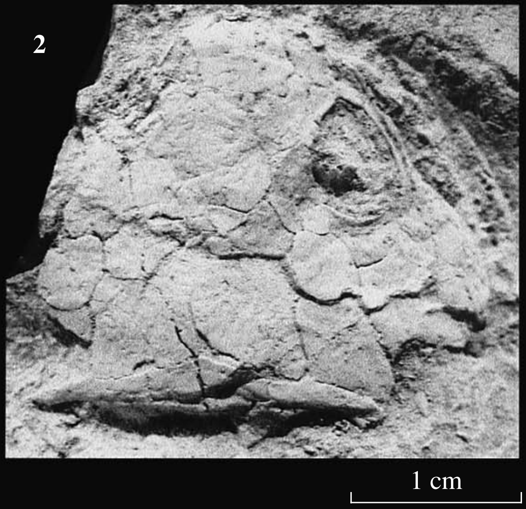
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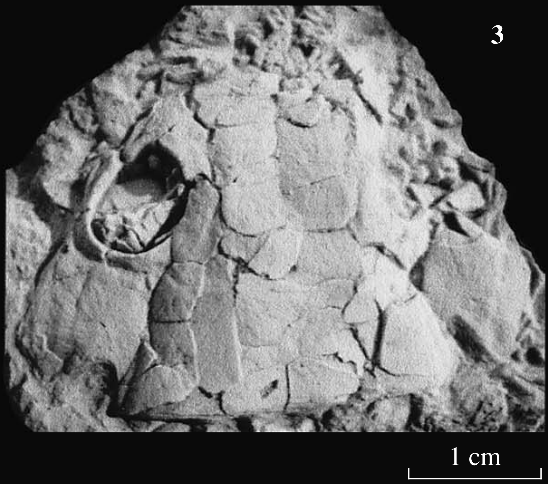
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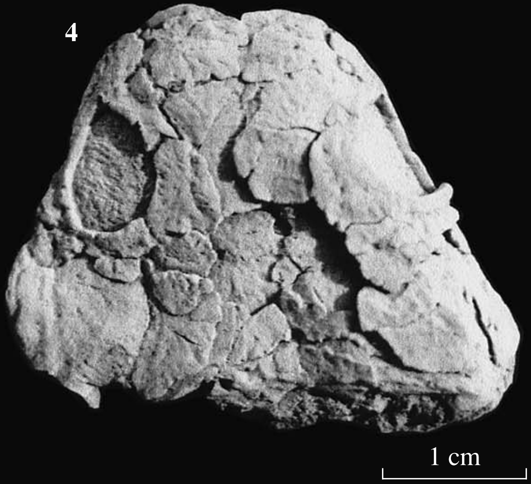
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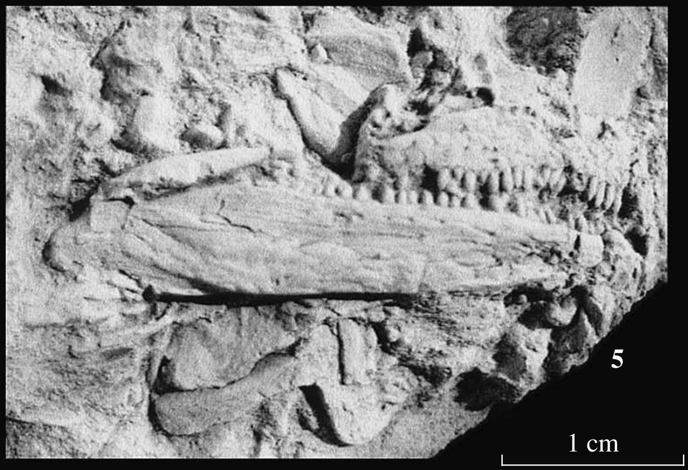
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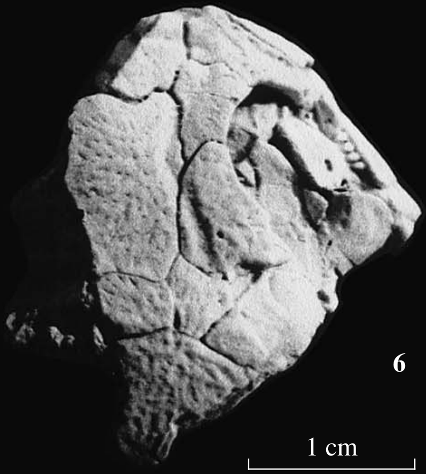
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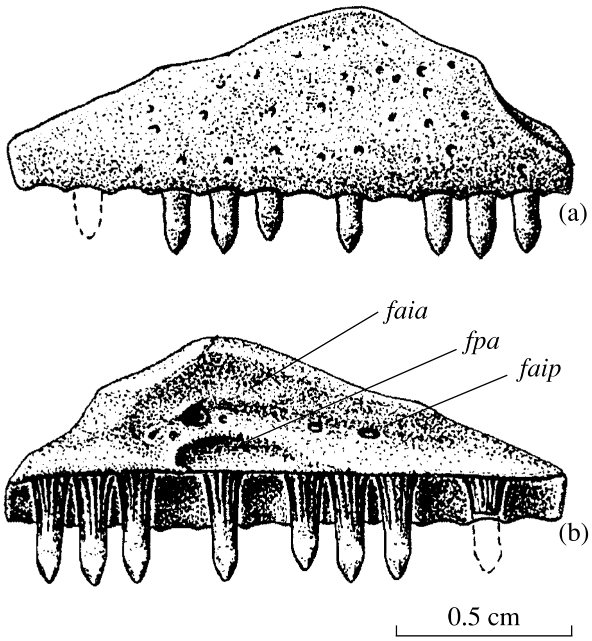

Fig. 17. *Microphon exiguus*, maxilla, holotype PIN, no. 3585/31: (a) labial and (b) lingual views.

The supratemporal is elongated and positioned at an angle to the longitudinal skull axis; occasionally, it substantially expands posteriorly (specimen PIN, no. 3585/92). The supratemporal is always larger than the intertemporal. The tabulars project toward the otic notches. The paroccipital processes are short, triangular or trapezoid, and positioned horizontally; between them and the ventrally directed occipital processes, there is a wide notch indicating that the posttemporal fossae remain open. On the dorsal side, the postparietals are larger than the tabulars; posteriorly, they strongly jut out into the parietals.

The squamosal is very large, its anterior edge closely approaches the orbit. The otic flank is S-shaped in outline. The quadratojugal is low and weakly projects ventrally; its anterior edge is in line with the posterior orbital wall.

The premaxillae have wide and short dorsal processes. The premaxillary fontanel is absent. The premaxilla is connected to the maxilla at the midlength of the naris. The premaxilla contains six teeth (specimen PIN, no. 3585/108).

The maxilla is short and high and has a well-developed ascending lamina (Fig. 17; Pl. 7, figs. 1a, 3a). The anterior foramen for the infraorbital artery is located in line with the fifth or sixth maxillary tooth; the posterior foramen for this artery is at the termination of the ascending lamina; sometimes, a small intermediate foramen is also present. The fossa containing the antorbital process is always well developed.

The bone contains a clearly differentiated alveolar canal from which the branches of arteries and nerves opened in the alveoli and on the strongly perforated labial surface. In the maxillae of the juveniles of the size class considered, the number of teeth ranges from 13 to 16. The latter value concerns skulls at least 30 mm in length (specimens PIN, nos. 3585/108, 114). Thirteen teeth were registered in an isolated maxilla (PIN, no. 3585/142) belonging to a skull the length of which is estimated as at least 25 mm (Pl. 7, fig. 3a). In other cases, even smaller juveniles have 14 or more teeth in the maxilla; in particular, an isolated 6-mm-long maxilla (PIN, no. 3585/204, skull length is estimated as 18–20 mm) contains 15 alveoli (Pl. 7, fig. 1a).

The relative positions of the bone boundaries on the ventral and dorsal surfaces of the skull roof are shown in Fig. 16b. It is of interest that the postparietals strongly expand on the ventral surface and their anterior edges are located half way between the parietal foramen and the occiput. The tabulars expand anteriorly to almost the same extent; in addition, the medial flanks of the tabulars form platelike projections extending toward each other and isolated by the end of the intercapsular crest; ventrally, these projections overlie the posterior region of the postparietals.

The parietals spread under all the adjacent bones, except for the tabulars and postparietals which occupy the posterior positions in the skull roof. The intertemporal, on the contrary, overlies all the adjacent elements and only its central region is seen on the ventral surface. The supratemporal is mainly closed from below by the medial expansion of the squamosal (having a wide plate for articulation with the parietal shield) and by the flanks of the parietals and tabulars spreading under this region. The quadratojugal strongly expands under the squamosal along the crest anteriorly framing the otic notch. The postfrontal is elongated on the ventral surface and spreads under the prefrontal, postorbital, and intertemporal.

Available material allows one to examine the main elements of the endocranial imprint (Fig. 16b). The parietal foramen is located in a small depression

Explanation of Plate 7

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Microphon exiguus Ivachnenko, 1983; jaws of juveniles; Donguz 6 locality (Orenburg Region, Orenburg District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon).

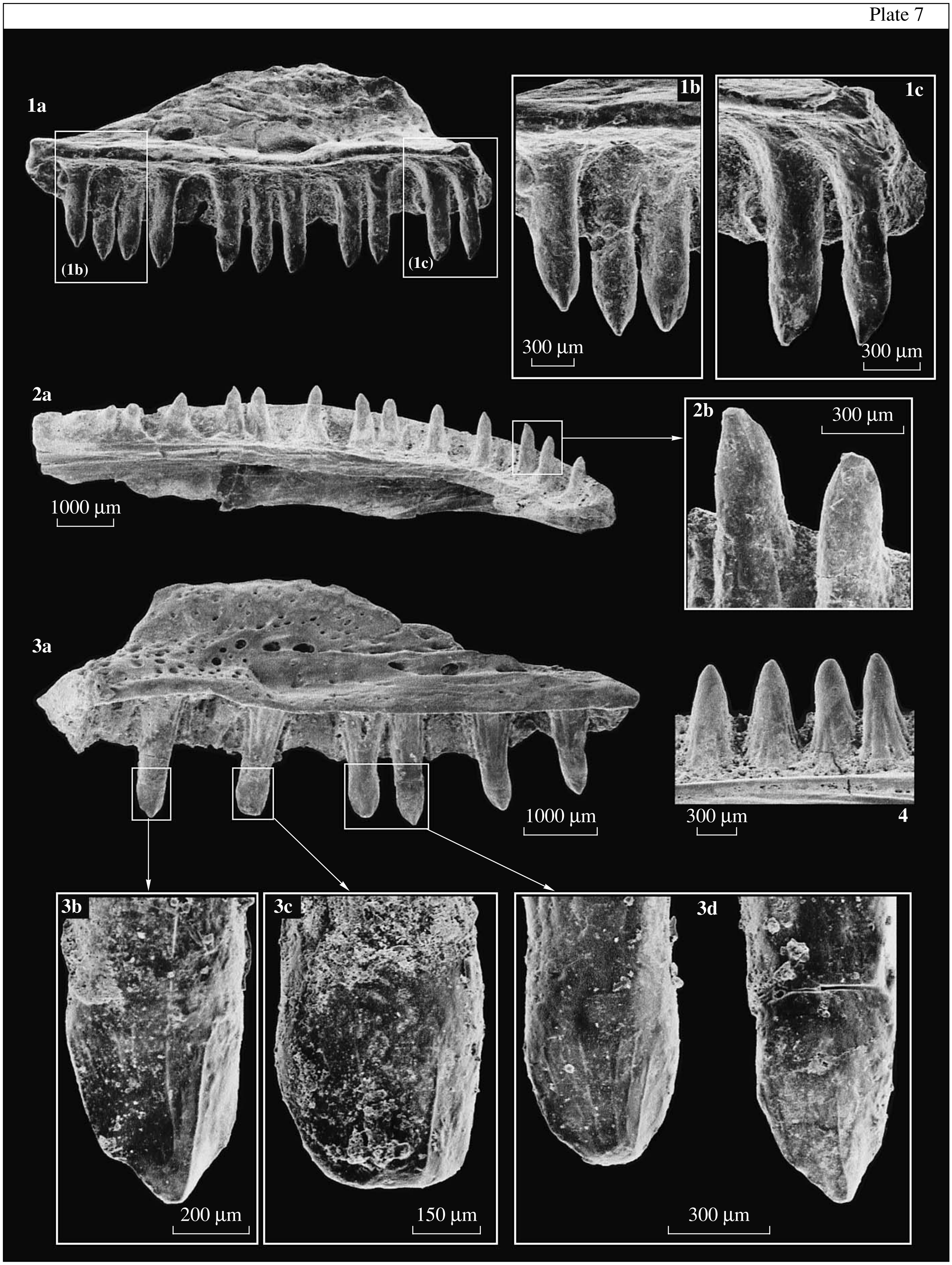
Fig. 1. Specimen 3585/204, left maxilla: (1a) general appearance, (1b) posterior teeth, and (1c) anterior teeth.

Fig. 2. Specimen PIN, no. 3585/141, left dentary: (2a) general appearance and (2b) teeth from the symphysial region.

Fig. 3. Specimen PIN, no. 3585/142, right maxilla: (3a) general appearance and (3b–3d) tooth crowns.

Fig. 4. Specimen PIN, no. 3585/139, fragmentary right dentary with the posterior teeth.

Plate 7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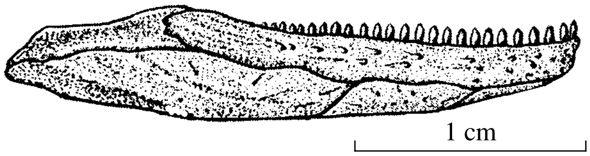

Fig. 18. *Microphon exiguus*, right ramus of juvenile lower jaw, reconstructed using specimen PIN, no. 3585/108, labial view.

bounded laterally by the orbitotemporal crests converging posterior to the foramen. Posteriorly, the crests form an integral crista mediocapsularis extending along the medial suture and reaching the occipital edge of the skull. Anterior to the parietal foramen, the orbitotemporal crests widely diverge laterally; upon approaching the parietal–frontal boundary, they abruptly curve and extend anteriorly almost parallel to each other, passing around the frontals. The occipital edge is thickened and forms a shelflike projection ventral to the concave roof of the parietals. The squamosal has two crests located anterior to the otic notch at an angle to each other and marking the position of the articular region of the palatoquadrate cartilage.

Palate. The vomers are long and expand toward the premaxillae; as a result, the choanae are teardrop-shaped, tapering anteriorly (Fig. 16c). The palatines jut out into the pterygoids to a greater extent than the much narrower ectopterygoids; the laterochoanal process is well-pronounced. The pterygoid flanges curve ventrally and are positioned at an angle of about 90° to the quadrate rami. Anterior to the parasphenoid rostrum, the anterior regions of the pterygoids come into wide contact with each other and are separated from the premaxillae by the vomers coming into narrow contact with one another. The parasphenoid has a wide rostrum. The parafenestral wings are undeveloped. In the basipterygoid region, the bone body forms short lateral projections spreading under the basal cartilaginous articulation between the palatoquadrate and the braincase. The posterior edge of the parasphenoid also has a small projection.

Available material enables one to discover certain structural features of the dorsal surface of the lateral palatal elements (Fig. 16d). The choanae are framed by low flanges formed by the vomerine and palatine margins curving dorsally. A deep groove of the postchoanal anastomosis of the infraorbital and palatine arteries is divided medially into two branches; the first passes along the posterior edge of the choana, and the second extends along the contact between the palatine and the ectopterygoid. Close to the boundary of the vomer, the palatine has a pair of relatively large foramina providing passage for blood vessels inside the bone; similar foramina are also present on the ectopterygoid (specimens PIN, nos. 3585/107, 114).

Lower jaw. The dentary is almost three times as long as the postdentary region of the mandible (Fig. 18; Pl. 6, fig. 5). The coronoid process is undeveloped. The splenial does not contribute to the formation of the symphysial facet and, in contrast to the postsplenial, virtually lacks expansion on the external side of the jaw. The crista angularis extends from the ossification center of the angular to the articular region and marks the bend of the bone. The posterior end of the dentary is shaped into a high plate widely overlapping the anterior region of the surangular. A row of supralabial foramina, accompanied by furrows directed dorsally or posteriorly, extends along the alveolar margin. The symphysial region is strongly pierced; in the posterior part of the bone, the foramina for blood vessels are not numerous. The lower jaw contains up to 25 teeth (specimen PIN, no. 2585/108). An isolated dentary (specimen PIN, no. 3585/141) belonging to a skull less than 20 mm in length contains 22 teeth (Pl. 7, fig. 2a).

Dentition. The structure of the juvenile marginal teeth widely varies because of the heterodonty observed even at early ontogenetic stages and the high rate of changes of the dental system in the course of individual development. In 20-mm-long skulls (specimen PIN, no. 3585/204; Pl. 7, figs. 1b, 1c), the crowns of the maxillary teeth already have a small projection on the anteriorly facing part of the cutting edge. On the lingual side, they have two or three prominent ridges converging apically. The apices are flat, slightly inclined lingually, and displaced somewhat posteriorly relative to the central position. The tooth bases are round in cross section, isolated folds are observed only in some teeth.

In a dentary belonging to an animal of approximately the same size (specimen PIN, no. 3585/141; Pl. 7, fig. 2b), only anterior teeth have a projection on the cutting edge, whereas the posterior teeth are conical; these features are retained in larger animals (specimen PIN, no. 3585/129; Pl. 7, fig. 4). In both the maxilla and the dentary, the highest teeth are observed in the middle of the tooth row; the anterior teeth from the lower jaw are very small.

In 23–30-mm-long skulls, the basal region of the tooth crown is weakly thickened and the lateral projections are usually developed better than those of smaller individuals and present on either side of the crown. The number of ridges on the lingual side becomes approximately twice as great. The tooth bases acquire intensive plication, deep grooves on their external side closely approach the boundary of the enamel cover.

In specimen PIN, no. 3585/108 (skull approximately 30 mm long), the dentition is preserved in both jaws (Pl. 6, fig. 5). The teeth of the upper jaw project beyond the alveolar margin to a substantially greater extent than in the lower jaw where only the tooth crowns project dorsally. The lower teeth are almost symmetrical, the basal region of the crown is thickened, and the apices are flat. In the premaxillary teeth, the crowns are higher and wider and have well-developed lateral projections; in the maxillary teeth, these projections are relatively weak; and in the lower teeth, they are virtually undeveloped.

The material from the type locality includes isolated maxillae belonging to large animals the skulls of which were about 55 mm long (specimens PIN, nos. 3585/26, 101). The teeth from these specimens are distinguished by more thickened crowns and longitudinally extended tooth bases oval in cross section. Numerous ridges on the lingual side have become closely spaced undulating threads. The number of folds on the teeth bases has increased considerably in comparison with earlier developmental stages. It is noteworthy that all crowns bear marks of intensive wear, i.e., the apices are blunt and the lateral projections (presumable denticles) on the cutting edge are smoothened. The teeth in an isolated dentary of an adult show a similar wear pattern [specimen PIN, no. 3585/24, skull length is estimated as at least 75 mm: Bulanov (2000, pl. 10, fig. 7)].

The vomer of specimen PIN, no. 3585/107 has at least five large conical teeth alternating with teeth of smaller size. On the palatine, the mediochoanal row is continued by large shagreen teeth arranged in a longitudinal field extending along the boundary of the pterygoid. The postchoanal row is incompletely formed; in particular, the palatine and ectopterygoid of specimen PIN, no. 3585/114 have seven large teeth (possibly, one or two empty alveoli are also present), which are distributed unevenly (located at different distances from each other) and not arranged in a line. The large palatine teeth have low and conical crowns, the lingual side of which is covered by ridges; the tooth bases are plicate and round in cross section.

The anterior part of the parasphenoid body and the rostrum are covered by rows of small teeth radially diverging from the ossification center. On the pterygoids, they expand onto the bases of the quadrate rami (specimens PIN, nos. 3585/25, 108). It is not improbable that the medial flanks of the vomer and ectopterygoid lacked shagreen teeth (specimens PIN, nos. 3585/107, 114).

Surface ornamentation. In all skulls shorter than 23 mm in length (specimens PIN, nos. 3585/25, 92, 109, 110, 203), the surface relief is undeveloped; the membrane bones are covered by narrow furrows originating from numerous foramina accumulated mainly around the ossification centers. In some cases, the surface relief is absent at later developmental stages (specimen PIN, no. 3585/207, 31-mm-long skull). In the smallest individual that shows the initial stages of formation of ornamentation, the skull is 24 mm long (specimen PIN, no. 3585/140); a weak surface relief is observed in the central part of almost every skull roof bone.

In a skull about 35 mm in length (specimen PIN, no. 3585/114), the primary elevations between the furrows are replaced by ridges of the same orientation; at the ossification centers, the foramina for blood vessels are surrounded by superficial fossae. This pattern is especially prominent on the parietal and frontal (Pl. 6, fig. 6), the peripheral areas of which, however, remain almost smooth. The surface ornamentation is relatively weak on the nasale, prefrontale, postfrontale, and lacrimale.

Seismosensory system. In juveniles, the grooves of the seismosensory system are distinctly seen (Figs. 16a). The supraorbital groove originates at the edge of the premaxilla and extends along the upper edge of the naris through the ossification center of the nasal. Within the lacrimal, the groove abruptly curves and passes above the orbit along the prefrontal, the external flank of the frontal, and the postfrontal. Posteriorly, as the groove comes onto the intertemporal (PIN, no. 3585/92) or, more often, on the parietal (specimens PIN, nos. 3585/89, 110, 114, 203, etc.), it breaks; in some cases, it continues without gaps to form the postorbital commissure (specimen PIN, no. 3585/140). This commissure branches off on the postorbital. The temporal branch of the supraorbital groove passes over the caudal process of the postorbital and extends posteriorly along the boundary between the supratemporal and squamosal and, then, along the external edge of the supratemporal.

The infraorbital groove is observed in the posterior region of the lacrimal, from which it passes onto the jugal; in the postorbital region of the jugal, the groove is connected to the postorbital commissure. Within the squamosal, the groove extends toward the quadrate–articular articulation, bypassing the ossification center of the bone.

Any trace of the ethmoid and occipital commissures is absent at this ontogenetic stage. On the lower jaw, only the posterior part of the mandibular branch is imprinted; this groove passes through the upper part of the angular above the angular crest.

Endocranium. Ossified endocranial structures have not been registered in juveniles.

Adult skull. According to original estimates, the cranial fragments and isolated membrane bones of *M. exiguus* from the Poteryakha 2 locality belong to skulls up to 80 mm long.

At this ontogenetic stage, the occipital edge of the parietal shield becomes slightly concave (Fig. 19a; specimen PIN, no. 3713/60; Pl. 8, fig. 1). The preorbital region is developed to a substantially lesser extent than the postorbital region of the skull, as in juveniles; this is evidenced by the preservation of the square shape of the nasal (specimen PIN, no. 3713/86; Pl. 8, fig. 2).

Available material allows one to judge a number of structural details of the ventral surface of the skull roof (Fig. 19b). The parietal foramen is located in a deep funnel-shaped depression. Anteriorly, the orbitotemporal crests weakly diverge laterally and reach the ossification centers of the frontals; this zone is covered by relatively small ridges (Pl. 8, fig. 3a). The lateral regions of the tabulars form dome-shaped areas for the attachment of the auditory capsules; anteromedially to these areas, there are extended depressions most likely

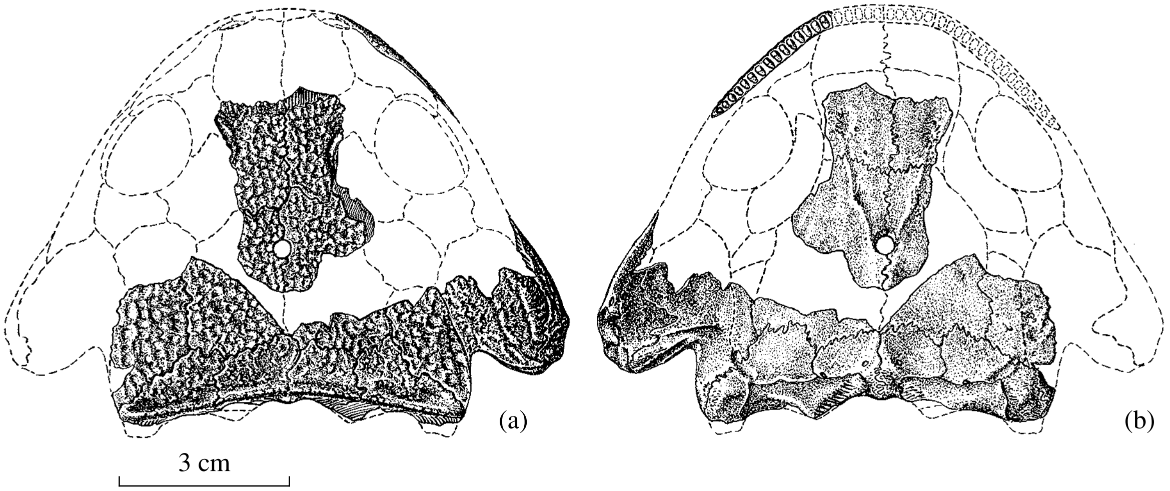

Fig. 19. *Microphon exiguus*, adult skull roof, reconstructed using specimens PIN, nos. 3713/45, 48, 53, and 60: (a) dorsal and (b) ventral views.

providing an attachment area for the end of the ascending ramus of the pterygoid (Pl. 8, fig. 1b). The crests on the squamosals are positioned similarly to those of juveniles (Pl. 8, figs. 4a, 5a, 6a). On the ventral side, the anterior edges of the postparietals and tabulars are in line with each other.

The ornamented surface clearly shows certain segments of the seismosensory grooves that are indiscernible at early developmental stages. This primarily concerns the occipital commissure extending along the edge of the parietal shield (specimen PIN, no. 3713/60; Pl. 8, fig. 1). Within the squamosal, there is an additional jugal groove passing below the main branch of the infraorbital groove and connected to this groove closer to the lower edge of the otic notch (specimens PIN, nos. 3713/53, 75; Pl. 8, figs. 4a, 5a, 6a). In the anterior part of the dentary, there is an imprint of the symphysial segment of the mandibular canal originating from the boundary of the postsplenial, extending anteriorly along the lower edge of the bone, and abruptly curving dorsally posterior to the symphysis (Pl. 9, figs. 1a, 2a, 3a).

In addition, the skull roof surface has depressions similar in shape and position to those of *Discosauriscus* and usually considered to be associated with electrically sensitive organs (Klembara, 1994b). One of these depressions medially adjoins the main (dorsal) branch of the infraorbital groove, being located between this groove and the edge of the otic notch (specimens PIN, nos. 3713/53, 75; Pl. 8, figs. 4a, 5a). The other depression is located at the end of the groove of the occipital commissure in the lateral region of the tabular (specimen PIN, no. 3713/60; Pl. 8, fig. 1).

The maxilla of adults contains 15–18 teeth (specimens PIN, nos. 3713/45, 72, Fig. 20; Pl. 9, fig. 4). In some cases, the ascending lamina of the maxilla is absent [specimen PIN, no. 3713/46: Bulanov, (2000, pl. 11, fig. 6)]; this is probably a form of individual variation. The dentary contains 24–27 teeth (specimens PIN, nos. 3713/51, 52, respectively). The labial surface of the posterior plate of the dentary is covered by numerous furrows for blood vessels. The furrows converge to one or two foramina located opposite the posterior end of the tooth row.

The crowns of the marginal teeth are markedly inflated, covered lingually by narrow undulatory threads, and have slightly flattened apical regions (Pl. 9, figs. 6, 7, 8). The cutting edge usually has three or four small denticles merging in an integral serrated ridge and often smoothened by wear. The crowns of the premaxillary teeth are higher and broader and have a larger

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Explanation of Plate 8

Microphon exiguus Ivachnenko, 1983; fragments of adult skull roof; Poteryakha 2 locality (Vologda Region; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon).

Fig. 1. Specimen PIN, no. 3713/60, occipital region of the parietal shield: (1a) dorsal and (1b) ventral views.

Fig. 2. Specimen PIN, no. 3713/86, right nasal: (2a) dorsal and (2b) ventral views.

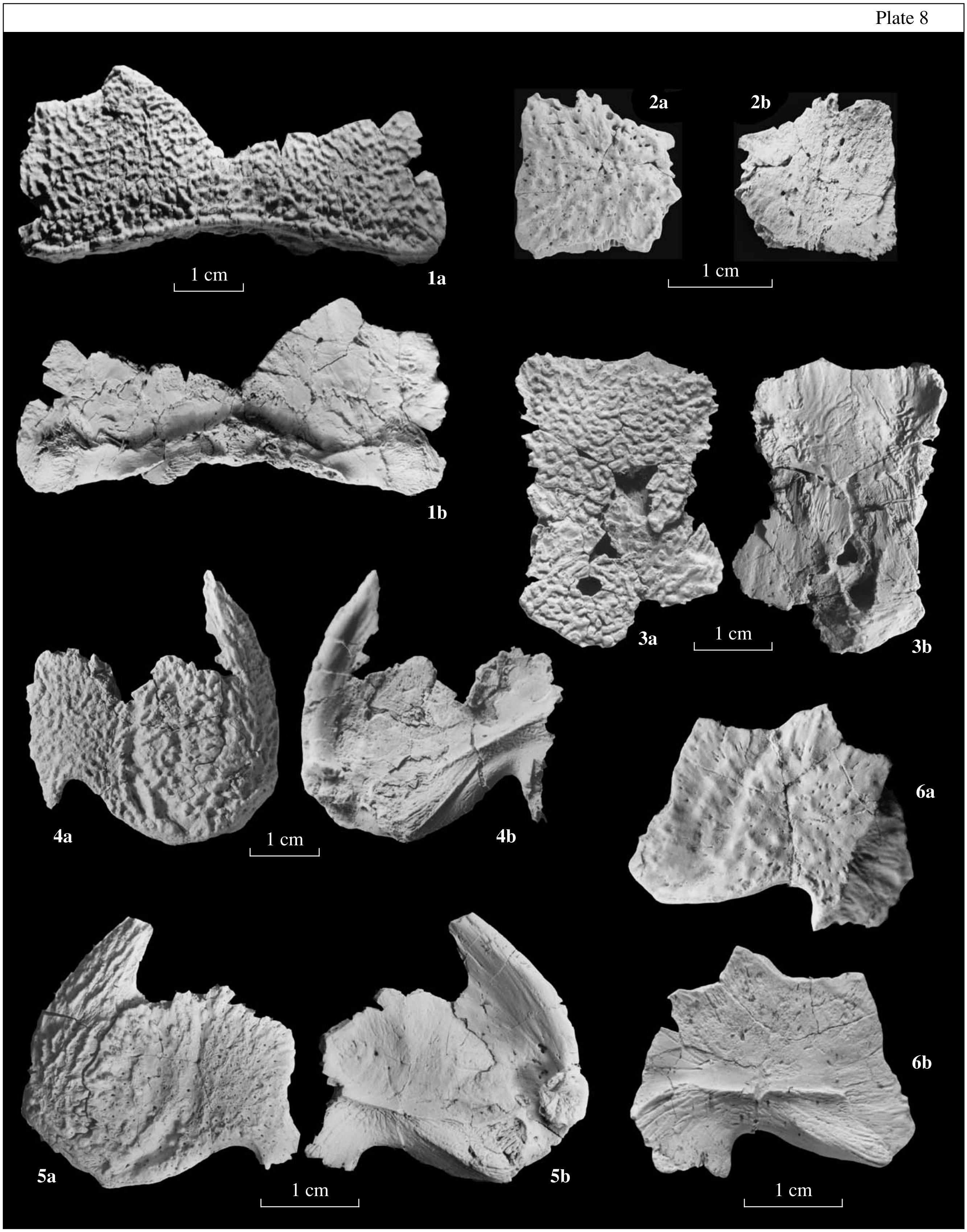
Fig. 3. Specimen PIN, no. 3713/48, fragment of the interorbital region: (3a) dorsal and (3b) ventral views.

Fig. 4. Specimen PIN, no. 3713/53, right zygomatic region: (4a) ventral and (4b) dorsal views.

Fig. 5. Specimen PIN, no. 3713/75, left zygomatic region: (5a) dorsal and (5b) ventral views.

Fig. 6. Specimen PIN, no. 3713/49, left squamosal: (6a) dorsal and (6b) ventral views.

Plate 8



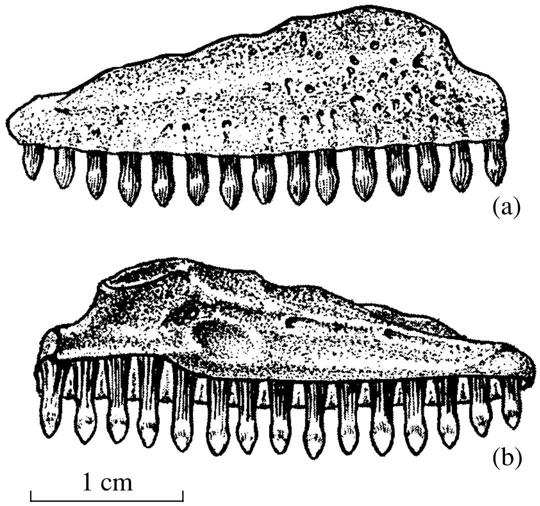


Fig. 20. *Microphon exiguus*, right maxilla, reconstructed using specimen PIN, no. 3713/45: (a) labial and (b) lingual side.

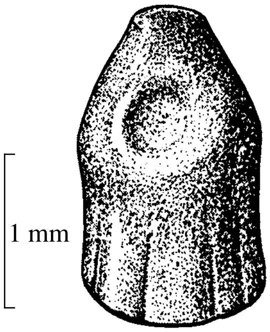


Fig. 21. *Microphon exiguus*, mandibular tooth 18, specimen PIN, no. 3585/24, labial view.

number of supplementary denticles than the maxillary teeth (Pl. 9, figs. 10, 11).

The teeth in the only known dentary of a large *M. exiguus* from the type locality lack apical crown regions and terminate in broad round facets because of wear. The labial side of the teeth has rounded pits formed by the teeth of the opposing jaw as a result of occlusion (Fig. 21). Isolated strongly worn teeth were found in the Poteryakha 2 locality (Pl. 9, fig. 9).

Available material allows one to examine the subsequent developmental stages of surface ornamentation. IN the majority of elements, the joint tuberculate pattern of the surface relief predominates; it is composed of tubercles mainly connected by bonds which form short ridges widely varying in shape and orientation (Pl. 8, figs. 1a, 3a). The tubercles appear as a result of disintegration of straight ridges formed between the furrows of the primary larval sculpture, the rudiments of which are observed in juveniles. Among available fragments, only the anterior part of the quadratojugal shows elements of radial ridged ornamentation (specimens PIN, nos. 3713/53, 75, Pl. 8, figs. 4a, 5a). Sometimes, the relief is composed of irregular cells formed by a more complete fusion between neighboring tubercles; this type of ornamentation is observed, in particular, in the central part of the parietals of specimen PIN, no. 3713/60.

At the same time, the postparietals and tabulars retain a surface relief composed of separate high tubercles at the definitive stage; fusion between tubercles is extremely poorly pronounced (specimens PIN, nos. 3713/60, 61).

On the dentary, the sculpture composed of separate or merged tubercles is present only in the anterior region where the bone is pierced by numerous foramina (Pl. 9, figs. 1a, 2a, 3a).

Microphon gracilis Bulanov, sp. nov.

The material on *Microphon gracilis* comes only from the Babintsevo locality and includes remains of juveniles. Some specimens of this species housed at SGU (collected by G.I. Tverdokhlebova in 1976) were used by Ivakhnenko (1987) for the description and reconstruction of *Raphanodon (= Karpinskiosaurus)*

Explanation of Plate 9

Microphon exiguus Ivachnenko, 1983; jaws and teeth of adults; Vologda Region; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon; all specimens, except for Figs. 5, 10, and 12, from the Poteryakha 2 locality.

Fig. 1. Specimen PIN, no. 3713/52, right dentary: (1a) labial and (1b) lingual views.

Fig. 2. Specimen PIN, no. 3713/51, left dentary: (2a) labial and (2b) lingual views.

Fig. 3. Specimen PIN, no. 3713/50, left dentary: (3a) labial and (3b) lingual views.

Fig. 4. Specimen PIN, no. 3713/45, right maxilla, labial lingual view.

Fig. 5. Specimen PIN, no. 4547/4, right ectopterygoid, ventral view; Poteryakha 1 locality.

Fig. 6. Specimen PIN, no. 3713/71, maxillary tooth, lingual view.

Fig. 7. Specimen PIN, no. 3713/177, crown of maxillary tooth, lingual view.

Fig. 8. Specimen PIN, no. 3713/175, crown of marginal tooth, lateral view.

Fig. 9. Specimen PIN, no. 3713/173, crown of premaxillary tooth, lingual view.

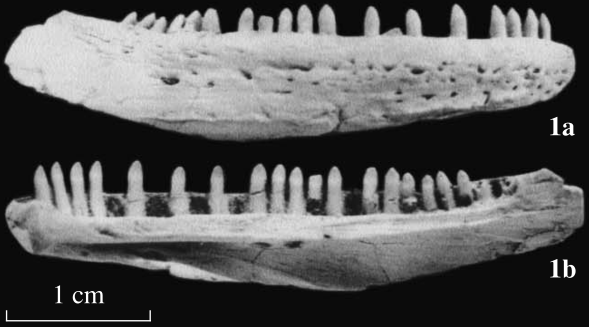
Fig. 10. Specimen PIN, no. 4723/2, crown of premaxillary tooth, lingual view; Kochevala 2 locality.

Fig. 11. Specimen PIN, no. 3713/174, crown of premaxillary tooth, lingual view.

Fig. 12. Specimen PIN, no. 3709/29, crown of resorbed tooth, dorsal view; Navoloki locality.

Fig. 13. Specimen PIN, no. 3713/176, crown of resorbed tooth, ventral view.

Plate 9


1a
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2a
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3a
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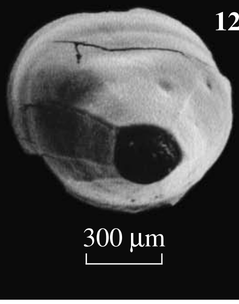
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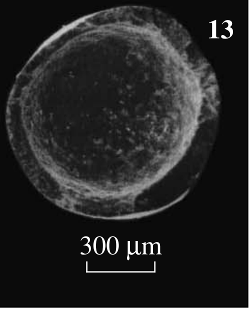
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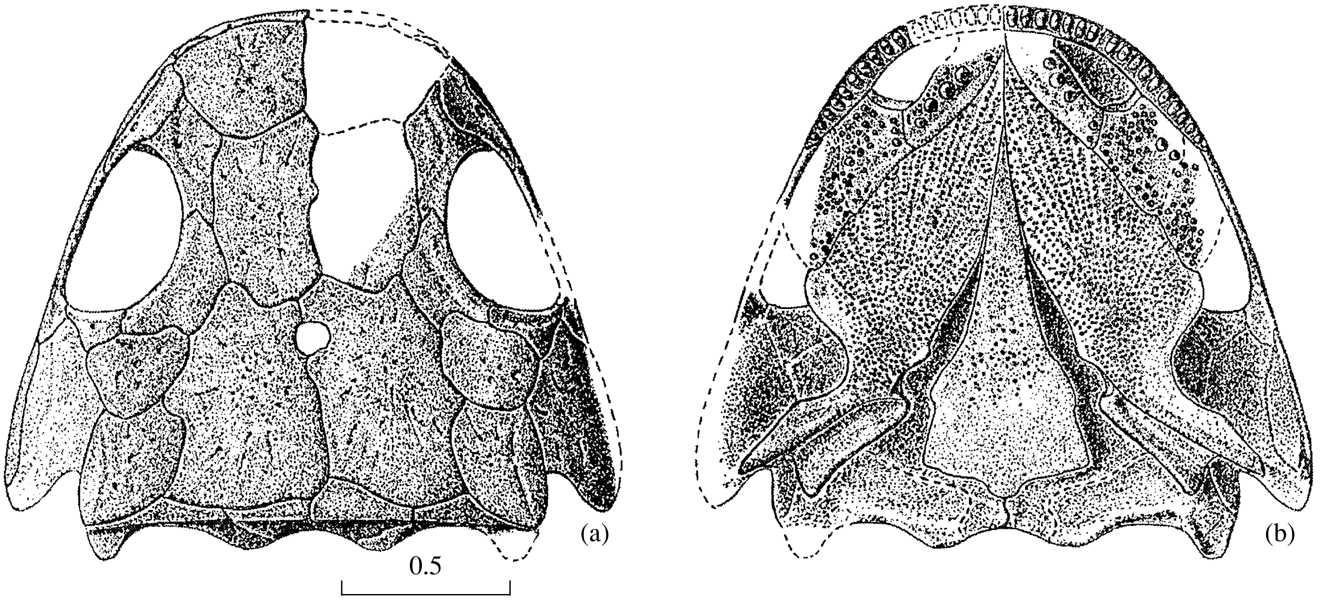


Fig. 22. *Microphon gracilis* sp. nov., juvenile skull, reconstruction based on holotype PIN, no. 4617/110: (a) dorsal and (b) ventral views.

ultimus. New material has shown clear morphological distinctions between the two forms and allowed for the establishment of a new species, *Microphon gracilis* sp. nov. This species is similar in cranial structure to *Microphon exiguus*, represented in the type locality (Donguz 6) by animals of the same ontogenetic stage; this allows for a correct comparison between these species.

Adult *M. gracilis* has not yet been found. Many specimens are poorly preserved because of specific burial conditions in the locality, skeletal elements often became disarticulated and occurred in the host rock as separate accumulations of fossils. It is not improbable that, in addition to natural postmortem disarticulation, this was associated with the consolidation and plastic deformation of the enclosing rock (argillaceous siltstone) in the course of diagenesis; this inference is substantiated by the strong lateral compression of some skulls (e.g., specimen PIN, no. 4617/189).

General characteristics. The skull is rounded parabolic in plan, the preorbital region is widened, and the zygomatic regions are abruptly inclined to the plane of the parietal shield; occasionally, the latter is observed in fossil material (e.g., specimen SGU, no. 104B/2024, Fig. 23). The skull length estimated on the basis of the skulls and their fragments from the collection under study ranges from 12 to 28 mm (specimens SGU, no. 104B/2010 and PIN, no. 4617/170, respectively); however, certain isolated bones found in the locality belong to 40-mm-long skulls (PIN, no. 4617/115, pterygoid).

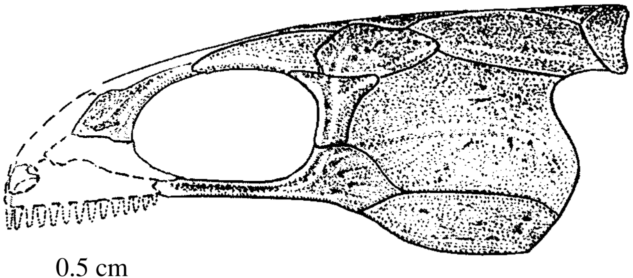


Fig. 23. *Microphon gracilis* sp. nov., juvenile skull, specimen SGU, no. 104B/2024, lateral view.

The occipital edge of the parietal shield is straight. The orbits are large and oval. The otic notches are relatively shallow and terminate at most at the midlength of the supratemporals. The jaw condyles are located substantially anterior to the occiput. The postorbital skull region is much longer than the preorbital region. The nares face mainly anteriorly.

Skull roof. The parietals are large and extended. Their anterior regions enter the interorbital region (Fig. 22a). A small and round (occasionally, oval, e.g., in specimen PIN, no. 4617/109, Fig. 24) pineal foramen is located in the anterior quarter of the parietals immediately posterior to the transverse plane of the posterior orbital rim. The frontals expand anteriorly (occasionally, abruptly expand; e.g., in specimen PIN, no. 4617/109) and are displaced far from the orbital rims by the contact between the prefrontal and the postfrontal. The nasals are very broad, especially in the anterior region.

In the majority of specimens, the prefrontal is smaller than the postfrontal; however, the right side of the holotype shows the inverse ratio. A very short postorbital is located far from the supratemporal. The latter bone does not expand posteriorly. The intertemporal is irregularly isometric in shape and only slightly smaller

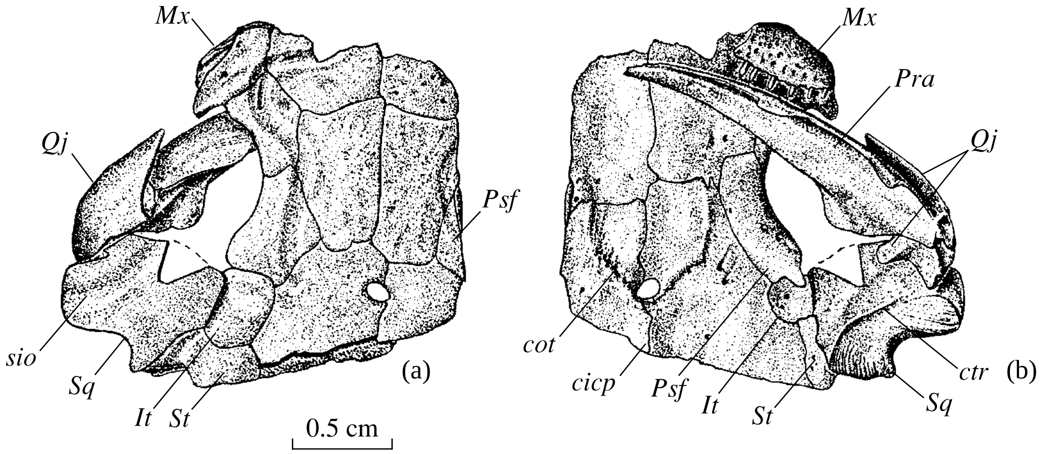


Fig. 24. *Microphon gracilis* sp. nov., incomplete juvenile skull, specimen PIN, no. 4617/109: (a) dorsal and (b) ventral views.

than the supratemporal; laterally, it comes into extensive contact with the squamosal. The anterior edge of the jugal comes into narrow contact with the lacrimal, which weakly expands under the orbit. A short postorbital region of the jugal only slightly wedges in the suture between the quadratojugal and the squamosal. The lacrimal is low and does not contain a canal for the nasolacrimal duct. In the holotype, the right septomaxilla is preserved; it looks like a wide crescentic plate with a nonclosed septomaxillary foramen.

On the dorsal surface of the smallest individuals (holotype and specimen SGU, no. 104B/2010), the bones of the occipital region are virtually undeveloped; the postparietals weakly jut out into the parietals and the tabulars project toward the otic notches. The paroccipital processes are short and trapezoidal, they are separated from the occipital processes by wide notches; this suggests that the posttemporal fossae were open.

The squamosal is very large and comes into wide contact with the intertemporal, its anterior edge closely approaches the orbital rim. The quadratojugal terminates opposite the posterior orbital margin and strongly projects ventrally with reference to the jugal.

In specimen PIN, no. 4617/190, the left orbit contains a fragmentary sclerotic ring composed of three rectangular plates; several isolated elements are located near this region.

The premaxilla is broad; it has a wide and short dorsal process, the external side of which contains several relatively large foramina. Premaxillary fontanel is absent. The premaxilla contains seven teeth (holotype and specimen PIN, no. 4617/185).

The maxilla is short and high; on the anterior edge, it has a postnasal process directed anterodorsally (specimens PIN, nos. 4617/111, 112; Pl. 10, figs. 1a, 2a) and probably articulated with the nasal, strongly expanding laterally; therefore, the lacrimal is isolated from the naris. A contact between the elements under consideration most likely occurred in the holotype, the postnasal process of which is rudimentary; as a form of individual variation, the process could be undeveloped in some large individuals (specimen PIN, no. 4617/175, Pl. 10, fig. 3a).

Externally, the bone surface is pierced by numerous foramina. The main foramen for the infraorbital artery is located at the midlength of the maxilla above the fossa for the antorbital process of the olfactory capsule. In the 15–28-mm-long skulls, the bone contains 10–13 teeth (holotype and specimen PIN, no. 4617/112, respectively).

The ventral surface of the skull roof of *Microphon gracilis* is closely similar in structure to that of *M. exiguus* (Figs. 24b, 25). The parietal foramen is located in a small depression between the orbitotemporal crests of

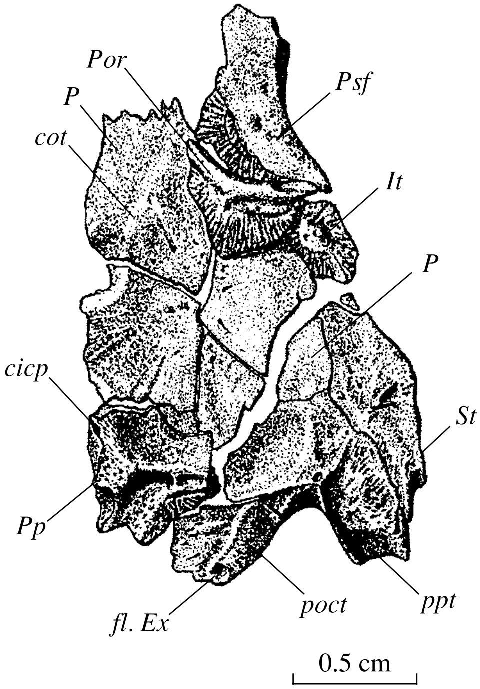
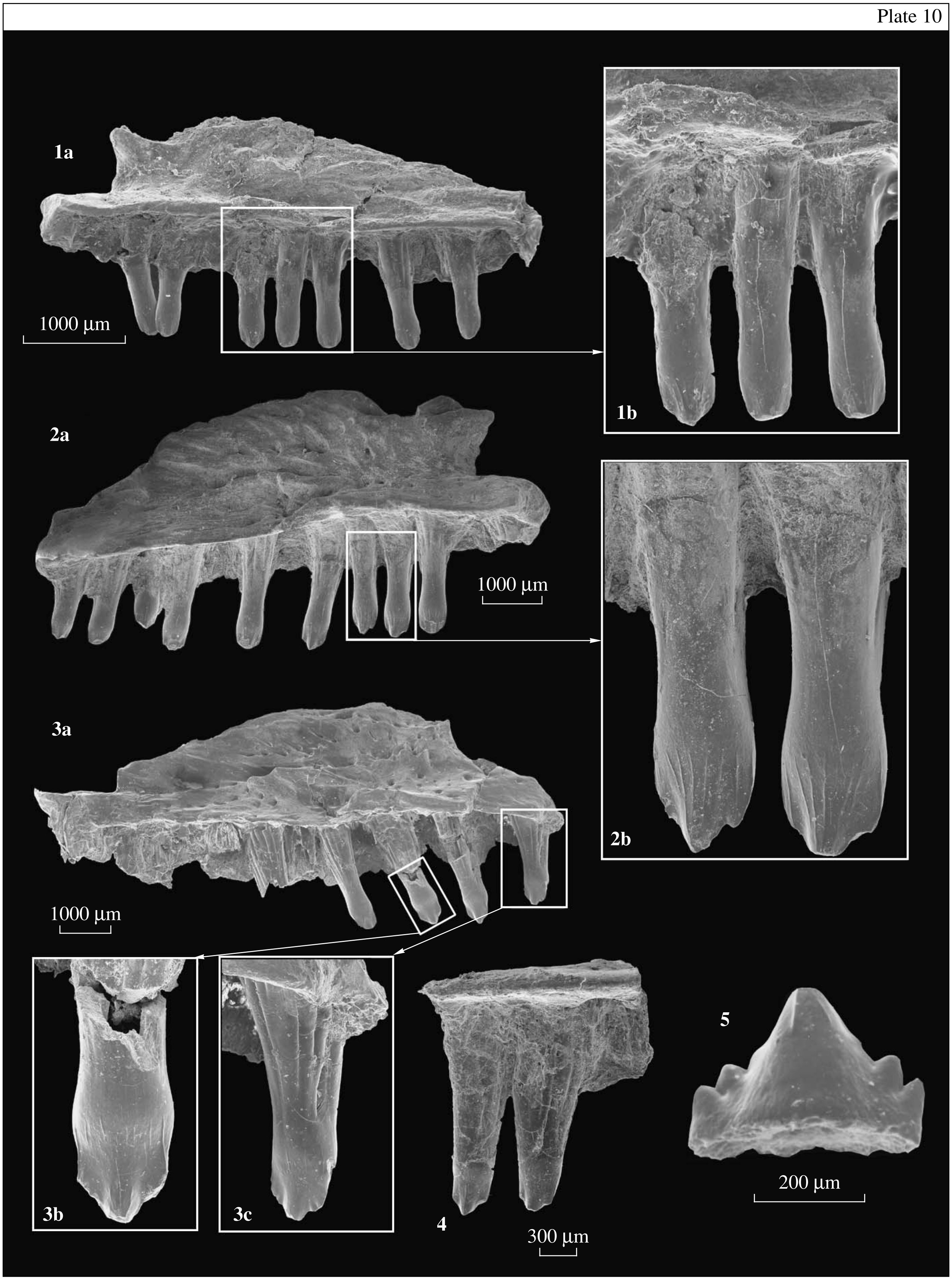


Fig. 25. *Microphon gracilis* sp. nov., fragment of juvenile skull roof, specimen PIN, no. 4617/170, ventral view.

Plate 10



Explanation of Plate 10

Microphon gracilis sp. nov.; upper jaws and teeth of juveniles; Babintsevo locality (Orenburg Region, Grachevskii District; Upper Permian, Upper Tatarian Substage, Northern Dvina Horizon).

Fig. 1. Specimen PIN, no. 4617/112, right maxilla, lingual view: (1a) general appearance and (1b) teeth from the middle of the tooth row.

Fig. 2. Specimen PIN, no. 4617/111, left maxilla, lingual view: (2a) general appearance and (2b) teeth from the anterior part of the tooth row.

Fig. 3. Specimen PIN, no. 4617/112, left maxilla, lingual view: (3a) general appearance and (3b, 3c) teeth from the anterior part of the tooth row.

Fig. 4. Specimen PIN, no. 4617/182, fragmentary maxilla, lingual view.

Fig. 5. Rudimentary crown of mandibular tooth, specimen PIN, no. 4617/180, lingual view.

the endocranial imprint; posterior to the foramen, the crests fuse with one another. Anterior to the parietal foramen, the crests diverge laterally; further anteriorly, they abruptly curve and extend almost parallel to each other, passing around the frontals. The intercapsular crest is low; on the sides of this crest, the concave roof of the parietals forms depressions that are limited posteriorly by the ventral projection of the skull roof extending across the tabulars and postparietals and providing attachment facets for the elements of the occipital ring and the auditory capsules. The attachment facet for the opisthotic on the ventral surface of the paroccipital process of the tabular is rugose. Anteromedial to this facet, the tabular has a shallow depression where the upper edge of the ascending ramus of the pterygoid was probably attached. The facet for the exoccipital is a spherical depression on the ventral end of the occipital process (Fig. 25). The transverse crest on the ventral side of the squamosal marks the position of the quadrate ramus of the pterygoid, it is substantially displaced anteriorly with reference to the edge of the otic notch (specimens PIN, nos. 4617/109, 119–121; SGU, no. 104B/2024). The posteromedial region of the quadratojugal is an inverted cup-shaped protrusion covering externally the articular region of the palatoquadrate.

Specimens PIN, nos. 4617/109 and 170 allow one to judge the relative positions of bone boundaries on the ventral and dorsal surfaces of the skull roof. In the axial region, the anterior bones usually overlie the posterior bones. The parietals widely spread under all adjacent elements, except for the tabulars and postparietals occupying the posterior positions. The dorsal surface of the tabulars is almost entirely reduced; however, on the ventral side, they strongly expand anteriorly and medially, widely spreading under the postparietals, parietals, and supratemporals. Ventrally, the supratemporal is partially covered by the parietal; laterally, it is covered by a wide temporal process of the squamosal connecting the zygomatic region to the parietal shield. The intertemporal occupies an external position, only its central region is seen ventrally; this region is pierced by the foramina providing passage for nerves and blood vessels to the skin.

Palate. The choanae are elongated teardrop-shaped, becoming narrower anteriorly in parallel with the expansion of the vomers (Fig. 22b). Anterior to the pterygoids, the vomers come into narrow contact with one another and isolate the pterygoids from the premaxillae. The palatine processes of the premaxillae are undeveloped. The vomer and the palatine contact at the posterior end of the choana. The palatine lacks a laterochoanal process. The ectopterygoid is substantially smaller than the palatine.

The palatine rami of the pterygoids frame the anterior region of the parasphenoid rostrum and come into relatively wide contact with one another. The lateral elements of the palate are arranged in line and only slightly jut out into the pterygoids. The ventrally curving pterygoid flanges are positioned at an angle of approximately 90° to the quadrate rami of the pterygoids.

The posterior region of the parasphenoid expands and gradually becomes a broad rostrum terminating opposite the posterior edge of the choanae. The lateral edges of the bone form projections in the region of the basipterygoid processes, a small process is also present at the posterior margin of the bone. The parafenestral wings are undeveloped.

Lower jaw. Specimen PIN, no. 4617/180 allows one to judge the structure of the lower jaw of *M. gracilis* (Fig. 26). Between the anterior edge of the prearticular located opposite the eighth mandibular tooth and the symphysis, there is a narrow notch bounded ventrally by the splenial and, dorsally, by the expanded anterior region of the dental area and the precoronoid adjoining this area posteriorly. The splenial closely approaches the symphysis; however, it does not contribute to the formation of the articular surface. The postsplenial is of the same length but wider, expanding dorsally on the external side of the jaw.

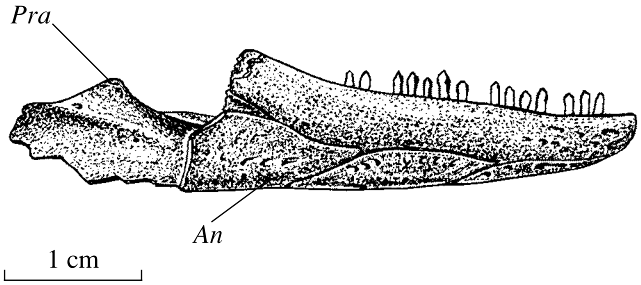


Fig. 26. *Microphon gracilis* sp. nov., right ramus of the lower jaw, specimen PIN, no. 4617/180, labial view.

The coronoid process is covered lingually by longitudinal furrows. The internal wall of the adductor cavity gradually lowers posteriorly and deviates medially to form a projection located at an angle of approximately 30° to the horizontal plane. In the articular region of the jaw, the prearticular abruptly expands dorsally. The lower jaw includes three toothed coronoids, the boundaries of the coronoids are located opposite the thirteenth and, probably, eighteenth mandibular teeth. The external surface of the anterior region of the dentary is pierced by numerous foramina. The lower jaw contains 24 teeth (specimen PIN, no. 4617/180; skull about 30 mm in length).

Dentition. In 15-mm-long skulls, the marginal teeth are weakly folded, the tooth bases are round in cross section, the crowns are unicuspid, and the apex is slightly flattened. The tooth bases of larger animals are intensively folded, compressed laterally, and oval in cross section (Pl. 10, figs. 1b, 2b, 3b, 3c, 5). The proximal region of the crowns is thickened; on each side of the high central apex, the cutting edge has one to three well-pronounced supplementary denticles clearly isolated from each other and often showing wear marks that appeared during their lifetime (Pl. 10, fig. 4). The lingual side of the tooth crowns is covered by prominent ridges converging to the apex and extending to the lateral denticles.

On the palate of the holotype, each vomer retains only three large teeth located along the medial wall of the choanae. The surface of the palatines and ectopterygoids is covered by smaller teeth (using available material, it is difficult to determine the arrangement of these teeth); at this developmental stage, the postchoanal tooth row consists of only two relatively large teeth located posterior to the choanae.

The palatine rami of the pterygoids are covered by numerous rows of small teeth diverging radially from the ossification centers; thus, the palatal teeth are absent from only the ventrally curving margins of the pterygoid flanges. The toothed fields cover the bases of the quadrate rami of the pterygoids and expand posteriorly to the midlength of these rami.

Surface ornamentation. In all specimens of the size range under study, the membrane bones of the skull roof are covered externally by narrow radial furrows diverging from the foramina located at the ossification centers.

Seismosensory system. In the smallest known individual (specimen SGU, no. 104B/2010, parietal shield with the interorbital region, estimated skull length is about 13 mm), only the temporal branch of the supraorbital groove of the seismosensory system is discernible. This groove emerges on the postorbital and passes onto the intertemporal and, then, onto the external margin of the supratemporal.

In the holotype (skull about 15 mm in length), the seismosensory canals are weakly imprinted but are substantially more complete (Fig. 22a). The temporal branch of the supraorbital groove extends along the boundary between the intertemporal and the squamosal and passes onto the postorbital, bypassing the intertemporal, in contrast to that of specimen SGU, no. 104B/2010. Above the orbit, the groove is marked only on the right side of the skull where it covers a small area of the frontal at the contact between the postfrontal and the prefrontal. In the preorbital region, the groove forms an abrupt flexure and passes through the ossification center of the nasal. In the anterior part of the prefrontal, the surface of the groove contains a large foramen for the superficial ramus of the facial nerve responsible for innervation of the anterior segment of the supraorbital canal. A furrow for this nerve originates from the foramen and passes onto the nasal.

The infraorbital groove is distinctly seen on the jugal where it is presented as a series of deep lacunae most likely formed by the nerves and blood vessels associated with the seismosensory canal rather than by the canal itself. Posterior to the orbit, this groove is connected to a well-pronounced groove of the postorbital commissure; subsequently, it passes onto the squamosal where, being clearly seen, it passes laterally far beyond the ossification center. The holotype lacks a trace of the occipital commissure.

In specimen PIN, no. 4617/109 (skull about 22 mm long; Fig. 24), the grooves of the lateral line organs are broad and continuous over the entire extent; this is an important distinction from *M. exiguus* of the same size. The groove is broken only at the transition of the supraorbital groove from the postfrontal to the parietal; judging from the depth of the grooves, this apparently shows an actual division of the seismosensory canals of this animal. A continuation of the groove is observed on the intertemporal. On the lacrimal, the anterior region of the infraorbital canal is imprinted.

Endocranium. At the ontogenetic stage considered, the palatoquadrate and braincase lack cartilage bones.

Age variation. Available material shows a relatively narrow range of size variation. The ontogenetic variation is observed mainly in the number of marginal teeth and the complication of their crowns. As the skull increases in length from 15 to 28 mm, the number of maxillary teeth increases from 10 to 14. The tooth bases become longer and more intensively folded, the proximal regions of crowns become thicker and wider in comparison with the uppermost part of the bases. Supplementary denticles appear on the cutting edge and their number increases in subsequent tooth generations; on each side of the central apex, the cutting edge has up to three denticles.

In skulls less than 15 mm in length, the seismosensory grooves on the surface of the skull roof are discontinuous. As the skull reaches 21 mm in length, the primary grooves merge to form an integral network; breaks are only observed in the supraorbital groove at the point where it passes onto the parietal (or intertemporal) and in the anterior region of the skull, within the upper jaw arch, where the furrows are hardly discernible because the labial surface of the premaxilla and maxilla is considerably perforated (the occipital edge of the parietal shield where the occipital commissure usually pass, is not preserved in available specimens of the size class considered).

Microphon arcanus Bulanov, sp. nov.

The holotype (PIN, no. 3711/1) is an incomplete maxilla with 11 alveoli, six of which contain teeth (Figs. 27a, 27b). Three teeth (the first, second, and eighth) were lost as a result of disintegration preceding the burial. The maxilla is relatively low and has a small notch in the anterior edge (probably, the greater part of the ventral wall of the naris was formed by the premaxilla). Posterior to the nares, the upper margin of the maxilla has an internally inclined articular facet for the anterolateral edge of the lacrimal. The anterior foramen for the infraorbital artery is in line with the fifth maxillary tooth; posteroventral to this foramen, opposite the posterior edge of the choana, there is a fossa connected to the antorbital process.

The tooth crowns are strongly thickened proximally and the lingual inclination of the apices is weak (Figs. 27c, 27d). Massive crests formed by the fusion of the lateral denticles are observed on the cutting edge on either side of the central apex. Lingually, the crowns are covered by numerous narrow ridges converging to the central apex and extending to the lateral crests. The tooth bases are intensively folded and, at the level of tooth attachment, round in cross sections; toward the crown, the cross section gradually becomes extended oval. Each preserved tooth shows traces of wear during the animal's lifetime, i.e., blunted central apices, smoothened edges of the lateral crests, and wear marks on the ridges of the lingual side of the tooth crowns.

Genus *Kotlassia* Amalitzky, 1921

Kotlassia prima Amalitzky, 1921

Until recently, *Kotlassia prima* was only known from the type locality and presented by an almost complete skeleton (holotype PIN, no. 2005/74) and an isolated skull (specimen PIN, no. 2005/75), which were examined by a number of researchers (Amalitzky, 1921; Sushkin, 1925, 1926; Hartmann-Weinberg, 1935; Bystrow, 1944; Ivakhnenko, 1987). During the initial preparation, the specimens were strongly damaged. In particular, on the skull roof of specimen PIN, no. 2005/75, the majority of bones were removed and it virtually became a mold of the inner surface of the dermatocranium. This specimen provides no way of studying the structure of the palatal complex. The skull of the holotype is more informative; however, it is incompletely preserved (a large part of the palate and the zygomatic region on the left side are lost) and deformed, the state of the skull roof surface allows one to trace only some boundaries between individual ossified elements. This is part of the reason for the differences between the earlier reconstructions of *Kotlassia* proposed by different researchers. Another reason for the erroneous ideas concerning this genus was the assignment of certain other amphibians from the same locality to this form. In particular, certain specimens of *Karpinskiosaurus secundus* were originally described by Amalitzky as a species of *Kotlassia* (*K. secunda* Amalitzky, 1921) and the bone armor of the chroniosuchid *Chroniosuchus licharevi* was also assigned to this genus (Hartmann-Weinberg, 1935; Bystrow, 1944).

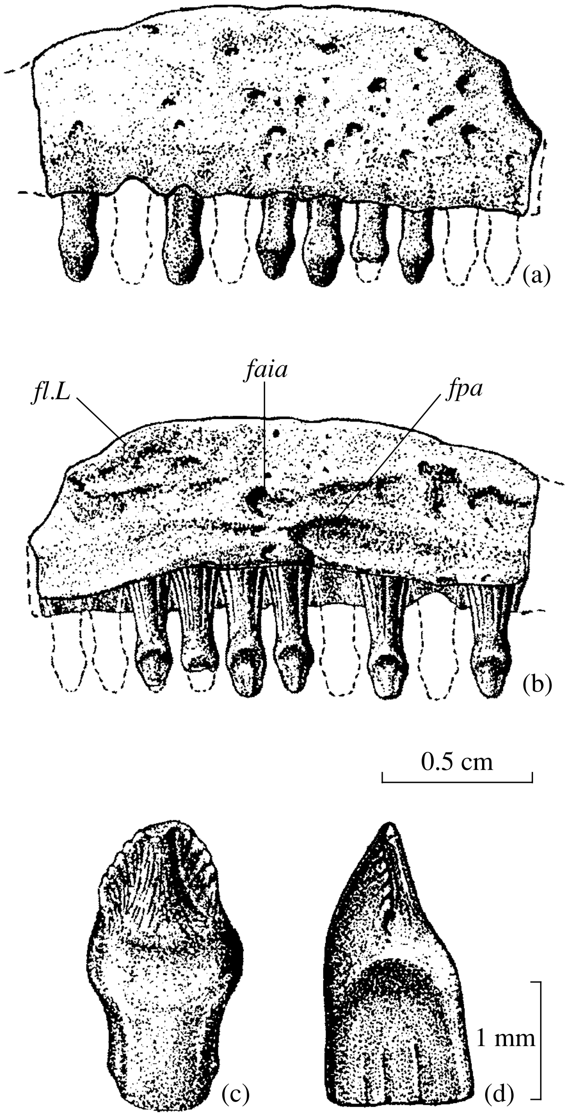


Fig. 27. *Microphon arcanus* sp. nov., right maxilla, holotype PIN, no. 3711/1: (a) labial view; (b) lingual view; (c) crown of maxillary tooth, lingual view; and (d) crown of maxillary tooth, lateral view.

The skull of *Kotlassia prima* is reconstructed here on the basis of the holotype only (Figs. 30, 31). New data on the genus *Microphon*, which has much in com-

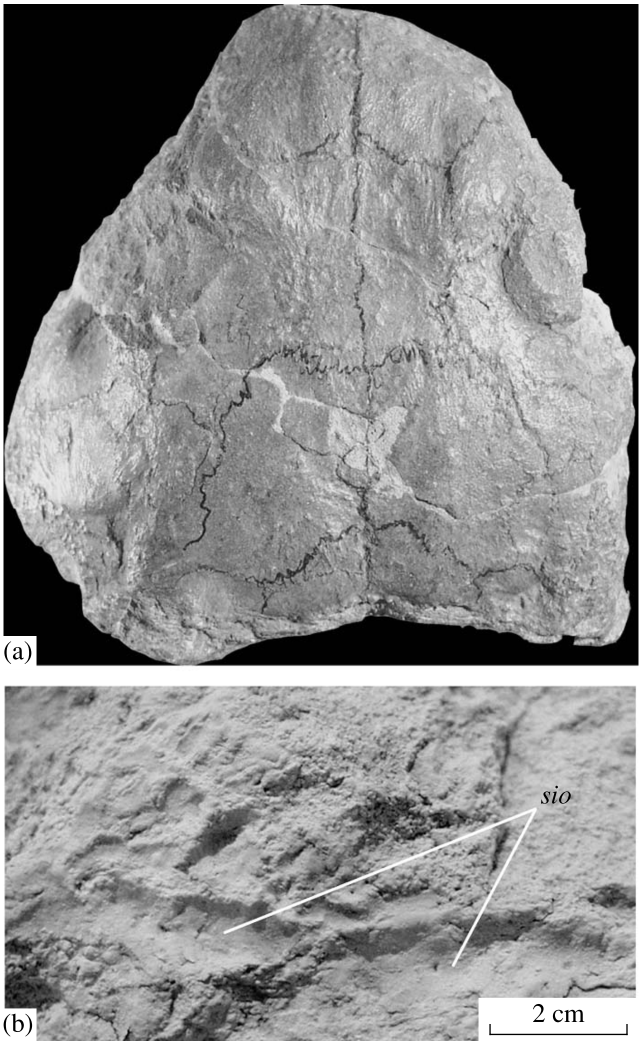


Fig. 28. *Kotlassia prima*, skull, specimen PIN, no. 2005/75: (a) dorsal view and (b) segment of the infraorbital seismosensory canal, left side.

mon with *Kotlassia* and is widespread in the earlier beds, are of great importance in the understanding of available data. Because of the poor preservation of the type material, isolated specimens of *Kotlassia prima* (fragmentary jaws, bones of the palatal complex, numerous teeth, vertebrae, etc.) found in the recently discovered Gorokhovets locality are of considerable importance for the characteristics of this species.

Notwithstanding its relatively poor preservation, the holotype provides us with the most significant data on *Kotlassia prima.* It is especially important as a source of information about the endocranial structure of kotlassioids, in the majority of which the endocranium either ossified to a lesser extent or not at all (Utegeniidae) or was extremely poorly preserved in available specimens (e.g., in *Biarmica* and *Leptoropha*).

A reexamination of the other kotlassian species, *K. grandis* Tverdochlebova et Ivachnenko, 1994, has shown that it is a karpinskiosaurid closely related to *Karpinskiosaurus ultimus.*

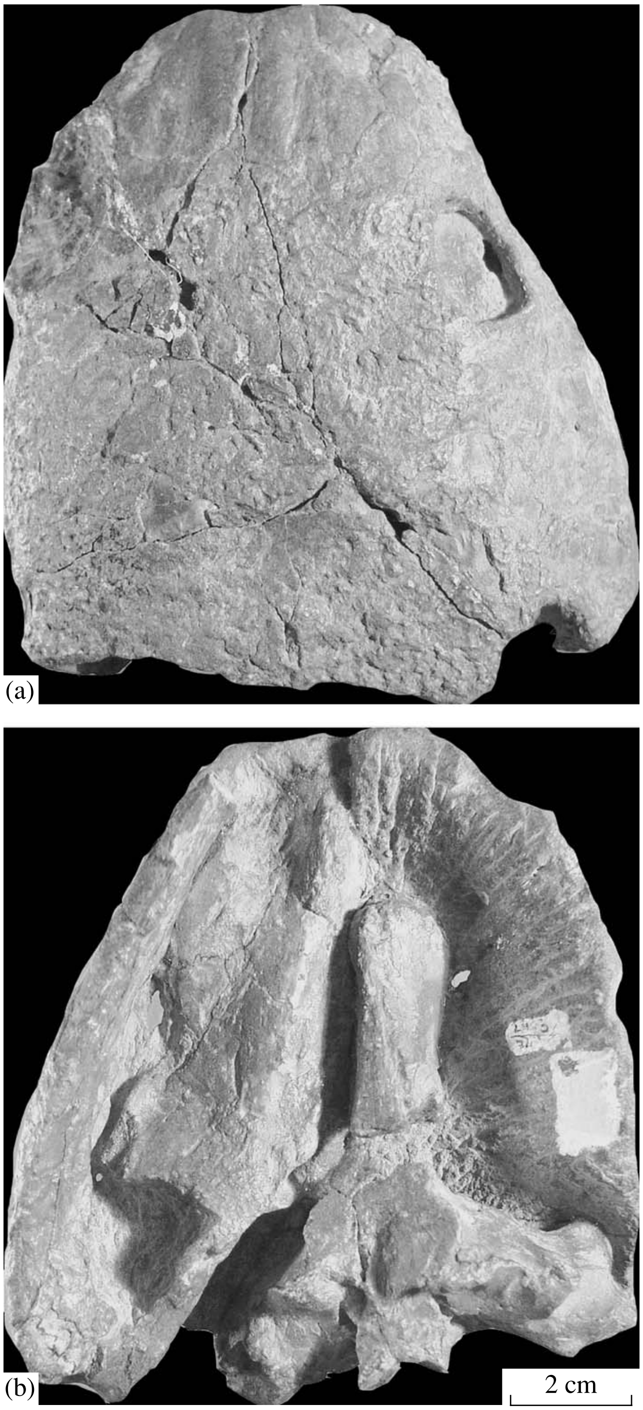


Fig. 29. *Kotlassia prima*, skull, holotype PIN, no. 2005/74: (a) dorsal and (b) ventral views.

General characteristics. The skull of *Kotlassia prima* is characterized by the high position of its zygomatic region, which is inclined at an angle of about 40° to the central part of the skull roof (specimen PIN, no. 2005/75), and an almost flat parietal shield

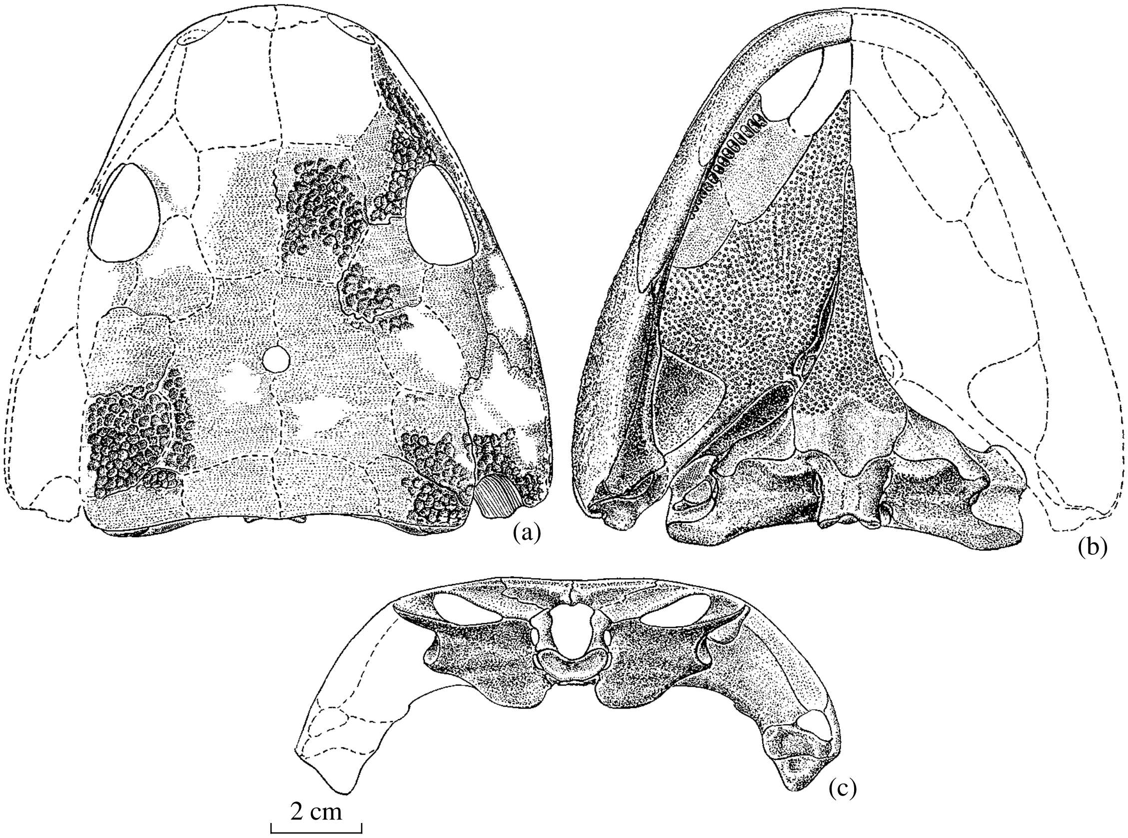


Fig. 30. *Kotlassia prima*, skull, reconstructed using holotype PIN, no. 2005/74: (a) dorsal, (b) ventral, and (c) rear views.

(a retreating parietal shield of the holotype is accounted for by deformations; in specimen PIN, no. 2005/75, the same effect is attributable to the absence of membrane bones in the axial part and the concave ventral surface of the parietals, as, e.g., in adult *Microphon exiguus*). The orbits are relatively small, round, and displaced anteriorly with reference to the midlength of the skull. The posterior orbital rim of the holotype is located at the midlength of the skull; in specimen PIN, no. 2005/75, which is somewhat smaller, it is in a more posterior position. The preorbital region is widened; however, it is developed to a greater extent than that of *Microphon* because of relatively longer nasals. The occipital edge of the skull is concave, especially in specimen PIN, no. 2005/75. The small and round parietal foramen is located substantially posterior to the posterior orbital rim. The otic notches are small, narrow, and rounded; their anterior edges are approximately in line with the midlength of the supratemporal. The external nares face mainly anteriorly and are only slightly turned laterally. The jaw condyles are located somewhat anterior to the occipital condyle. Along the midline, the skulls of the holotype and specimen PIN, no. 2005/75 are approximately 120 and 105 mm long; taking into account the posteriorly projecting tabulars, they are 125 and 116 mm long, respectively.

Skull roof. The parietals are small and narrowed in the anterior part and terminate short of reaching the interorbital region. The frontals are widened rostrally and extend to the level of the anterior orbital rim. The nasals are extended and widened anteriorly. It is difficult to estimate the size of the external surface of the postparietals of the holotype. In specimen PIN, no. 2005/75, judging by the imprint in the host rock, the anterior edges of the ventral side of the postparietals are located halfway between the occipital edge and the parietal foramen. It is highly unlikely that the dorsal flanks of the postparietals were developed to such a great extent; these bones undoubtedly had wide underlying plates for the parietals and occupied a substantially smaller area on the dorsal surface, similar to those of other kotlassioids.

The prefrontal and postfrontal are approximately equal in size and come into wide contact with each other. The postorbital is triangular in shape and located far from the supratemporal. The intertemporal is large, equal to, or somewhat larger than, the supratemporal. The tabular becomes narrower toward the otic notch. The massive paroccipital processes of the tabulars are well preserved in the holotype, their wide ventral laminae overlie the paroccipital processes of the opisthotic. These processes are turned ventrally and posteromedially to frame laterally and partly ventrally the posttemporal fossae, which are widely open posteriorly. The occipital processes also rest on the opisthotics, their tips adjoin the well-ossified exoccipitals.

The squamosal is very large, the otic notch is approximately two-thirds as wide as the occipital flank of this bone. The jugal strongly expands posteriorly behind the orbit. It is impossible to judge the relationships of the jugal with the lacrimals and maxillae in either specimen. The anterior edge of the quadratojugal is in line with the posterior orbital rim.

Judging from the size of the nares, the dorsal processes of the premaxillae were broad. The maxillae are not preserved; using available specimens, it is impossible to outline the positions of these bones.

Certain structural details of the ventral surface of the skull roof of *Kotlassia prima* are reconstructed on the basis of the bone imprints on the internal mold of specimen PIN, no. 2005/75 (Fig. 28a). The position of the parietal foramen in this specimen is determined by the point where the well-pronounced imprints of the orbitotemporal crests extending from the interorbital region come close together. Posterior to the foramen, the crests merge into a well-pronounced crista mediocapsularis, which is imprinted in the host rock as a groove passing back along the medial suture to the occipital edge of the parietal shield. The groove isolates wide elevations showing that the surface of the parietals and, partially, the postparietals were convex. Judging from the imprints of the foramina and canals for blood vessels, the ossification centers of the parietals were located caudal to the parietal foramen in the posterior regions of these bones. The thickened margins of the bones framing the orbital rim are imprinted in the host rock as wide grooves. However, in the region of the prefrontals, there are dome-shaped elevations in the imprint; medially, the orbitotemporal crests approach these elevations. Another flat and wide elevation, the presence of which in the holotype is attributable to the absence of nasals, extends along the suture between the latter bones. Judging from the imprint, the margins of the nasals adjoining the external nares were probably thickened and formed a low ridge.

Palate. The holotype allows one to examine the structural features of the palatal complex of *Kotlassia*, since the parasphenoid and membrane bones on the right side of the palatoquadrate complex are almost completely preserved (Fig. 30b).

The choanae are large and oval. The boundaries between the lateral elements of the palate are traced only partially. The vomer is not seen in the specimen; probably, it was not preserved in the burial or was lost during preparation. The palatine has a well-pronounced short laterochoanal process. Along the boundary with the maxilla, the palatine has transversely broken bases of large teeth in the postchoanal row, which show a plicate structure characteristic of this form. The ectopterygoid is somewhat narrower and, most likely, longer than the palatine. As a result of deformation, this element is displaced from its natural position and its posterior region is pushed onto the pterygoid; this is evidenced by the outlines of the bone and by the posteromedial orientation of teeth of the postchoanal row passing from the palatine onto the ectopterygoid.

The pterygoid has a well-pronounced flange, which abruptly projects into the adductor cavity and is positioned at an angle of about 70–80° to the quadrate ramus. Medially, the latter borders a clearly ossified quadrate and adjoins the ventral edge of the occipital flank of the squamosal. The ascending lamina forms a cup-shaped cover around the auditory capsules; its dorsal projection falls in the region of the anterior wall of the prootic almost in line with the anterior margins of the tabulars (the ventral edges of these bones). The fossa of the basipterygoid articulation is small and faces anteromedially, the articular facet faces posterolaterally and somewhat dorsally.

The rostrum of the parasphenoid is relatively narrow, its anterior edge is in line with the posterior edges of the choanae. Parafenestral wings are absent; however, immediately posterior to the region of the basipterygoid articulation, the bone forms small and round lateral projections spreading under the medioventral region of the prootic. In the center of the posterior region of the parasphenoid, there is a depression bounded anteriorly by a field of shagreen teeth and extending to the posterior end of the bone. The latter looks like a caudally directed projection attached to the anterior region of the basioccipital.

Lower jaw. In the holotype, the right ramus of the lower jaw is in the natural position and partially covered laterally by the quadratojugal; this provides no way of studying the surangular. The left ramus is not preserved. In specimen PIN, no. 2005/75, the mandibular rami are absent.

On the labial side of the lower jaw, the sutures between membrane bones are difficult to trace because of poor preservation. The anterior edge of the angular is approximately at the midlength of the mandible. The boundary of the dentary is established on the basis of changes in the pattern of surface sculpturing. The boundary between the splenials is hardly discernible; on the external side of the jaw, either bone somewhat expands dorsally.

The lingual side is largely formed by an extensive prearticular closely approaching the symphysis and covering medially the articular region, which is only slightly elevated (Fig. 30d). The coronoid process is high and projects far above the tooth row. It is formed by the posterior coronoid, the contact of which with the surangular is quite distinct. The boundaries between the coronoids are difficult to determine. A small oval Meckel's foramen opens anteriorly opposite the coronoid process between the prearticular, angular, and, possibly, postsplenial. The anterior edge of the adductor cavity is in line with the posterior end of the ectopterygoid. The medial wall of the cavity is only slightly lowered posteriorly. Toward the jaw joint, the upper edge of the prearticular gradually turns laterally, the angle of deviation is at most 40°; therefore, the cavity gradually increases in width. In the ventral view, the lower edge of the jaw gradually becomes sharper posteriorly.

Dentition. In each specimen from the Sokolki locality, the bones of the upper and lower jaws are either lost or strongly damaged; therefore, the number of marginal teeth remains uncertain. The fragmentary maxilla of the holotype contains several well-preserved teeth from the middle of the tooth row, which allows one to examine the dental structure in *Kotlassia*. The material collected by Amalitzky includes an isolated tooth (specimen PIN, no. 2005/2689) undoubtedly belonging to this form; however, it is approximately 1.5 times as large as the maxillary teeth of the holotype.

The crowns of marginal teeth of *Kotlassia* are very simple in structure. They lack supplementary denticles and have sharp cutting edges on either side of the crown. The flat apices are blunted by wear and moderately curved lingually; in all specimens, the lingual side lacks ridges. The tooth bases are compressed laterally and strongly extended transversely relative to the jaws. The pulp cavity has a well-developed plication; however, only in the near-crown region, do the folds adjoin each other laterally, whereas at the attachment to the bone, they are isolated.

The postchoanal row of large palatine teeth is completely formed and extends along the palatine–maxillary boundary from the posterior edge of the choana to the anterior edge of the adductor cavity. The teeth are not preserved; however, the palatine and ectopterygoid bear plicate stumps of the tooth bases; similar to the marginal teeth, the bases are closely spaced and, at the anterior end of the row, clearly lengthened. Posteriorly, the cross section of the teeth gradually becomes round and decreases in diameter. The palatine bears eight (or nine) teeth, the ectopterygoid bears at least eight.

The parasphenoid rostrum is covered by small teeth. The posterior boundary of the shagreen field is clearly seen on this element and frames anteriorly an extended depression in the posterior region of the bone. Because of poor preservation, the teeth on the pterygoid are seen only near the ossification center, namely, in the region of the basipterygoid articulation and within the quadrate ramus.

Surface ornamentation. The skull roof of specimen PIN, no. 2005/75 virtually lacks surface sculpturing.

In the holotype, the sculpture is also strongly damaged; however, it is satisfactorily preserved in places; this allows one to gain general insight into the surface relief on the greater part of the skull roof. The relief of *Kotlassia* is almost entirely composed of small and, occasionally, irregular cells, which are rather prominent in some elements of the right side, in particular, on the tabulars, the posterior region of the supratemporal, along the otic notch on the squamosal, and in some areas of the frontals and prefrontals. On the lacrimal, the sculpture was most likely different somewhat and reminiscent of the joint tuberculate pattern; however, isolated cells are clearly seen in the region of the lacrimal of specimen PIN, no. 2005/75.

On the lower jaw, the relief composed of ridges diverging from the ossification center on the labial side of bone is characteristic of the angular. The external surface of the dentary has a relatively weak wrinkled surface sculpturing; apparently, the ornamentation of this bone was mainly composed of longitudinal ridges located between numerous foramina for blood vessels and nerves and formed by joint tubercles.

Seismosensory system. The fact that *Kotlassia* had the seismosensory system is evidenced by the presence of a well-pronounced segment of the infraorbital groove on the left side of specimen PIN, no. 2005/75 (Fig. 28b). In the holotype, the right jugal bears wide and extended furrows below the orbit; these furrows are larger than the elements of surface sculpturing and probably contributed to the formation of the infraorbital groove. Several cells united in a row on the lacrimal are most likely the anterior extension of the groove. Because of poor preservation, it is impossible to determine whether or not the other bones had the grooves of the lateral line system (note that, in a number of sites, the surface relief of *Kotlassia* is reconstructed on the basis of the relief pattern in adjacent areas).

Endocranium. The endocranium of *Kotlassia* experienced rather complete ossification; the holotype shows ossified auditory capsules (prootic and opisthotic), tympanic region (stapes), and occipital ring (basioccipital and exoccipitals); the sphenethmoid in the axial part and the quadrate and articular in the region of the jaw joint also underwent ossification (Figs. 30b, 30c).

The internal walls of the auditory capsules did not ossify. The oval fenestra faces mainly laterally and slightly posterodorsally. It is located at the edge of a short tube, the anterior wall of which is formed by the prootic, while the posterior wall is formed by the opisthotic.

The prootic is underlain proximally by the parasphenoid; the dorsodistal region of the bone is covered by the tabular. A wide groove extends from the upper external edge of the bone along the ventral side of the capsule to the oval fenestra; posteriorly, it is limited by the paroccipital process of the opisthotic. Anterior to the oval fenestra, the anterior segment of the groove becomes narrower and passes onto the surface of the auditory capsule to the basipterygoid articulation; it most likely provided passage for blood vessels.

As is seen on either side of the holotype, the opisthotics lack contacts with the basioccipital, being separated from the latter by a nonossified space. It was probably connected to the exoccipital; however, this cannot be stated with confidence. Dorsally, the opisthotics were attached to the dermatocranium through the paroccipital and the occipital processes of the tabulars; ventrally, they came into narrow contact with the posterior edges of the lateral expansions of the parasphenoid body.

The stapes is preserved on the right side of the holotype only. It is short, shaftlike, and slightly S-shaped in distoproximal view. The base of the bone abruptly expands and its medial edge rests on the upper edge of the oval fenestra. The distal end is directed dorsally toward the supratemporal; however, this is unlikely the natural position of the bone. The foramen for the stapedial artery is absent.

The occipital condyle is entirely formed by the basioccipital and has a concave articular surface. Dorsally, the columnar exoccipitals are attached to the lateral edges of the basioccipital and frame laterally a wide and oval foramen magnum. The supraoccipital did not ossify.

Because of deformation, only the left sphenethmoid is seen in the holotype; it is attached to the cultriform process along the entire extent. The posterior edge of the bone is pressed in and curves anteriorly to form a wide notch providing passage for nerves II, III, and IV.

The quadrate is very well ossified; however, in the specimen, it closely adjoins the articular; therefore, it is impossible to examine the articular surface of the jaw condyle. The paraquadrate foramen is large.

Superfamily Seymourioidea Williston, 1911

Family Karpinskiosauridae Sushkin, 1925

Subfamily Discosauriscinae Romer, 1934

Genus *Ariekanerpeton* Ivachnenko, 1981

Ariekanerpeton sigalovi (Tatarinov, 1968)

The material on *Ariekanerpeton sigalovi* comes from the Sarytaipan locality (Tajikistan) and includes hundreds of specimens covering a wide age range from the larval stage to adult animals with skulls up to 60 mm long. A large number of specimens are larval imprints. Some larvae are squamate and show external gills. The state of specimens recommends examination of the skeletal structures with the use of plastic contact copies of natural imprints in the solid thin-layer siltstone. The copies are worse in quality than those of *Utegenia shpinari*; therefore, it is not always possible to recognize minute morphological details. Nevertheless, this approach gives insight into the cranial morphology of *Ariekanerpeton*.

In the original description, the form from the Sarytaipan locality was correctly assigned to discosauriscids closely resembling European *Discosauriscus*; therefore, it was referred to as a new species of this genus, *D. sigalovi* (Tatarinov, 1968). Subsequent study, involving extensive material collected by the researchers of the PIN in 1975, substantiated the establishment of *Ariekanerpeton* as a separate genus distinguished from *Discosauriscus* (Ivakhnenko, 1981). This statement was later corroborated by Laurin (1996c) who indicated that *Ariekanerpeton* and North American *Seymouria* are closely similar to each other.

General characteristics. The collection includes the imprints of larvae whose body is at most 50 mm long. Plastic models were produced for the skulls ranging in length from 11.5 to 58 mm (specimens PIN, nos. 2079/800 and 600, respectively).

The preorbital skull region is narrow. The nares face mainly laterally. The occipital edge of the parietal shield is straight in juveniles and becomes concave somewhat in adults. The orbits are almost oval but angular and sharply outlined. The position of the jaw condyles changes in ontogenetic development; in the largest individuals, they are apparently in line with the occiput. The otic notches terminate opposite the anterior edges of the supratemporals; in larvae, they occasionally terminate at the midlength of these bones.

Skull roof. The parietals are widened at their midlength; anterolaterally and posteriorly, they are strongly cut out by the postfrontals and the medially expanding supratemporals, respectively (Fig. 31a). The parietal foramen is relatively large and round or, more commonly, irregularly oval; sometimes, it is located at the boundary of the frontals (specimens PIN, nos. 2079/242, 608). The frontals are as long as the orbits, always widened anteriorly, and project somewhat along the medial suture into the preorbital region. The nasals slightly taper anteriorly.

The prefrontal is shorter than the postfrontal. These bones come into narrow contact above the orbit. The postorbital is very small and never adjoins the supratemporal. The anterior end of the jugal extends anteriorly beyond the midlength of the orbit, the postorbital region of the jugal is very short (Pl. 11, fig. 2).

The lacrimal is high and becomes slightly lower toward the naris. The infraorbital process terminates opposite the orbital center and overlies the anterior region of the jugal. Incomplete ossification of the posterior region of the external wall of the duct, occasionally observed in *Discosauriscus* (Klembara, 1997), has not been registered in *Ariekanerpeton*. Some specimens (e.g., PIN, nos. 2079/324, 510) show the presence of the septomaxilla; however, poor preservation hinders the discovery of structural details of this bone.

The broad supratemporal markedly juts out into the parietal and has a slightly concave lateral flank. The intertemporal is always smaller than the supratemporal. In large animals, the tabulars are substantially larger than the postparietals and more strongly project anteriorly with reference to the latter bones. The external edge of the tabular forms a large segment of the margin of the otic notch. The paroccipital processes are short, trapezoidal, and separated by notches from the occipital plates. The tabulars of large animals are larger than, or equal to, the postparietals. In specimen PIN, no. 2079/309, the right postparietal is abnormally enlarged so that it surpasses the total area of both tabulars (Pl. 11, fig. 3). In specimen PIN, no. 2079/608, a small separate bone is located between the parietal and

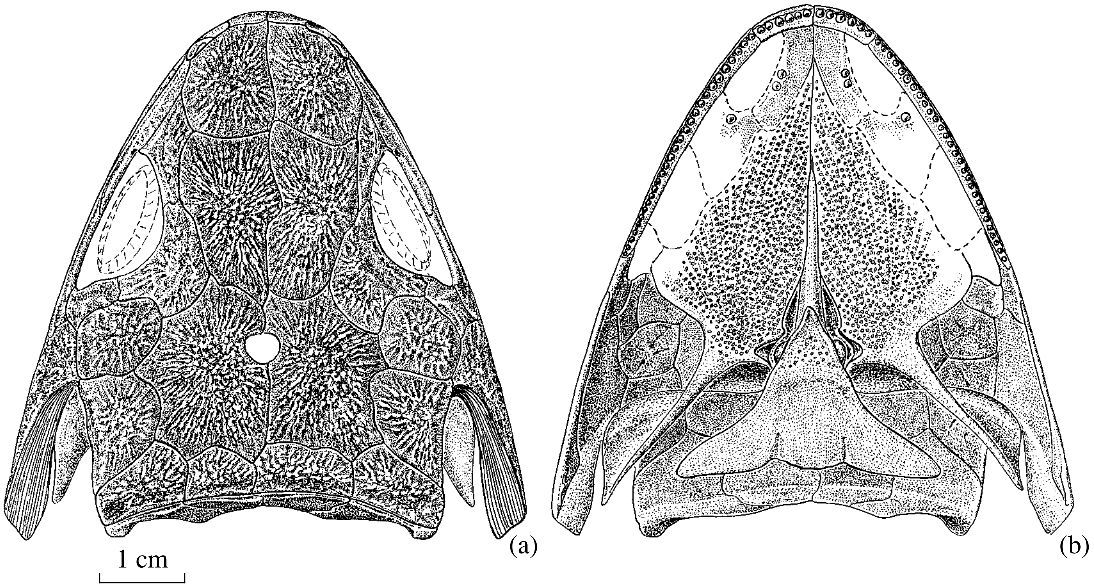


Fig. 31. *Ariekanerpeton sigalovi*, adult skull, reconstructed using specimens PIN, nos. 2079/600, 133, 332, 638, and 830: (a) dorsal and (b) ventral views.

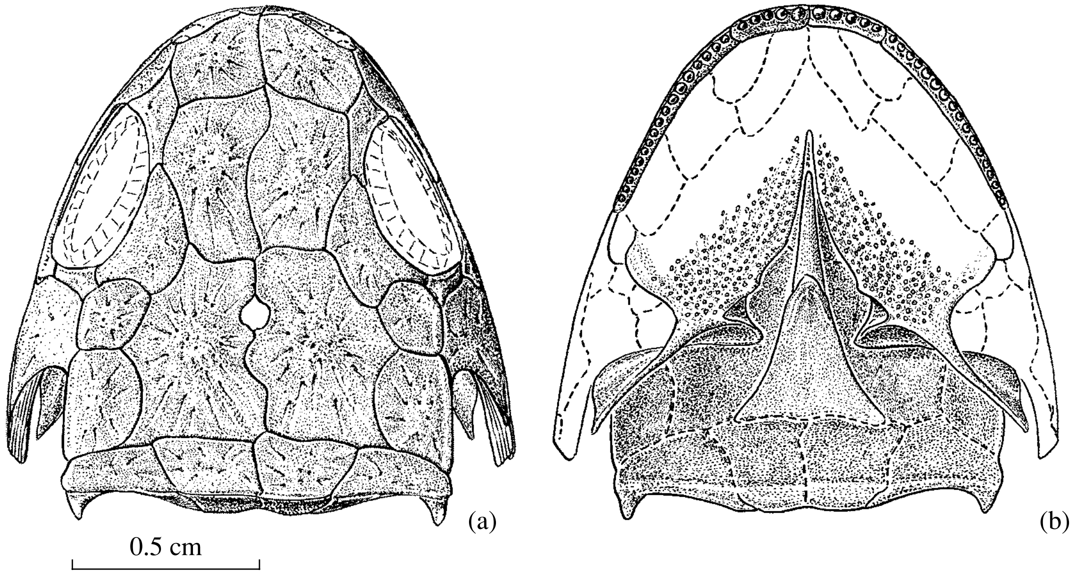


Fig. 32. *Ariekanerpeton sigalovi*, larval skull, reconstructed using specimens PIN, nos. 2079/436 and 764: (a) dorsal and (b) ventral views.

the left postparietal; a considerably larger additional bone is present in the same position in specimen PIN, no. 2079/394 (Pl. 11, fig. 5).

The squamosal is short and has a broad plate on the occipital flank. The quadratojugal is very low and only slightly projects ventrally with reference to the jugal.

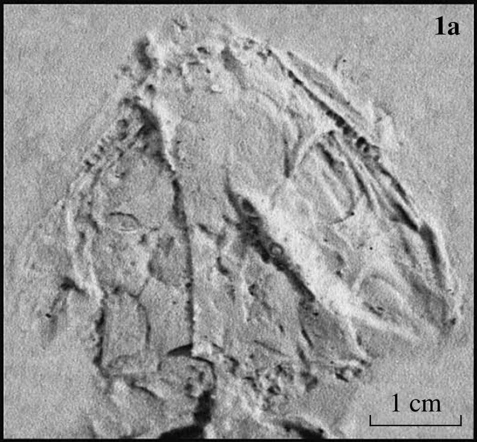
The premaxillae have narrow (one-third as wide as the dental area) and, most likely, short dorsal processes (specimens PIN, nos. 2079/21, 247). Nevertheless, in specimen PIN, no. 2079/608, the processes of the premaxillae are long and concave medially; this suggests the presence of the premaxillary fontanel. Normally, the bone contains six or, occasionally, seven teeth (specimen PIN, no. 2079/253).

The maxilla is high and strongly perforated externally and terminates opposite the posterior orbital rim. It contains up to 33 teeth (specimen PIN, no. 2079/324).

Palate. In almost all specimens examined in this study, the lateral palatal elements are covered ventrally

Plate 11

1a



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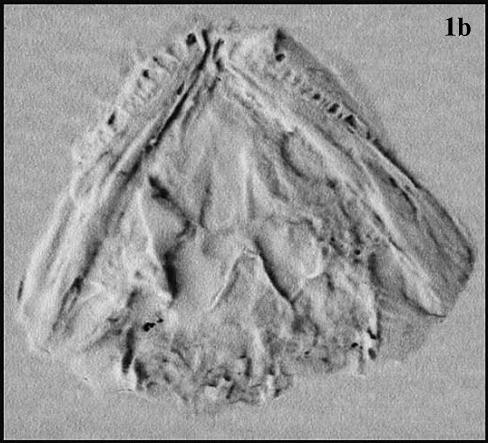

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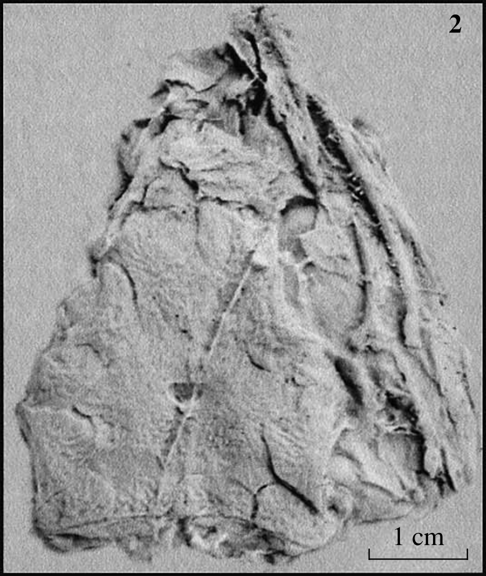

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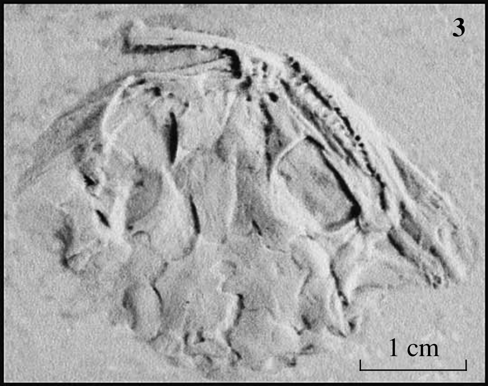

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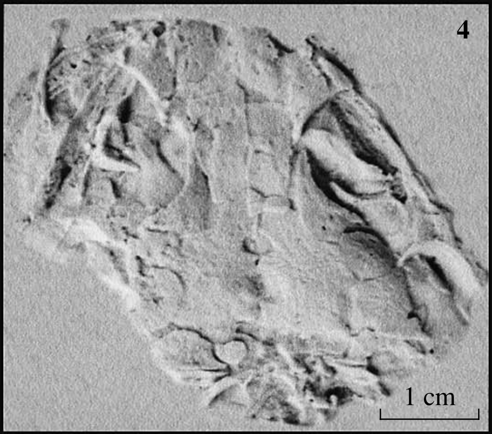

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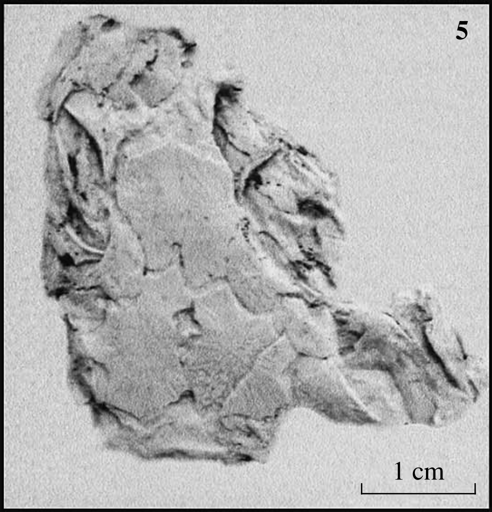


by the lower jaws located under the skull; therefore, the structure of these bones remains uncertain.

The vomer is narrow (specimens PIN, nos. 2079/247, 253; Fig. 31b). The palatine rami of the pterygoids wedge in the vomers and extend to the midlength of these bones. The angle between the pterygoid flanges and the quadrate rami of the pterygoids is 80–85°. The parasphenoid has a very narrow rostrum equal in length to the bone body. The thin platelike margins of the rostrum underlain by the palatal regions of the pterygoids become medially a thickened ridgelike axial part; in all likelihood, the latter part opened on the ventral surface even in adults. The posterior region of the parasphenoid forms widely spaced parafenestral wings oriented laterally and slightly posteriorly (specimens PIN, nos. 2079/247; Pl. 12, fig. 1b).

Lower jaw. The postdentary region composes one-third of the lower jaw length (Fig. 31c). Anteriorly, the surangular increases in height; however, the jaw lacks a well-outlined coronoid process. The internal wall of the adductor cavity is formed by the prearticular; posteriorly, it becomes lower and, in the articular region, is inclined at an angle of 60° to the vertical. The splenials weakly expand on the external surface of the jaw; the postsplenial is substantially longer than the splenial, its posterior end closely approaches the ossification center of the angular.

A long and pointed caudal process of the dentary extends posteriorly beyond the coronoid projection and covers a large part of the anterior region of the surangular. Ventrally, the dentary is underlain by the external flanks of the splenial and postsplenial.

Dentition. The bases of the marginal teeth are round in cross section and regularly plicate. The crowns are unicuspid; in the anterior teeth, they are markedly flattened and slightly curve lingually (specimens PIN, nos. 2079/133, 324). Because of incomplete preservation, other structural details are indiscernible in the available material. Premaxillary teeth 3 and 4 and maxillary teeth 4–7 are sharply distinguished from the others by height, width, and intensive plication at the tooth bases (Pl. 12, fig. 2).

Approximately at the midlength of the vomer, there are two palatal teeth of the mediochoanal row; they are relatively small compared to the marginal teeth (specimens PIN, nos. 2079/247, 253). The palatine has only one tooth of this type posterior to the choana (holotype PIN, no. 2079/1, specimen PIN, no. 2079/431). Actually, it could be a greater number of large palatine teeth, as in *Discosauriscus*; however, it is impossible to examine the dentition of the lateral palatal elements in the majority of specimens.

The medial margin of the palatine has a longitudinal field of large shagreen teeth. The anterior regions of the pterygoids, including the pterygoid flanges, are covered by numerous rows of small teeth, converging to the region of the basipterygoid articulation. Occasionally, these rows are slightly arched (specimen PIN, no. 2079/324). On the parasphenoid, a small toothed field is marked only near the ossification center (specimens PIN, nos. 2079/324, 500); the rostrum and the parafenestral wings lack teeth.

Surface ornamentation. In skulls shorter than 27 mm in length, the surface of membrane bones of the skull roof remains smooth and only covered by numerous narrow furrows extending radially from the central part and closely approaching the bone edges (Pl. 11, fig. 3; Pl. 12, fig. 1a). In larger individuals, the spaces between the furrows are occupied by flat ridges, which are relatively high around the ossification centers and smoothened toward the bone edges. Well-pronounced ridges cover even small membrane bones adjoining the parietals and forming the orbital rim, in particular, the anterior flanks of the postparietals and tabulars, the medial part of the supratemporals, the postfrontals, and the postorbital part of the jugals (specimen PIN, no. 2079/396, skull is approximately 29 mm long). Radial ridged relief usually prevails on skulls approaching 41 mm in length (specimens PIN, nos. 2079/21, 373; skull length estimated as 40.5 and 38.5 mm, respectively).

As the skull is greater than 30 mm in length, separate tubercles are formed on the ridges. The tubercles appear by narrowing the ridges at the points where the furrows alternating with the ridges contain foramina for blood vessels. The initial stage of this process is observed in specimen PIN, no. 2079/431 (the skull is approximately 32 mm long) in which the tuberculate relief is formed in the only sector of the right parietal (Pl. 11, fig. 5). In general, the relief changed more synchronously. In the ossification centers where the formation of tubercles follows the other pattern rather than disintegration of ridges, the tubercles are occasionally con-

Explanation of Plate 11

Ariekanerpeton sigalovi (Tatarinov, 1968); skull casts, dorsal view; Sarytaipan locality (Tajikistan, Leninabad District; Lower Permian).

Fig. 1. Holotype PIN, no. 2079/1: (1a) dorsal and (1b) ventral views.

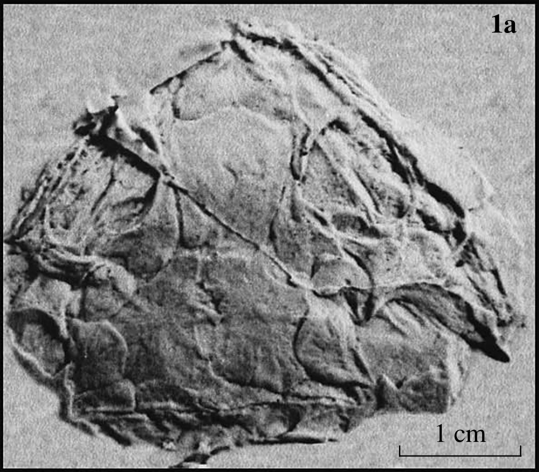
Fig. 2. Specimen PIN, no. 2079/600.

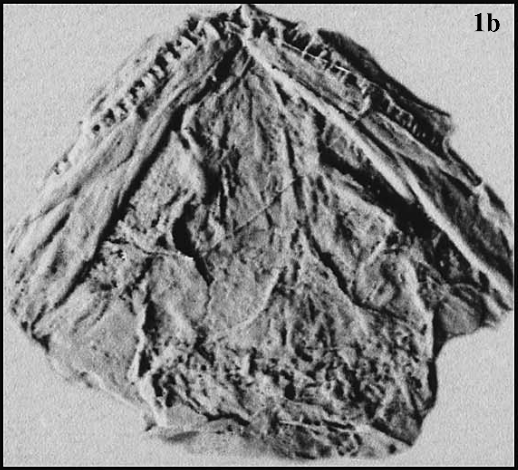
Fig. 3. Specimen PIN, no. 2079/309.

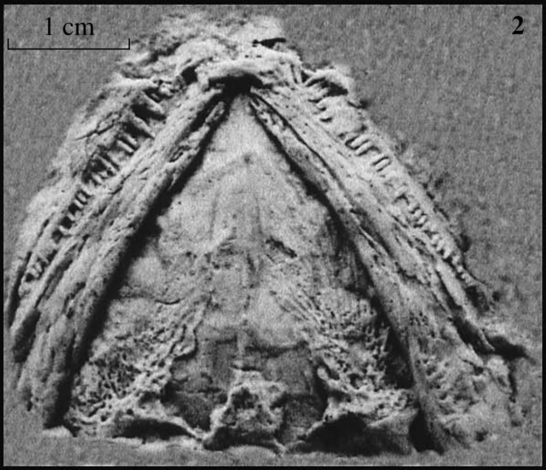
Fig. 4. Specimen PIN, no. 2079/394.

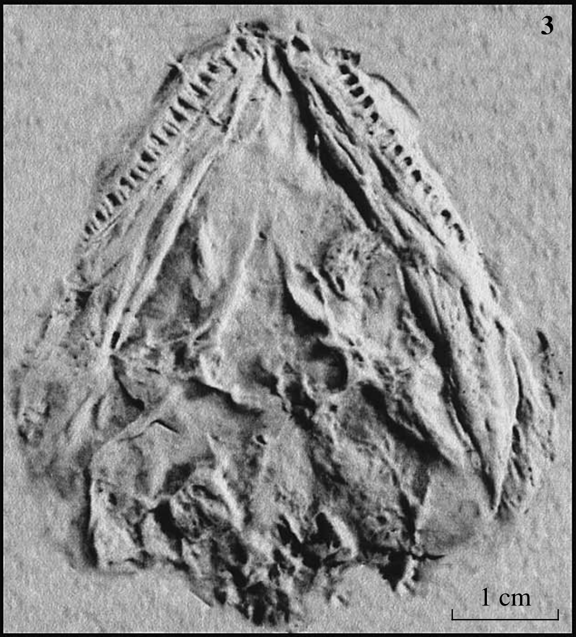
Fig. 5. Specimen PIN, no. 2079/431.

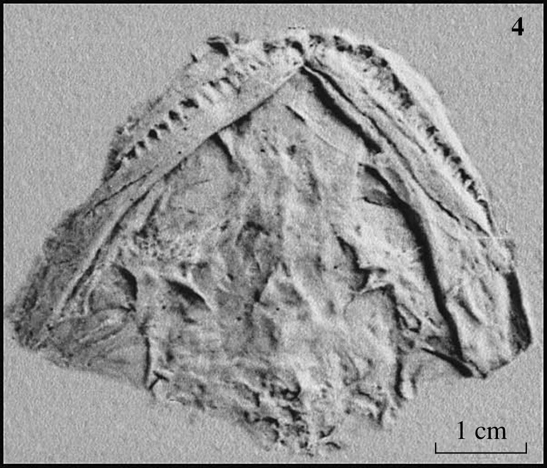
Plate 12

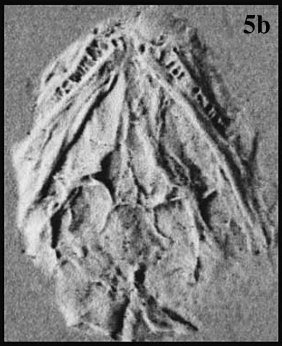












nected by bonds (e.g., on the nasals of specimen PIN, no. 2079/332, the skull is approximately 37 mm long).

In skulls greater than 35 mm in length, the tuberculate relief often prevails (specimens PIN, nos. 128, 332; the skulls are 35.5 and 37 mm long, respectively). However, in this case, the relations between the tubercles and radial ridges are always evident, since the ridges are incompletely disintegrated even in the largest available specimens (PIN, no. 2079/600; Pl. 11, fig. 2) where they are retained in the marginal areas of the bones.

On the lower jaw, a well-developed radial ridged relief is observed on the angular and, to a lesser extent, on the postsplenial. A similar relief is also formed in the symphysial region of the dentary; however, the greater part of this bone lacks ornamentation and is covered by furrows extending mainly posteriorly from the labial foramina for blood vessels.

Seismosensory system. Because of incomplete preservation of the specimens under study, the grooves of the lateral line system located on the skull roof are usually hardly discernible, if at all.

The supraorbital groove emerges on the nasal at the boundary of the premaxilla and extends laterally between the ossification center and the upper wall of the naris (Fig. 31a). As the flexure is formed, the groove comes onto the prefrontal and bypasses the lacrimal, extending close to its upper edge (specimens PIN, nos. 2079/199, 242). The prefrontal has a large foramen providing passage for the superficial ramus of the facial nerve to the neuromasts of the anterior region of the supraorbital seismosensory canal. At the contact between the prefrontal and the postfrontal, the groove passes to the adjacent area of the external margin of the frontal. It passes through the central part of the postfrontal and always comes onto the intertemporal and, further along, onto the postorbital; opposite the caudal process of the latter bone, the postorbital commissure branches off. The temporal branch extends posteriorly along the boundary between the squamosal and the intertemporal; subsequently, it comes onto the external margin of the supratemporal and extends to the otic notch (Pl. 11, fig. 3). The groove of the occipital commissure is clearly pronounced in skulls greater than 27 mm in length; in specimen PIN, no. 2079/247, it appears before the formation of surface sculpturing on the bones of the occipital edge of the parietal shield (Pl. 12, fig. 1a). The connection with the supraorbital groove occurs at the lateral end of the tabular occupied by a large depression (specimens PIN, nos. 2079/247, 332) that is a homologue of depressions located in the same position in *Discosauriscus* from Moravia (Klembara, 1994b). Similar elements are present on the postfrontals and their positions are also associated with the seismosensory grooves (specimens PIN, nos. 2079/396, 434).

The groove of the infraorbital canal emerges in the posterior part of the lacrimal (specimen PIN, no. 2079/309; Fig. 31c); it passes along the jugal under the orbit and comes onto the squamosal; in the posterior part of the latter bone, it extends along the edge of the otic notch. This segment of the canal is poorly imprinted and hardly discernible.

Endocranium. In *Ariekanerpeton* with skulls greater than 27 mm in length (specimens PIN, nos. 2079/247, 638), the basioccipitals and exoccipitals ossified (Pl. 12, figs. 1b, 4). The exoccipitals appear as short and wide columns expanded somewhat at the lower and upper ends. The short basipterygoid processes of the basisphenoid are observed in skulls greater than 40 mm in length and shaped into hemispheres (specimens PIN, nos. 2079/324, 638; Pl. 12, figs. 2, 4). The auditory capsules and jaw condyles remain nonossified.

Larval skull. The material under study includes larvae, the smallest of which has a 11.5-mm-long skull (specimen PIN, no. 2079/800).

A larval skull shorter than 15.5 mm has large orbits and a short preorbital region (Fig. 32). The anterior edge of the otic notches is usually located posterior to the anterior edge of the supratemporal (specimens PIN, nos. 2079/309, 764, 823). The jaw condyles are located substantially anterior to the occipital edge, which remains straight at this stage. The parietal foramen is in line with the posterior orbital rim; occasionally, it nearly approaches the boundary of the frontals (specimens PIN, nos. 2079/398, 823). The frontals extend far into the interorbital region and, as in the definitive state, have markedly widened anterior regions slightly wedging along the medial suture in between the posterior regions of the shortened nasals.

The intertemporal is smaller than the supratemporal, the prefrontal is smaller than the postfrontal; and the

Explanation of Plate 12

Ariekanerpeton sigalovi (Tatarinov, 1968); skull casts, dorsal view; Sarytaipan locality (Tajikistan, Leninabad District; Lower Permian).

Fig. 1. Specimen PIN, no. 2079/247: (1a) dorsal and (1b) ventral views.

Fig. 2. Specimen PIN, no. 2079/324, ventral view.

Fig. 3. Specimen PIN, no. 2079/133, ventral view.

Fig. 4. Specimen PIN, no. 2079/638, ventral view.

Fig. 5. Specimen PIN, no. 2079/500: (5a) dorsal and (5b) ventral views.

postorbital is short, as in adults. The bones composing the occipital edge of the parietal shield are well developed; at the same time, the tabulars are always shorter than the postparietals and occupy a smaller area. The tabulars are substantially narrowed laterally. Specimen PIN, no. 2079/218 has only one postparietal in the central position.

In skulls approximately 20 mm in length, the maxilla contains about 20 teeth (specimens PIN, nos. 2079/500, 866). The premaxillae have relatively high dorsal processes the medial edges of which closely join each other (specimen PIN, no. 2079/866). The rostral region of the parasphenoid was completely open on the ventral surface.

The skull roof lacks surface ornamentation. Of the grooves of the seismosensory system, the supraorbital segment of the supraorbital groove is usually observed (specimens PIN, nos. 2079/218, 686); occasionally, the temporal branch (located on the supratemporal) of this groove (specimen PIN, no. 2079/436, 823) and (or) the postorbital commissure (specimens PIN, nos. 2079/347, 436) are also registered.

Subfamily Karpinskiosaurinae Sushkin, 1925

Genus *Karpinskiosaurus* Sushkin, 1925

Karpinskiosaurus ultimus (Tchudinov et Vjuschkov, 1956)

The type material on *Karpinskiosaurus ultimus* comes from the Pron'kino locality and consists almost exclusively of jaws. Using these specimens, Tchudinov and Vjuschkov (1956) established a separate species of the genus *Nycteroleter* Efremov, 1938, *N. ultimus*. Ivakhnenko (1987) excluded this form from *Nycteroleter* and assigned it to leptorophid seymouriamorphs as a separate genus, *Raphanodon*. The reconstruction given in the cited work was based mainly on the material from the Babintsevo locality where jaws of similar structure were accompanied by incomplete skulls.

Subsequently, it was shown that some of these skulls and all jaws from the type locality belong to the genus *Karpinskiosaurus*. This caused the abandonment of the generic name *Raphanodon* and recognition of *Karpinskiosaurus ultimus* (Bulanov, 2002), distinguished from the type species *K. secundus* of the genus mainly by the depth of the otic notch and a weak lingual inclination of the apices of the marginal teeth.

The description given below is based exclusively on the material from the Babintsevo locality. The comparison with the specimens from the Pron'kino locality is based mainly on the jaws. In addition, material from Pron'kino includes the typical tabular (specimen PIN, no. 521/84) characterized by the cellular surface relief and posterolaterally extended otic flank, an isolated auditory capsule (specimen PIN, no. 521/133), and an isolated quadrate (specimen PIN, no. 521/130); the attribution of the latter two specimen is open to question.[1]

The Babintsevo locality yielded both larval and postmetamorphic animals, showing substantial morphological differences in marginal dentition. The larval marginal teeth are clearly tricuspid in structure, whereas the crowns of postmetamorphic animals lack supplementary denticles. One may question the assignment of the two clearly different forms to the same species, the more so as the other seymouriamorph with serrated marginal teeth, i.e., *M. gracilis*, was found in this locality. However, the morphology of the latter species was rather thoroughly examined (see above), and morphogenetic changes of the dental system were investigated on the basis of rather representative material. As the skull is 15 mm long or shorter, larval *K. ultimus* has 22 teeth in the maxilla, while *M. gracilis* of the same size has only ten teeth retaining an unicuspid structure. As the skull of *M. gracilis* becomes twice larger, the number of serrated teeth in the maxilla is at most 13; the closely related species *M. exiguus* has at most 18 maxillary teeth even at the definitive ontogenetic stage. The serration patterns of the tooth crowns are also substantially different; in contrast to *M. gracilis*, larval *K. ultimus* has a pair of large triangular supplementary denticles comparable in size to the central apex.

Other cranial characters also corroborate the above interpretation. In particular, in specimen SGU, no. 104B/2031, the parasphenoid has a long rostrum lacking shagreen teeth and narrow parafenestral wings; these characters have not been registered in any kotlassioids (they may not be interpreted as larval features, since in *Utegenia*, the presence of a toothed rostrum is observed even at the earliest known developmental stages). It is remarkable that the premaxillae have a high ascending process with a concave medial edge; this feature is atypical of *M. gracilis*; however, it is observed in large-sized *Karpinskiosaurus* having an extended fontanel between these processes and certain other features.

It should be noted that all isolated jaws of *K. ultimus* showing unicuspid crowns do not correspond in size to the larvae and belong to relatively large animals.

The collection studied contains eight fragmentary skulls, three of which (specimen SGU, nos. 104B/2031, 2033, 2034) belong to larvae, while the others are postlarval animals with skulls up to 40 mm in length (specimens SGU, nos. 104B/2008, 2009, 2032; PIN,

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[1] In addition to the cranial fragments, Vjuschkov (1957) described two forms on the basis of postcranial skeletal specimens from the same locality. In contrast to cranial specimens, they were correctly referred to as seymouriamorphs, *Kotlassia* sp. and *Buzulukia butsuri*. It is highly probable that the second form (holotype is an incomplete vertebral column) is a synonym of *Karpinskiosaurus ultimus*, since its spinous processes are very similar to those of *Karpinskiosaurus* (*K. secundus*) from the Sokolki locality excavated by Amalitzky. The taxonomic position of *Kotlassia* sp. is uncertain; however, the assignment of these specimens (isolated vertebrae) to the genus *Kotlassia* is questionable.

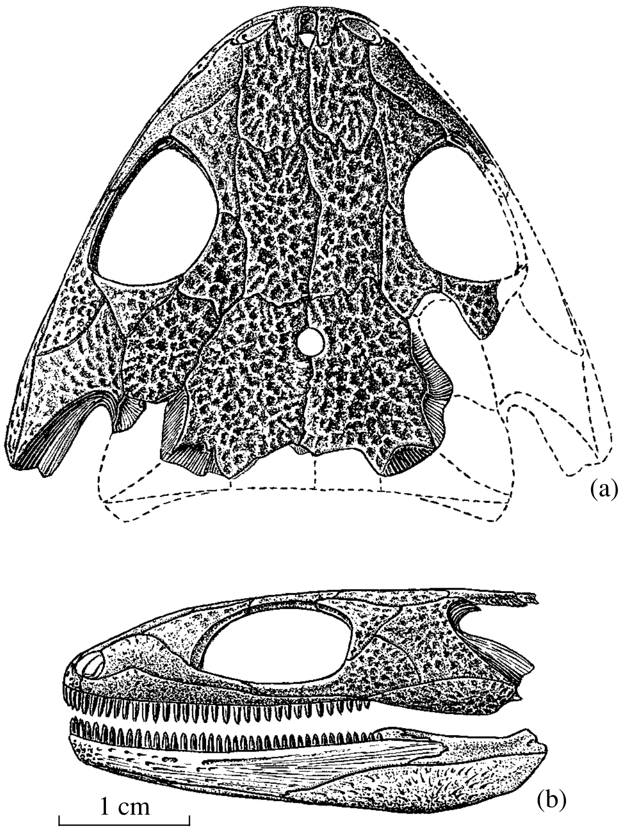


Fig. 33. *Karpinskiosaurus ultimus*, skull of postmetamorphic individual, reconstructed using specimen PIN, no. 4617/158: (a) dorsal and (b) lateral views.

nos. 4617/158, 188). The most informative is specimen PIN, no. 4617/158 providing the basis for the description given below. Additional material includes isolated jaws and dermatocranial bones from the same locality.

Some jaws from the type locality belong to much larger individuals.

General characteristics. A skull about 40 mm in length has mainly oval and only slightly angular orbits (i.e., the orbital margin abruptly curves at certain points) displaced somewhat anteriorly (Fig. 33a). The occipital region is not preserved in available specimens; however, by analogy with *K. secundus*, it was probably concave. The anterior edge of the otic notches is in line with the suture between the supratemporal and the intertemporal. The jaw joint is positioned anterior somewhat to the occiput because of the small sizes of the animals under study. The external nares are positioned at an angle of about 45° to each other.

Skull roof. The parietals are relatively small, only slightly widened posteriorly, and weakly notched on the lateral side of the intertemporal and supratemporal. The parietal foramen is round (Pl. 13, fig. 1a). The nasals are somewhat narrower than the frontals. Both the frontals and the nasals are constant in width over the entire extent. The frontals are as long as the orbits and the nasals are shorter by one-third. Each nasal has an anterior projection isolated from its counterpart by a median suture and articulated with the dorsal processes of the premaxillae.

The prefrontal of postmetamorphic animals is longer than the postfrontal; above the orbit, these bones

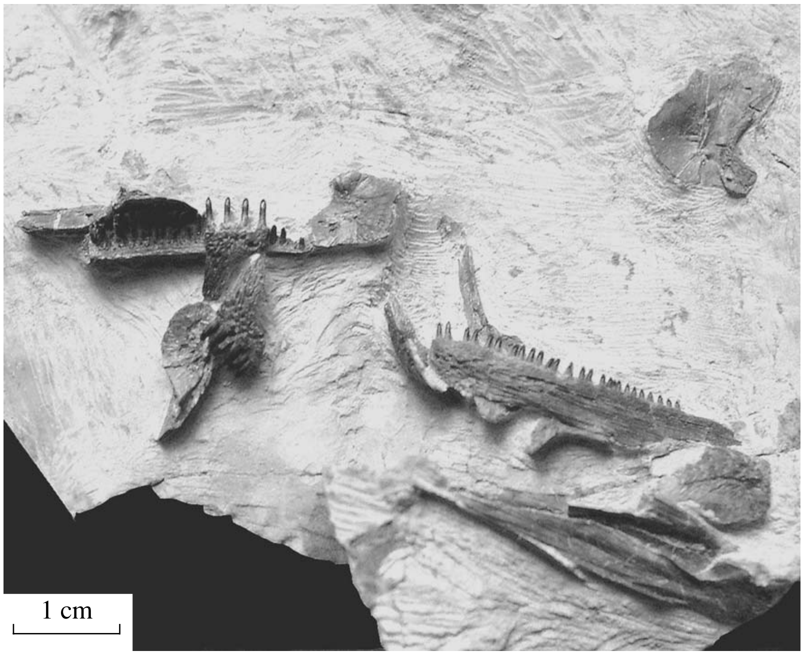
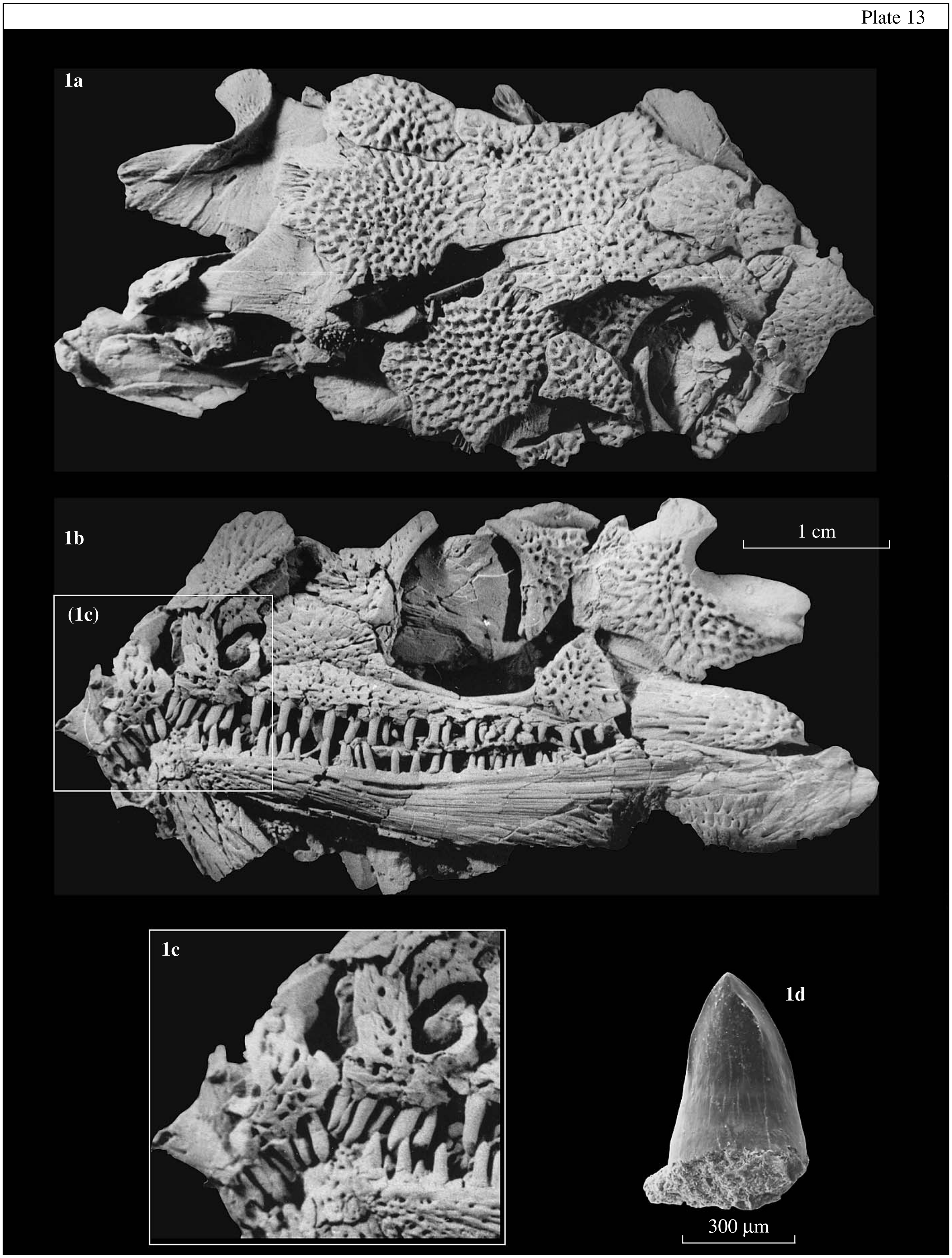


Fig. 34. *Karpinskiosaurus ultimus*, fragmentary skull of postmetamorphic individual, specimen PIN, no. 4617/188, dorsal view.

Plate 13



Explanation of Plate 13

Karpinskiosaurus ultimus (Tchudinov et Vjuschkov, 1956); Babintsevo locality (Orenburg Region, Grachevskii District; Upper Permian, Upper Tatarian Substage).

Fig. 1. Specimen PIN, no. 4617/158, skull of postmetamorphic individual: (1a) dorsal view, (1b) lateral view, (1c) nasal region, and (1d) rudimentary marginal tooth.

come into narrow contact with each other. The postorbital is regularly triangular. The lacrimal is high and has a long infraorbital process extending to the midlength of the orbital rim and overlying a large part of the jugal. The canal of the nasolacrimal duct is completely enclosed in the bone. It begins with a single foramen in the anterior wall of the orbit and opens in the anteroventral margin of the lacrimal. The septomaxilla is a large navicular plate, the posterior edge of which contains the septomaxillary foramen (Pl. 13, fig. 1c).

The postorbital region of the jugal is well developed. A very large and extended intertemporal was most likely larger than the supratemporal. The tabulars are lost in all specimens; however, one can propose that their ventral flanks were markedly reduced because the parietals have special underlying plates. This relationship is observed on either side of the skull of specimen PIN, no. 4617/158; at the same time, it is atypical of seymouriamorphs. The postparietals spread under the parietals.

The squamosal is relatively small and has a posteriorly widened horizontal process articulated with the axial region. The otic notch entirely covers the occipital flank of this bone shaped into a smooth plate gradually expanding posteriorly.

The premaxillae have high dorsal processes coming into separate contacts with the nasals because of the presence of the premaxillary fontanel. The premaxilla contains six teeth (specimens SGU, nos. 104B/2031, 2034; PIN, no. 4617/158). In specimen PIN, no. 4617/188, the left premaxilla contains seven teeth, as distinct from the right premaxilla (Fig. 34).

The ascending lamina of the maxilla is undeveloped (Fig. 35; Pl. 13, fig. 1b). The anterior face of the dental area has a relatively deep fossa for the attachment of the premaxilla. The groove for the infraorbital artery extends from the posterior edge of the maxilla along its internal side and terminates in a foramen (often, a number of foramina) located opposite the sixth or seventh marginal teeth. Immediately below, in line with the posterior edge of the choana, there is a round fossa for the antorbital process of the olfactory capsule. The groove for the artery contains five or six evenly distributed foramina facing posteriorly and providing passage for a blood vessel to the bases of the marginal teeth.

The maxilla is strongly perforated externally. A row of upper labial foramina extends along the alveolar margin; beginning from the central part of the maxilla, the furrows originating from the foramina merge to form a superficial canal directed posteriorly. Occasionally, one or two relatively large foramina are observed posterior to the nares. In a skull about 40 mm in length, the maxilla contains 30 teeth (specimen PIN, no. 4617/158).

Palate. The vomerine structure is unknown. The palatine (specimen SGU, no. 104B/2032, Fig. 36) has a well-pronounced laterochoanal process. The anteromedial edge has a plate for articulation with the vomer; on the ventral side, the line of contact between these ele-

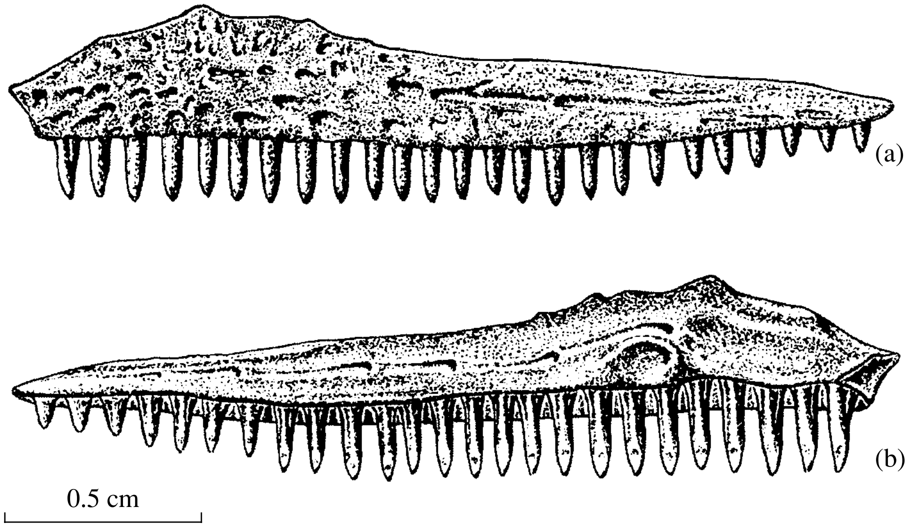


Fig. 35. *Karpinskiosaurus ultimus*, left maxilla of postmetamorphic individual, reconstructed using specimens SGU, nos. 104B/2011 and 2013: (a) labial and (b) lingual views.

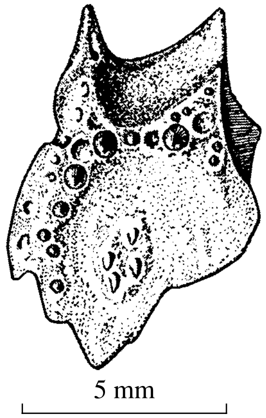


Fig. 36. *Karpinskiosaurus ultimus*, right palatine, based on specimen SGU, no. 104B/2032, ventral view.

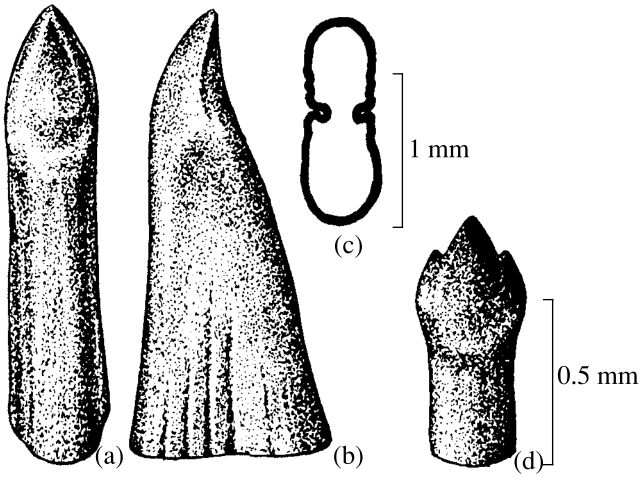


Fig. 37. *Karpinskiosaurus ultimus*, marginal teeth: (a) maxillary tooth of postmetamorphic individual, lingual view (specimen SGU, no. 104B/2015); (b) the same, lateral view; (c) the same, cross section of the tooth base at the point of attachment to the maxilla; (d) larval premaxillary tooth 3, labial view (specimen SGU, no. 104B/2033).

ments is oriented longitudinally with reference to the skull axis. The palatine has alveoli for five large teeth, four of which are positioned along the posterior wall of the choana. The fifth tooth is displaced somewhat caudally and located near the boundary of the maxilla. The alveoli of large teeth (two of which are empty) alternate with smaller teeth. The posterior region of the medial flank lacks teeth. In the central region of the palatine, only a small area is covered by shagreen teeth. The outline of the posterior edge of the palatine suggests that the ectopterygoid was relatively narrow.

The parasphenoid has widely spaced and parafenestral wings oriented somewhat posteriorly (Pl. 13, fig. 1a).

Lower jaw. The dentary is 3.5 times as long as the postdentary region. The posterior region of the surangular contains a small surangular foramen open posteriorly. The splenial is substantially shorter than the postsplenial (the earlier assertion concerning the equal length of these elements is erroneous); either bone does not expand on the external side of the jaw. Apparently, the anterior element does not contribute to the formation of the symphysis. The coronoid process is weakly developed (Fig. 33b; Pl. 13, fig. 1b).

The internal wall of the adductor cavity is formed by the prearticular and becomes lower posteriorly, toward the jaw joint. The upper edge of the wall gradually curves medially to form a horizontal plate anterior to the condyle. In the region of the articular, the prearticular increases in height. The Meckel's foramen is either absent or small and slitlike (specimen PIN, no. 4617/188).

The dentary is extended, the maximum height is at the midlength of the jaw; the posterior region is narrow and extends far posterior beyond the coronoid process. The symphysial region is strongly perforated externally; the foramina located in this region face mainly posteriorly and are accompanied by narrow, rectilinear, and nonanastomosing furrows extending throughout the bone to the boundary of the angular (specimens PIN, nos. 4617/158, 188). Beginning from the second quarter of the bone, the upper labial foramina are located in a narrow and deep groove extending caudally along the alveolar margin; the posterior part of the groove lacks foramina. The groove of the Meckel's cartilage is deep, especially in the anterior part where the lower edge of the dentary closely approaches the dental area. The branches of the mandibular artery penetrated to the bases of the teeth through the evenly distributed small foramina on the ventral side of the dental area. This suggests the absence of a generalized alveolar canal inside the bone.

Dentition. In the largest animals from the collection under study, the marginal teeth have small crowns with slightly flattened and weakly lingually curved apices. The lateral denticles are absent, the thin-walled bases are extended oval in cross section and strongly extended longitudinally. At the center of the extended lateral sides, there are one or two deep folds abruptly projecting in the pulp cavity toward similar elements on the opposite side. Other folds are much shallower and located on the lateral sides only.

The palatal teeth are somewhat smaller than the marginal teeth and differ from the latter by nonfolded bases and conical nonflattened crowns. The pterygoids are covered by rows of high spikelike shagreen teeth. A field of shagreen is observed in the near-basipterygoid region of the parasphenoid. The posterior region of the bone at the base of the parafenestral wings is scattered with isolated small teeth.

Surface ornamentation. The skull roof is covered by a well-developed surface relief composed of small polygonal cells. The cells are elongated somewhat at the periphery of large bones of the axial and zygomatic regions (parietals, frontals, nasals, squamosals, and quadratojugals). The bones of the upper and lower jaw

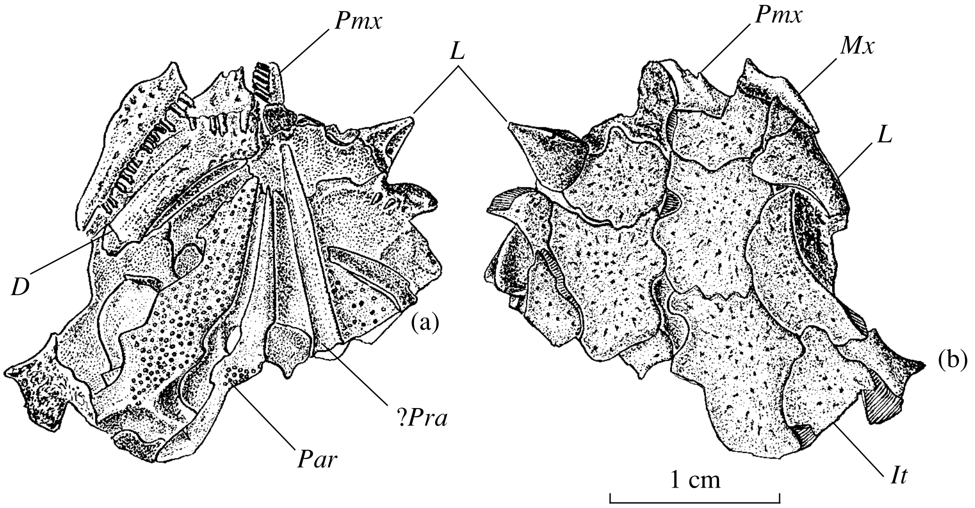


Fig. 38. *Karpinskiosaurus ultimus*, larval skull, specimen SGU, no. 104B/2031: (a) dorsal and (b) ventral views.

arches, prefrontals, lacrimals, and surangular are weakly ornamented. In the central part of the left postfrontal of specimen PIN, no. 4617/158, there is a deep fossa (Pl. 13, fig. 1) probably related to electrically sensitive organs; a similar fossa was described in the same position in *Discosauriscus* (Klembara, 1994b). On the other bones, including the postfrontal of the opposite side, similar structures are absent.

Seismosensory system. In postmetamorphic animals, grooves of the seismosensory system are entirely absent.

Endocranium. None of the available specimens shows cartilage bones in the ethmoidal and otico-occipital blocks. This may be a result of poor preservation. Specimen PIN, no. 4617/188 (skull about 40 mm long) has a well-ossified articular.

Larval skull. The skulls of larval *Karpinskiosaurus ultimus* are poorly preserved. The length of the smallest skull (specimen PIN, no. 104B/2033) is estimated as approximately 15 mm and that of the most completely preserved specimen (SGU, no. 104B/2031) is about 17 mm (Fig. 38).

In the structure of the larval dermatocranium, the increased relative size of the parietal, the anterior regions of which enter the interorbital area, attracts the attention. A large parietal foramen is located close to the boundary of the frontals. The orbits are large and the interorbital skull region is wide, while the preorbital region is short.

The prefrontal is substantially smaller than the postfrontal. The intertemporal is very large. The premaxillae have high dorsal processes, the concavity of the medial edges of which indicates the presence of the premaxillary fontanel. The lacrimal is high and has the infraorbital process extending far posteriorly; in the preorbital part of the bone, there are two or three large foramina located near the boundary of the maxilla. The septomaxilla lacks a distinct foramen for the nasolacrimal duct. The maxilla is short; in specimen SGU, no. 104B/2033, it is completely preserved and contains 22 teeth, the crowns of which are clearly tricuspid; in addition to the central apices, they have a pair of large supplementary denticles (Figs. 37d, 39). In the anterior teeth, the apices curve lingually; however, a stronger curvature is characteristic of six premaxillary teeth (specimen SGU, no. 104B/2031), which are somewhat larger than the maxillary teeth. The lower teeth are similarly serrated; in the symphysial region, they are very small (specimen SGU, no. 104B/2033). The bases of the marginal teeth lack plication.

The parasphenoid has narrow parafenestral wings directed posterolaterally and a narrow and long rostrum lacking small teeth, palatal teeth are observed only in the region near the basipterygoid. On the pterygoids, the shagreen teeth are arranged in sparse rows converging toward the ossification center; a small field of small teeth covers a part of the base of the quadrate ramus. The pterygoid flanges are weakly inclined ventrally and lack teeth.

Grooves of the seismosensory system are absent. The external surface of membrane bones of the skull

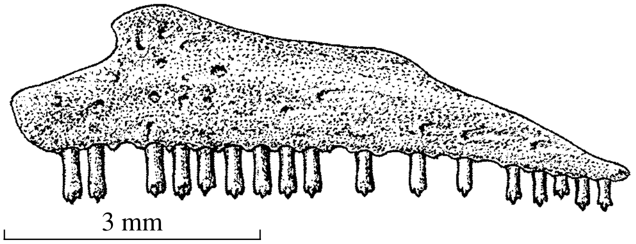
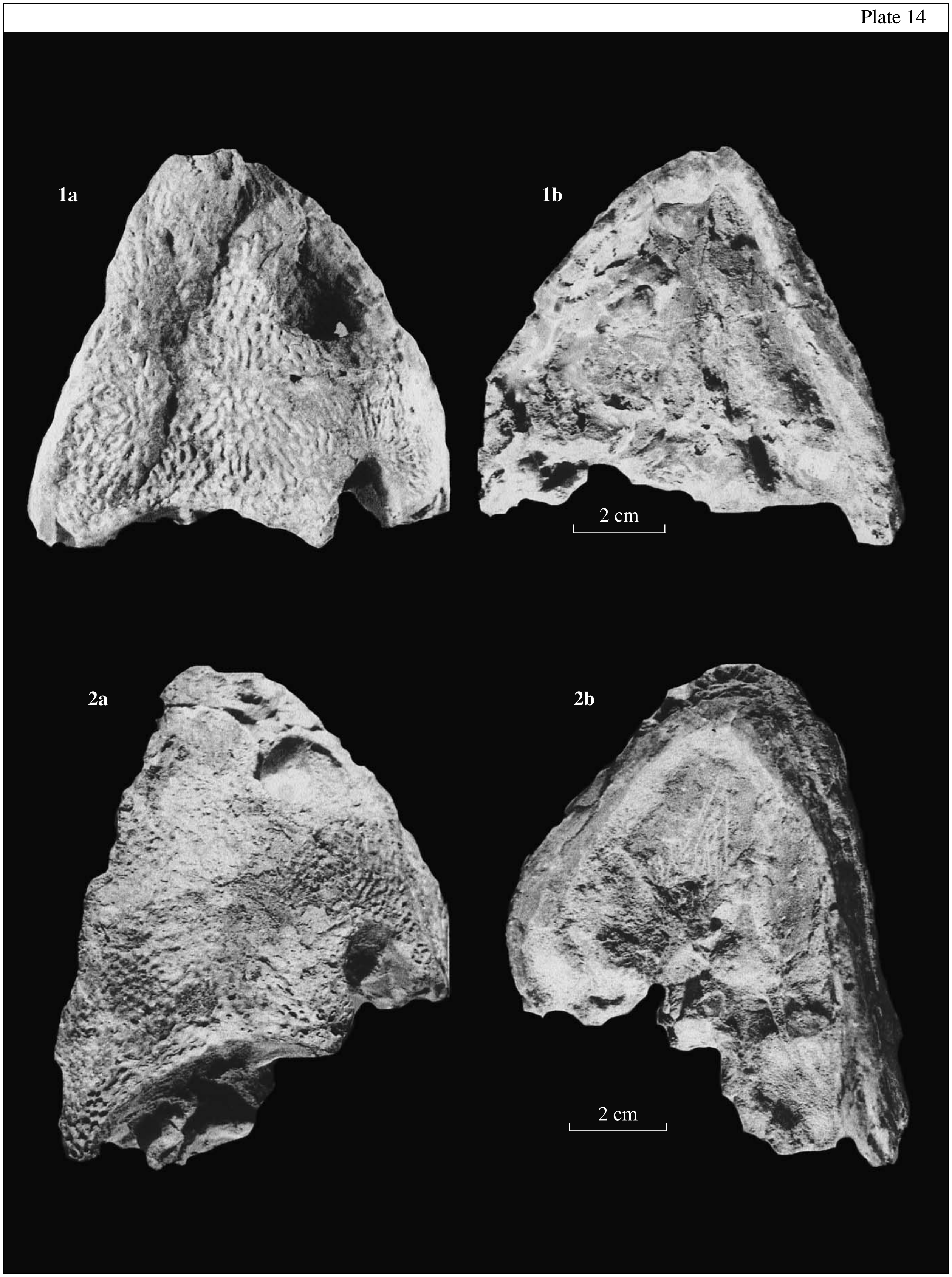


Fig. 39. *Karpinskiosaurus ultimus*, left maxilla of larva, reconstructed using specimen SGU, no. 104B/2033, labial view.

Plate 14



Explanation of Plate 14

Karpinskiosaurus secundus (Amalitzky, 1921); skulls; Sokolki locality (Arkhangelsk Region, Kotlasskii District; Upper Permian, Upper Tatarian Substage, Vyatka Horizon).

Fig. 1. Holotype PIN, no. 2005/81, skull: (1a) dorsal and (1b) ventral views.

Fig. 2. Specimen PIN, no. 2005/82 (holotype *K. neglectus*): (2a) dorsal and (2b) ventral views.

roof is almost smooth and covered by hardly discernible furrows occurring near the evenly distributed foramina for blood vessels.

Karpinskiosaurus secundus (Amalitzky, 1921)

The genus *Karpinskiosaurus* was established by Sushkin (1925) in the course of revision of seymouriamorphs from the Sokolki locality. The material included two specimens, an incomplete skeleton (PIN, no. 2005/81; Pl. 14, fig. 1) and an isolated skull (PIN, no. 2005/82; Pl. 14, fig. 2). These specimens were originally described by Amalitzky as *Kotlassia secunda.* Because of considerable distinctions in the structure of the cranial and postcranial skeleton, this form was ranked as a separate family, the Karpinskiosauridae.

Subsequently, Sushkin (1926) mentioned another species of *Karpinskiosaurus* from the same locality, *K. neglectus.* However, he gave only a brief diagnosis accompanied by neither the collection number of the specimen nor its figure. Apparently, Sushkin planned to prepare a detailed description in a subsequent paper; however, this was not performed, since the researcher suddenly passed away. Formal distinctions of *K. neglectus* from *K. secundus* concern cranial proportions, the pattern of surface sculpturing, and the shape of the postparietals (dermosupraoccipitals).

It should be pointed out that, in neither the original description of seymouriamorphs from the Northern Dvina nor subsequent works, Sushkin indicated the collection numbers of the type specimens. The numbers were presented by Bystrow (1944); however, he assigned all specimens collected by Amalitzky to one species, *Kotlassia prima.* Bystrow (1944, pp. 410, 411) indicated that Sushkin had established *Karpinskiosaurus neglectus* on the basis of specimen PIN, no. 2005/82, skull [information on the absence of this specimen from the collection of the PIN is erroneous (Bulanov, 2002)]. A comparison between the two holotypes casts doubt on the validity of *K. neglectus.*

Actually, the holotype *K. secundus* (PIN, no. 2005/81) differs from the holotype *K. neglectus* (PIN, no. 2005/82) in the dimensions of cells of the surface relief; however, the external surface of the skull roof of the latter specimen is strongly damaged; therefore, the relief is seen in only some sites. It is relatively prominent on the tabulars; however, these elements are damaged in *K. secundus.* Since ornamentation on the occipital edge and large bones of the axial region widely varies in many seymouriamorphs, e.g., kotlassiids and *Seymouria baylorensis* (Laurin, 1996a), there is a good probability that a similar differentiation was characteristic of *K. secundus.*

The differences in cranial proportions are undoubtedly associated with the considerable deformation of the specimens. This complicates reconstruction of the *Karpinskiosaurus* skull; at the same time, it is hardly probable that actual differences between the species of this genus concern the general structural pattern. The difference in postparietal shape should not be taken into account, since in the holotype *K. neglectus*, these bones are damaged and their initial shape can be reconstructed only partly. The study of the two specimens (as indicated above, they are strongly damaged) has not shown other significant differences. Thus, the validity of *Karpinskiosaurus neglectus* is highly questionable; therefore, this species should be regarded as a junior synonym of *K. secundus.*

Additional material on *K. secundus* from localities of the same -age includes mainly isolated jaws with teeth showing the characteristic curvature of the apices (Adamovka and Blumental 3 localities) and isolated teeth (Gorokhovets).

General characteristics. Both skulls experienced similar deformation; specimen PIN, no. 2005/82 is preserved somewhat better than the holotype, although in contrast to the latter, it has undergone a substantial longitudinal deformation (Fig. 40; Pl. 14, fig. 2).

The skull is almost triangular in plan because its preorbital region is short and narrow. The orbits are rounded rectangular, their posterior rim is approximately at the midlength of the skull. The nares face mainly laterally. The occipital edge is strongly concave because of the laterocaudally projecting tabulars. The zygomatic regions are in an almost vertical position. The otic notches are round in shape, jut out into the lateral edge of the parietal shield, and terminate anteriorly short of reaching the boundary between the supratemporal and the intertemporal. The jaw condyles are in line with the posterior edges of the tabulars. Along the midline, each skull is 75 mm long; taking into account the tabulars projecting posteriorly, the skulls are 85 mm long.

Skull roof. The parietals are relatively small and taper anteriorly. The parietal foramen is small and round. The frontals are extremely poorly preserved; their boundaries with the parietals are apparently located anterior somewhat to the posterior orbital rim. Judging from the width of the interorbital region, the frontals were narrow; the same concerns the nasals, the boundaries of which are more distinct in the specimens. The postparietals are small and most likely only weakly jut out into the posterior flanks of the parietals.

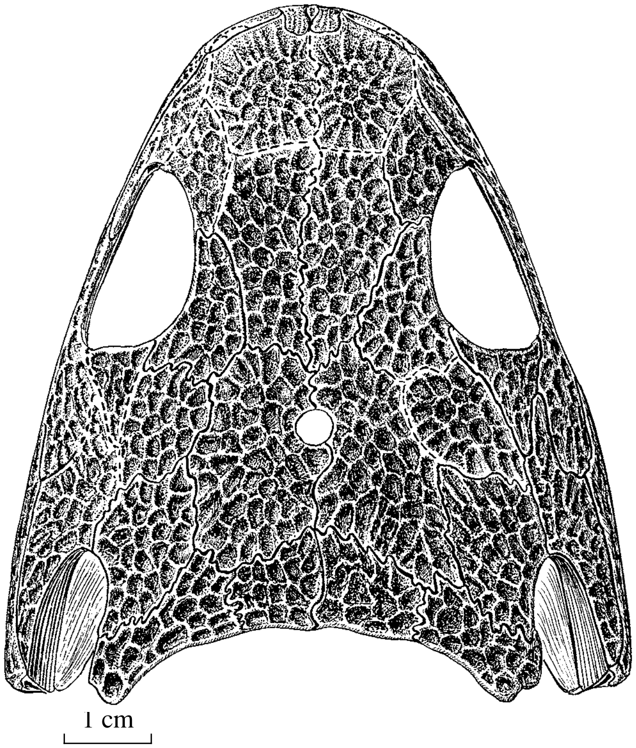


Fig. 40. *Karpinskiosaurus secundus*, skull, reconstructed using holotype PIN, no. 2005/81 and specimen PIN, no. 2005/82: dorsal view.

The premaxillae have narrow and high dorsal processes, between which an oblong fontanel is retained. The upper expanded margins of the processes are attached to the nasals and connected to one another (specimen PIN, no. 2005/82).

The maxilla is preserved satisfactorily on only the left side of specimen PIN, no. 2005/82. The anterior region of the bone is perforated externally by numerous foramina, the posterior end of the bone is in line with the posterior orbital wall. The maxilla apparently contained about 30 teeth.

The prefrontal and postfrontal are approximately equal in size and come into narrow contact above the orbit. The postorbital is triangular and has a well-pronounced caudal process; behind the orbit, the jugal expands far posteriorly to come in broad contact with the postorbital. The intertemporal and supratemporal are approximately equal in size (specimens PIN, nos. 2005/81, 82). The intertemporal is extended, the supratemporal tapers posteriorly and has a strongly concave otic flank.

The tabulars expand at the otic notches and form te posterolateral projections slightly inclined ventrally. Since the small paroccipital processes adjoin the well-developed vertically positioned occipital plates, the posttemporal fossae are completely closed in the caudal projection (Fig. 40b).

Although the postorbital region is elongated, the squamosal is very small; its anterior edge is located far from the orbit, halfway between the orbital rim and the edge of the otic notch (specimens PIN, nos. 2005/81, 82). The quadratojugal only slightly projects ventrally with reference to the alveolar edge of the maxilla, which most likely spread under the anterior region of the quadratojugal (specimen PIN, no. 2005/82).

Lower jaw. The lower jaws of both specimens are strongly damaged; therefore, they show only a limited set of structural features. The prearticular is shortened because the splenial considerably expands on the internal side, has a long posterior projection, and reaches the coronoids. In the region of the adductor cavity, the dorsal margin of the prearticular slightly curves medially. The Meckel's foramen was either absent or slitlike. The splenial apparently terminated short of reaching the symphysis. The angular and surangular are covered externally by surface sculpturing.

Palate. The palatal complex of each skull is extremely poorly preserved. The majority of membrane bones were damaged during primary preparation; therefore, it is difficult to determine the positions of the bone boundaries (Pl. 14, figs. 1b, 2b). The parasphenoid has a long and narrow rostral region extending onto the ventral surface (in either specimen); apparently, this is not a result of deformation. The parasphenoid body slightly expands in the region of the basipterygoid articulation; the posterior region of the bone has long and narrow parafenestral wings substantially deviating dorsally (holotype PIN, no. 2005/81). The pterygoids have triangular depressions for the basipterygoid processes of the basisphenoid; anterior to the depressions, there are small notches.

Dentition. Only specimen PIN, no. 2005/82 retains teeth; for the most part, they are lost or extremely poorly preserved. Nevertheless, it is clear that the crowns of the maxillary teeth are hooked and covered by ridges on both the internal and external sides.

Medial to the choana, the vomer has three large teeth arranged in a line; a pair of similar teeth are preserved on the palatine posterior to the choana; their crowns are conical, covered by ridges on either side, and lack flattening. Because of poor preservation, it is impossible to elucidate the distribution of shagreen teeth on the palatal surface.

Surface ornamentation. On the skull roof, cellular type relief prevails (holotype PIN, no. 2005/81). The postorbital region of the jugal and the caudal process of the postorbital of specimen PIN, no. 2005/82 are covered by extended cells (Fig. 40c). The radial ridged relief is observed on the quadratojugal, angular, and surangular. In addition, in holotype PIN, no. 2005/81, ridged sculpturing is observed in the peripheral region of the squamosal.

Seismosensory system. Within the intact regions of the skull roof, the grooves of the seismosensory system are not traced.

Endocranium. The endocranial elements ossified well. The weakly laterally projecting basipterygoid processes of the basisphenoid are well preserved in

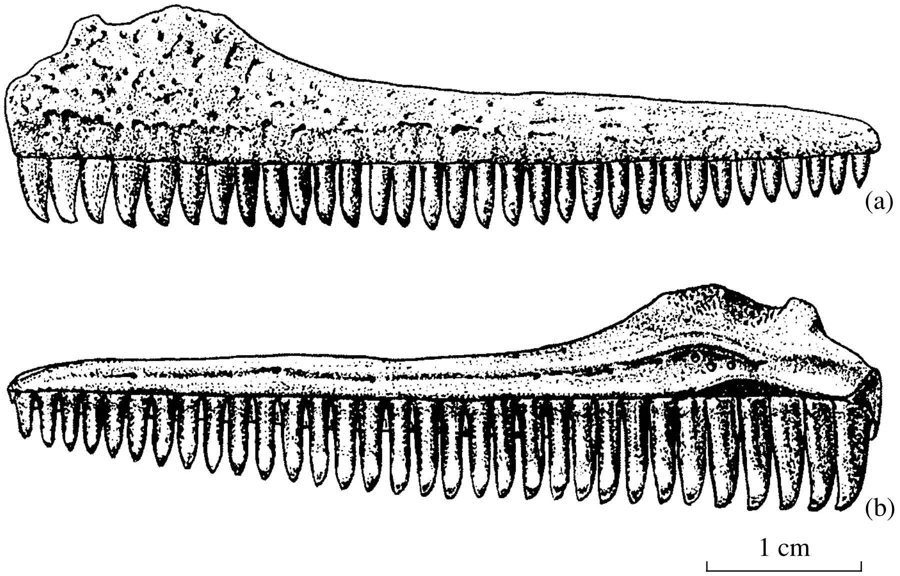


Fig. 41. *Karpinskiosaurus secundus*, left maxilla, reconstructed using specimens SGU, nos. 104B/322 and 323: (a) labial and (b) lingual views.

skull PIN, no. 2005/82. Each specimen of *Karpinskiosaurus secundus* retains both the quadrate and the articular. The bones of the occipital ring (except for the supraoccipital) ossified well; however, the occiput of the holotype is strongly damaged; in specimen PIN, no. 2005/82, the occiput is covered posteriorly by the anterior cervical vertebrae. The auditory capsules also completely ossified; however, the study of these elements necessitates additional preparation of the specimen.

The jaws from the Adamovka locality (of the same age as the type locality) were assigned to *K. secundus* on the basis of the similar structure of the marginal teeth. This material shows certain structural details of the maxilla. An important feature of the maxilla is the presence of a small ascending lamina (Fig. 41) posterior to the nasal notch (in specimen PIN, no. 2005/82, the maxilla also forms a dorsally oriented projection posterior to the nares). The anterior foramen for the infraorbital artery is in line with the sixth or seventh maxillary tooth; the other foramina located in the arterial groove are evenly distributed and face posteriorly. Externally, the bone is strongly perforated, especially in the anterior region.

The abruptly curving apices of the anterior maxillary teeth are directed mainly posteriorly because the alveoli deviate from the vertical position. As a result of longitudinal elongation, the tooth bases form broad buttresses; only the lateral sides of the bases are folded (Fig. 42).

CHAPTER 5. EVOLUTION OF THE SEYMOURIAMORPH SKULL

Dermatocranium

The skull of seymouriamorphs is short and parabolic in plan and has a poorly pronounced preorbital growth zone and extended postorbital region. The orbits are round or almost oval; occasionally, they are slightly angular or have notches in the anterior rim (*Seymouria*). At the definitive stage, the orbits are more or less displaced anteriorly or located at the midlength of the skull. In the case where the preorbital region is relatively weakly developed, the external nares face mainly terminally; in the skulls with an elongated preorbital region, the nares are turned laterally at an angle of up to 45°.

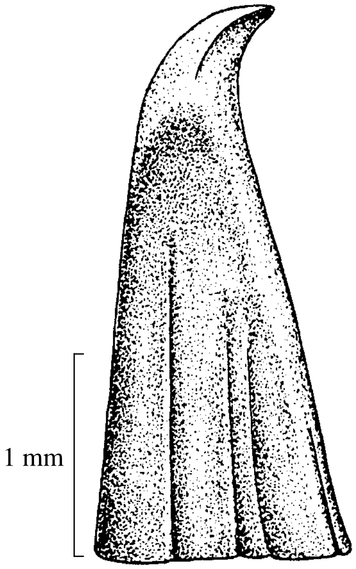


Fig. 42. *Karpinskiosaurus secundus*, maxillary tooth, based on specimen SGU, no. 104B/322, lateral view.

The skull is high; the zygomatic region is positioned steeply, almost vertically, and firmly attached to the parietal shield by the ventromedially expanded squamosal (synpareial pattern). In all seymouriamorphs the larval stage of which has been discovered, the occipital edge of the parietal shield is straight at early developmental stages; occasionally, this feature is retained in adults (*Utegenia* and *Leptoropha*); in the majority of adult forms, the occipital edge is concave to a greater or lesser extent.

The small parietal foramen is located anterior to the ossification centers of the parietals posterior to the posterior orbital rim near the boundary between the parietal and the frontal. The shape of the otic notches is associated with the depth and position of the jaw joint, the features changing in the course of ontogenetic development.

The skull is of the angustitabular type; in the dermatocranial structure, this manifests itself in the presence of contact between the postparietal and tabular; therefore, the ancestors of seymouriamorphs should belong to primitive reptiliomorphs. Seymouriamorphs possess the same set of membrane cranial bones as typical anthracosaurs; in particular, they retain separate intertemporals, postparietals, and tabulars; the lower jaw contains two splenials and three toothed coronoids.

The prefrontal and postfrontal are always connected to one another above the orbit. The lacrimal extends from the orbit to the external nares; however, in *Microphon gracilis*, it is most likely separated from the nares by the nasal process of the maxilla. This is caused by both a considerable development of the ascending lamina of the maxilla and a reduction of the nasolacrimal duct, largely determining the rate and extent of the lacrimal development (Medvedeva, 1959, 1975). The duct is present in the majority of members of the order; its canal is enclosed in the bone and opens by a single foramen in the anterior wall of the orbit and terminates in the anteroventral margin of the lacrimal. In some cases, the lateral wall of the canal incompletely ossified, e.g., in *Utegenia* and *Discosauriscus* (Klembara, 1997).

Seymouriamorphs have a large septomaxilla freely positioned in the nasal cavity and, occasionally, forming a complete ring round the nasolacrimal duct at the point of its curvature at the exit from the olfactory sac (septomaxillary foramen), e.g., in *Utegenia, Discosauriscus* (Klembara, 1997), and *Karpinskiosaurus* (Bulanov, 2002). In seymouriamorphs with a reduced nasolacrimal duct, this bone is also present but lacks a distinct septomaxillary foramen. In this case, the presence of the septomaxilla is accounted for by the dual nature of the duct; in living amphibians, the anterior part of the duct (around which the septomaxilla develops) is formed by an expansion of the olfactory sac and, in contrast to the posterior part, covered by the ciliated epithelium (Medvedeva, 1959).

Initially, the membrane bones of the nasomaxillary region are only weakly consolidated; in particular, the upper jaw arch only adjoins the membrane bones of the palatal complex and skull roof; serrated sutures are occasionally formed only between the premaxillae and the nasals. In the course of evolution, a stronger attachment of the maxilla to the dermatocranium gradually developed by dorsal expansion of this bone, and is always well-pronounced in progressive parareptiles. The dorsal (ascending) processes of the premaxillae widely vary in length and width; in some cases, the premaxillary fontanel is present and retained at the definitive stage (*Karpinskiosaurus*). The latter feature is primarily associated with a low specialization of the premaxillary teeth and only a weak load falling on the premaxillae during feeding. In seymouriamorphs that, judging from the dental structure, experienced substantial load on the premaxillae, the dorsal processes closely adjoined each other. The palatine processes of the premaxillae are newly formed short projections observed in only *Seymouria baylorensis* (Laurin, 1996a). In other seymouriamorphs, these processes are absent and the premaxillae are only weakly attached to the palate; this is evident, among other things, from the fact that, in the burial conditions, these bones are the first to become disarticulated.

In the palatal structure, of special note is the fact that the pterygoid flanges abruptly project into the adductor cavities; in all cases, the flanges are completely formed by the pterygoids and often show a clear ventral inclination. At the definitive stage, the interpterygoid vacuities are preserved as narrow notches located anterior to the basipterygoid articulation. The parasphenoid has a long rostrum, terminating on a level with the posterior edge of the choanae. The bone expands posteriorly to form more or less developed parafenestral wings spreading under the base of the braincase.

The vomers are always long and narrow and connected to the palatines at the posterior edge of the choanae. The choanae are oval or narrowed somewhat anteriorly. Lateral to the choanae, the palatine forms an anterior projection (processus laterochoanalis) spreading under the antorbital process of the cartilaginous olfactory capsule; this process supports the maxilla at early ontogenetic stages. In the maxilla, the attachment area for the antorbital process is a fossa located under the anterior foramen for the infraorbital artery.

The subdivision accepted in the present work of seymouriamorphs into the superfamilies Kotlassioidea and Seymourioidea is based, in particular, on the differences in the dermatocranial structure (additional differences relative to the features of the jaw and palatal dentition are considered in the section *Dentition*).

The Kotlassioidea are characterized by the following characters: (1) relatively shallow otic notches, the anterior edge of which extends anteriorly at most to the midlength of the supratemporals; (2) substantially reduced dorsal flanks of the tabulars; they are smaller than, or equal to, the postparietals in size and do not participate in the formation of the lateral edge of the parietal shield; and (3) short and broad parafenestral wings of the parasphenoid.

All kotlassioids retain the posttemporal fossae open. The premaxillary fontanel between the premaxillae is registered as a form of individual variation in only the most primitive forms (*Utegenia*). Early members of the group are characterized by the presence of contact between the postorbital and the supratemporal; this contact is lost in only the most evolutionarily advanced kotlassiids likely because of a considerable increase in size of the squamosal, the main element of the zygomatic region. In the lower jaw of the majority of species (*Biarmica tchudinovi*, *Microphon gracilis*, and *Kotlassia prima*), the prearticular closely approaches the symphysis and isolates the splenial from the coronoid row. The arrangement of the listed elements in the Utegeniidae is not yet entirely known; therefore, this character is currently included in the diagnosis of the Kotlassiidae and absent from the diagnosis of the entire superfamily. In all seymourioids, the splenial substantially expands dorsally on the internal side of the jaw and is connected to the precoronoid.

Even Early Permian members of the group (Utegeniidae) show the complete set of diagnostic characters.

In *Utegenia shpinari*, the otic notches are very shallow; the anterior edge of the notches is weakly displaced anteriorly with reference to the occiput and, only rarely, reaches the midlength of the supratemporals. Although the tabulars are strongly developed on the ventral side, the dorsal surface of these bones looks like narrow strips terminating short of the otic notches. The parafenestral wings of the parasphenoid are very short.

In the cranial structure of *Utegenia*, of special note is the narrow preorbital region (accounted for by the relatively narrow nasals and premaxillae) and elongated maxillae approaching posteriorly the plane of the posterior orbital wall. The frontals are longer than the parietals and project deep into the preorbital region of the skull, wedging in between the nasals along the medial suture. The postorbital is connected to the supratemporal by a long caudal process. The paroccipital processes of the tabulars are isolated from the occipital processes by notches. At the definitive stage, the articular region of the lower jaw is located posterior to the occiput.

Evolutionary changes in the cranial structure of the Kotlassiidae are mainly associated with the transformation of the jaw apparatus and develop against a background of general fetalization. The gradual decrease in the number of marginal teeth is accompanied by the shortening of the maxilla and, as a result, the development of the ascending lamina at the anterior end of this bone; this reinforces the attachment of the maxilla to the lacrimal located above. In contrast to the maxillae, the premaxillae are widened because of the increase in the number and complexity of the premaxillary teeth; this is probably an important factor of expansion of the entire preorbital region.

Along with the reduction of the posterior part of the tooth row, the jaw joints displaced anteriorly and, at certain stage of evolutionary development, the postorbital region (providing the attachment area for the greater part of the adductor muscles) elongated. The latter feature is characteristic of Late Tatarian kotlassiids and accompanied by an increase in the size of the squamosal, which results in breaking off the contact between the supratemporal and the postorbital. Most likely, the development of the jaw muscles induced an increase in the consolidation of membrane bones in this region; this manifests itself in the reinforced attachment of the zygomatic region to the parietal shield (by an increase in size of the ventromedial plate of the squamosal), expansion of the ventral side of the jugal along the edge of the otic notch, and complex overlap of the elements forming the occipital edge (*Microphon*). In the lower jaw of kotlassiids, the coronoid process is formed.

Among the Leptorophinae, *Biarmica* is the least specialized form retaining a number of features of the ancestral group. The large orbits were most likely widened in the posterior part. The postorbital has a very long caudal process, passing round the intertemporal to come into contact with the supratemporal. The anterior edge of the otic notches is in line with the anterior edges of the tabulars. The tabulars are separated from the otic notches by a projection of the supratemporal. The squamosal remains small; nevertheless, its otic flank is shaped into a broad plate. The coronoid process is only weakly raised.

The quadrate–articular region is located anterior to, or, less probably, in the plane of the occiput. The number of marginal teeth remains large, although it is reduced in comparison with that of *Utegenia*. The maxilla lacks ascending lamina; however, it forms a relatively broad horizontal attachment facet for the lacrimal. The premaxilla is slightly widened and contains six teeth (whereas *Utegenia* normally has five). The premaxilla–maxilla boundary is displaced toward the lateral wall of the naris; however, the dorsal process of the premaxilla remains narrow, at most one-third as wide as the dental area.

At the same time, the parietals are relatively strongly developed and project deep into the interorbital region. The occipital edge of the parietal shield becomes concave. The parafenestral wings of the parasphenoid are short but strongly widened. Of special note is the position of the pterygoid flange in the adductor cavity, since it is inclined at a substantially smaller angle to the quadrate ramus of the pterygoid than that of other seymouriamorphs.

In *Leptoropha*, the maxilla has already become short and forms a high ascending lamina and a wide vertically positioned attachment facet for the lacrimal. Occasionally, as a form of individual variation, the lamina is absent; this is the primitive condition of the character. Apparently, the posterior end of the maxillae is in line with the midlength of the orbits. The orbits are regularly round in shape. The posterior regions of the nasals are preserved in the holotype and their structure suggests that the preorbital region was widened and shortened (the premaxillae of *Leptoropha* has not been found). The jaw joints of adults are positioned anterior to the occipital edge of the parietal shield; the occipital edge is straight, in contrast to that of *Biarmica*.

The postorbital is connected to the supratemporal, as in earlier kotlassioids. The postorbital region contains a relatively small squamosal located far from the orbit. A large part of the zygomatic region is formed by the quadratojugal covering the jugal posteriorly and partly dorsally, as that of some utegenians. Judging from the shape of the posterior end of the dentary, the coronoid process was positioned rather high.

Microphon exiguus and *M. gracilis* are characterized by a high and short maxilla even at early ontogenetic stages. Similar to *Leptoropha*, *M. exiguus* shows the absence of well-developed ascending lamina as a form of individual variation. In *M. gracilis*, the nasal process of the maxilla forms an additional contact between this bone and the nasal; as a result, the lacrimal is isolated from the naris. In the ontogeny of Recent *Pleurodeles waltlii*, the maxilla is formed in a similar manner; it expands over the external wall of the cartilaginous olfactory capsule in two directions, i.e., to the complex prefrontale–lacrimale (a protrusion is formed opposite the antorbital process) and to the lateral projection of the nasal; the maxilla adjoins the nasal posterior to the naris (Lebedkina, 1979).

The preorbital region is short and very broad in the two *Microphon* species; the premaxillae and their dorsal processes are widened and the nasals strongly expand laterally, especially in *M. gracilis.* In the ontogeny of *M. exiguus* (presented by adults, in contrast to *M. gracilis*), any significant elongation of the anterior skull region is not observed. The jaw condyles of juveniles are located anterior to the occiput; apparently, in the course of ontogenetic development, they retain the same position; this agrees with the retention of a short skull. Since the squamosal considerably increases in size, the postorbital is strongly shortened and loses a contact with the supratemporal. Apparently, the absence of distinct coronoid process of the lower jaw in young *M. gracilis* and *M. exiguus* should be regarded as a juvenile character. This inference is corroborated, among other things, by a strong development of the coronoid process not only in *Leptoropha* but also in *Kotlassia*, the dentition of which is substantially simplified. The structure of the maxilla in *Kotlassia* is not known, the boundary of this bone is not observed in available specimens; however, it is not inconceivable that the secondary simplification of crowns caused an increase in the number of marginal teeth and reverse elongation of the maxillae (see below). Apparently, this resulted in a greater elongation of the preorbital region (combined with the retention of considerable width) than in *Microphon* and a slight anterior displacement of the jaw joint with reference to the occiput.

In general, the Seymourioidea are more conservative morphologically. The diagnosis of this group includes the following characters of dermatocranium: (1) deep otic notches extending to the anterior edge of the supratemporals; (2) well-developed dorsal flanks of the tabulars, exceeding the postparietals in size and composing a large segment of the medial edge of the parietal shield; and (3) long and widely spaced parafenestral wings of the parasphenoid.

The small otic notches of *Karpinskiosaurus secundus* undoubtedly appeared as a result of secondary changes, since in the earlier species of the same genus (*K. ultimus*), they are developed to the same extent as in other seymourioids.

All members of the superfamily have a long maxilla occasionally connected to the quadratojugal, e.g., in *Karpinskiosaurus ultimus* (Bulanov, 2002) and *Seymouria baylorensis* (Laurin, 1996a). Only *Seymouria baylorensis* has a high maxilla, which is associated with the excessive development of maxillary teeth (Laurin, 1996a). A small ascending lamina at the anterior edge of the maxilla is observed in *Karpinskiosaurus secundus* possessing hooked marginal teeth used for holding objects, whereas the less specialized *K. ultimus* lacks such elements. A weakened attachment of the upper jaw arch to the dermatocranium is manifested in karpinskiosaurs by the presence of a well-developed premaxillary fontanel preserved up to the definitive stage (*K. secundus*).

The occipital edge is always concave in seymourioids of late developmental stages, especially in Late Permian karpinskiosaurids having tabulars strongly projecting posteriorly. Occasionally, the paroccipital and occipital processes of the tabulars adjoin each other to close the posttemporal fossae; this is never observed in kotlassioids. The lower jaw contains a short prearticular limited anteriorly by the splenial, which strongly expands dorsally; this is observed in *Discosauriscus*, *Karpinskiosaurus*, and *Seymouria*; in *Ariekanerpeton*, the state of this character is not known.

The basic reason for placing *Seymouria* in a separate family is a more complex articulation between the zygomatic regions and the parietal shield such that the squamosal covers medially and laterally the stout sharply projecting ventrally and longitudinally oriented crests formed by the external flanks of the tabulars and supratemporals (Watson, 1954; Laurin, 1996a). In other seymouriamorphs, these regions are connected by a single ventral plate located on the medial edge of the squamosal and spreading under the temporal region. In addition, seymouriids, including *Rhinosauriscus*, are distinguished by a strongly developed preorbital region; at the definitive stage, the nasals are equal in length to the frontals and the orbits are located at the midlength of the skull. The anterior orbital rim has a notch directed anteriorly. In the lower jaw of *Sey-*

mouria, the splenial contributes to the formation of the symphysial surface (Laurin, 1996a).

It should be noted that, currently, many of the features listed above, including the diagnostic characters, are not easily explained. In seymourioids, an increase in the depth of the otic notches is very likely associated with the formation of the cavity of the middle ear and development of the sound-transmitting system formed by the auditory ossicles. The functioning of these bones remains obscure for lack of understanding of the structure of the entire complex of the otic elements. The development of the sound-transmitting apparatus with the tympanic membrane, the space for which is provided by the increased otic notch, can only be conceived under the conditions of a terrestrial environment. This is evidence for the secondarily aquatic mode of life of some seymourioids (Karpinskiosauridae) the ancestors of which were ecologically similar to seymouriids and passed through a long nonaquatic evolutionary stage. The changes in general configuration and position of the posterior region of the palatoquadratum accompanying the increase in the depth of the otic notches are most likely responsible for the break of contact between the supratemporal and the postorbital in seymourioids. In the superfamily Kotlassioidea, contrastingly, the same result is achieved by an increase in the size of the squamosal. The contact between these bones occurs in the ontogeny of *Discosauriscus austriacus* as a common variant and shows the relationships between seymourioids and primitive kotlassioids. Apparently, the closing of the posttemporal fossae in the most advanced seymourioids is associated with the increased role of the sterno-occipital muscles attached to the expanded occipital plates of the tabulars; this also suggests a facultative terrestrial mode of life.

The data on the ontogenetic development of the Utegeniidae and Karpinskiosauridae give us an insight into the main trends in the changes of the seymouriamorph skull in the course of ontogeny. They are as follows: (1) a decrease in relative size of the orbits by the enlargement of bones contributing to its formation; as a result, the contacts between these bones become wider, the parietals disappear from the interorbital region, and the interorbital region is broadened; (2) the development of the preorbital growth zone mainly by the elongation of the nasals and lacrimals (as well as the prefrontals, caused partly by a decrease in relative size of the orbits); (3) posterior displacement of the jaw joints, which, at the larval stage, are located anterior to the occipital skull edge; this changes the shape of the otic notches; however, the quadrate rami of the pterygoids retain the same orientation, since the zygomatic regions occupy an almost vertical position; (4) curvature of the occipital edge of the parietal shield in all forms, except for *Utegenia* and *Leptoropha*; and (5) elongation of the jaw bones and an increase in the number of teeth.

The majority of the Kotlassiidae show the juvenile state of the above characters. This indicates a significant role of fetalization in the evolutionary development of this group. A certain mosaic in the combination of characters is accounted for by the incompleteness of the phylogenetic sequence reconstructed on the basis of a limited number of taxa showing only a small part of the past diversity.

Dentition

Dentition is an informative component of the terrestrial vertebrate skull and is widely used for taxonomic construction and ecological interpretation in studying various groups of extinct and extant tetrapods. Diversification of the morphology of the jaw apparatus as a complex structure and the wide range of trophic relations caused the development of widely varying types of tetrapod dentition. However, analogies caused by the similarity of consumed resources and frequently observed in the forms connected by only remote phylogenetic relationship are everywhere traced against this background. The detection of similar adaptations in extant and extinct groups is a productive method for the reconstruction of ecological and trophic relationships in early vertebrates, enabling one to reveal the position of particular species in the composition of extinct communities.

The importance of dental morphology for the taxonomy of higher tetrapods has no need of comment: the complex dental structure of many amniotes suggests broad potentials for the differentiation of taxa of various ranks. Recent amphibians, the overwhelming majority of which are obligate predators, are characterized by the homodont dental system; however, extinct amphibians include groups that follow the way of significant modification of the entire system or its components.

Seymouriamorphs are such a group. It is remarkable that the greatest specificity of dentition is observed in some kotlassioids. Against the background of well-pronounced pedomorphosis, this group shows amazingly consistent realization of multicomponent dentition, in which a complex structure of the marginal teeth is combined with specialized dentition of the palatal complex.

Many researchers studied the dental structure of seymouriamorphs. A key parameter traditionally considered in the descriptions of the taxa is the number of alveoli (tooth positions) in the upper and lower jaw bones. The crown shape is analyzed only in the case of nonstandard arrangement (Tchudinov, 1957; Ivakhnenko, 1987); otherwise, teeth are out of the scope of thorough examination. The data on the internal dental structure are limited to the results presented by Broili (1927) who demonstrated in cross sections a strongly plicate structure of the tooth bases in *Seymouria* that closely resembles that of labyrinthodonts and by Bystrow (1944) who performed a similar study of *Kotlassia prima.*

The presence of plicate dentin is a diagnostic character of the order, distinguishing it from the other parareptiles and inherited from anthracosauromorph amphibians. The dental structure of the latter has much in common with this group (plicate tooth bases, the pattern of teeth attachment, and distribution of teeth over the jaws and the palate), especially when the least specialized forms, such as the Utegeniidae, are included in comparison.

The presence of high teeth is characteristic of seymouriamorphs as a whole. At most one-third of the tooth height is the crown covered by a bright enamel-like substance (termed below the *enamel* for short). With rare exceptions, longitudinal ridges never extending beyond the enamel cover ornament the lingual side of the crowns. The basal part of the marginal teeth to approximately the midheight of the teeth is covered externally by a plate formed by the expansion of the external alveolar margin of the jaw bones. The superficial alveoli are closely spaced and separated from each other by thin septa. The tooth bases do not extend deep into the bone nor cover the extension of the alveolar margin (prototecodont attachment pattern). In general, the tooth height gradually decreases posteriorly and the smallest teeth occur at the posterior end of the tooth rows. Nevertheless, in the preorbital region, the teeth are usually more or less differentiated in size, i.e., the teeth located at the joint of the premaxilla and maxilla and in the symphysial region of the dentary are distinguished by smaller size from neighboring teeth (especially in the case of a strong size differentiation characteristic of some genera, such as *Utegenia* and *Ariekanerpeton*). These teeth are opposed to the largest teeth of the antagonistic jaw.

The number of marginal teeth in the seymouriamorphs is small as compared to the most of the anthracosauromorphs, on average at most 30–35 in the maxilla, and up to 40–45 in the mandible. A gradual increase in the number of marginal teeth (considerable or slight) occurs in the course of the ontogeny of each species.

Most part of the palate in seymouriamorphs is covered by numerous small shagreen teeth. Within the anterior region of the pterygoids, they are arranged in numerous rows radiating from the ossification centers located in the basipterygoid region. Every row is one or two teeth in width. In kotlassioids, this shagreen expands far posteriorly along the quadrate rami of the pterygoids and is developed on the parasphenoid rostrum where it is also arranged in radiating rows.

In addition, large teeth comparable in size to the marginal teeth are always present on the palate medial and superior to the choanae of seymouriamorphs. Another component of dentition is the teeth located on the coronoids, i.e., numerous teeth, larger (sometimes, considerably) than the shagreen teeth of the palatal complex, directed dorsolingually, according to the orientation of the bones holding these teeth.

In seymouriamorphs, tooth generations are constantly replaced. The resorption is preceded by the appearance of a rudimentary replacing tooth on the surface of the dental area opposite the old tooth, which is observed in some *Utegenia shpinary* (specimens PIN, nos. 2078/372, 383). The old tooth is initially destroyed on the lingual side of the base at the place of tooth attachment to the bone, where a round notch appears and subsequently breaks into the pulp cavity. As this hole appears, it first expands upwards; later on, resorption involves the lateral sides of the base. The labial tooth wall is the last to be resorbed, the alveolus becomes free, and the old crown comes out. In the localities where seymouriamorphs are regularly found, the bone beds usually contain numerous worn crowns quite suitable for the identification of known forms. In particular, the presence of *Microphon exiguus* in the Navoloki locality was first ascertained by isolated teeth collected from dissolved host rocks and, later, was corroborated by the finds of macrofossils. The preservation of rudiments in empty alveoli is a good indicator of autochthonous and subautochthonous burial types where specimens were not exposed to a substantial disarticulation or redeposition.

Calcification of the bases of a replacing rudiment begins not earlier than the old crown comes out. In seymouriamorphs, only one replacing crown is observed opposite to a resorbing tooth; apparently, this suggests a moderate rate of replacement.

Early Permian kotlassioids, the Utegeniidae (*Utegenia*), have the least specialized dentition resembling that of the Carboniferous Embolomeri and may be considered archetypical of all parareptiles. The basic features of such dentition are a large number of marginal teeth (about 30 in the maxilla and 40 in the mandible) characterized by simple crowns and round sections of the bases, the presence of two or three large teeth medial and posterior to the choana. The shagreen densely covers the parasphenoid rostrum and expands far posteriorly over the external side of the quadrate rami of the pterygoids toward the quadrate–articular joint. On the palatine and ectopterygoid, it forms two longitudinal fields (lateral and medial) separated from each other by an area lacking teeth. Within the medial field, small teeth continue the rows developed on the palatine region of the pterygoid; the lateral field is covered by larger and randomly oriented shagreen teeth.

Further evolution of kotlassioids was associated with the complication of the marginal tooth crowns mainly by thickening their near-basal region and the appearance of supplementary denticles on the cutting edge. The number and size of the denticles vary in different members of the family as well as in the ontogeny of the species presented in the collection by age series. As this takes place, the tooth bases expand longitudinally (labiolingually) and become oval or oblong-oval in cross section. The anterior teeth are specialized to a greater extent. The teeth from the posterior ends of tooth rows are less modified and retain their ancestral structure (especially in the dentary) even at the late ontogenetic stages: the lateral denticles are less developed or absent, the crowns are only weakly thickened, the apices are weakly inclined lingually, and the tooth bases are round in cross section (*Microphon*).

The degree to which the mentioned specialized features vary along the tooth row is not identical in different forms. In addition to the age variation, it is subjected to individual variation as well; this complicates taxonomic identification in the case where a representative sample is absent.

In the Kotlassiidae, the crowns are complicated in parallel with a gradual decrease in the number of marginal teeth; at the definitive stage, the genera from the Tatarian have approximately half as many teeth as the Utegeniidae. In addition, the size differentiation of the anterior upper teeth disappears almost completely, which is determined by the change of food object, in particular, the absence of the necessity of holding fast relatively large prey. In addition, the heterodonty manifested as the appropriate change of the crown shape along the tooth row increases.

At the same time, rows of large teeth comparable in size to the marginal teeth were formed on the palate. The first (mediochoanal) row extends across the vomer in parallel to the choanal edge. Caudally, it continues as a longitudinal field of large shagreen. The postchoanal row extends on the palatine and ectopterygoid along the maxillary edge from the posterior end of the choana to the anterior edge of the adductor cavity.

The lower regions of the tooth crowns of *Biarmica*, unlike those of *Utegenia*, are appreciably thickened; there are two well-pronounced supplementary denticles on either side of the central apex. The serrated crowns are registered in a large part of the tooth row; the bases are extended longitudinally (labiolingually) and oval in cross section. The number of teeth in the dentary is reduced to 30, the maxilla contains approximately 25 teeth; in the anterior region of the upper jaw, the teeth are only slightly differentiated in size.

The mediochoanal row of the palatal teeth of *Biarmica* most likely extended along the entire length of the vomer (in the fragmentary left vomer of the holotype, only five teeth are preserved). The postchoanal row is rudimentary and consists of only three teeth located in the anterior region of the palatine; however, these teeth are oriented along the boundary of the maxilla. Further posteriorly, the row is continued by small teeth expanding onto the ectopterygoid; the anterior region of the latter bone has one or two large teeth. The lateral and medial fields of shagreen teeth in *Biarmica* join on the ectopterygoid.

The dental system of *Leptoropha talanophora* is especially specific. The marginal teeth have the most thickened basal regions of the crowns forming a wide shelf posterior to the abruptly inclined apex. Since the pulp cavity is extremely enlarged, it penetrates into the crown to form a large recess, which is preserved even in completely developed teeth. The number of supplementary denticles on each side of the cutting edge increases to three or four; the denticles are enlarged, giving the *Leptoropha* teeth some resemblance to those of pareiasaurs; this was the main reason for the initial assignment of this form to primitive rhipaeosaurid pareiasaurs (Tchudinov, 1955, 1957). The tooth bases are heavily plicated, longitudinally elongated, and strongly compressed laterally, especially in the near-crown region. Sometimes, they are covered externally by a thin layer of the osseous tissue, a conjectured analogue of cement.

The medial flank of the dental area of the maxilla and dentary is elevated; therefore, the tooth bases lie in a deep groove between the medial flank and the alveolar edge. The spaces between teeth are usually filled with spongy tissue. This may be responsible for certain changes in the process of tooth replacement, i.e., a comparatively large new crown is formed in a narrow space between the edge of the dental area and the tooth base; after the beginning of resorption, it develops inside the pulp cavity of the tooth of the preceding generation (PIN, no. 161/106).

The number of marginal teeth in comparison with *Biarmica* is reduced to 19 in the maxilla and to 22 in the lower jaw. The palate of *Leptoropha* is partially preserved; however, certain diagnostic characters of kotlassioids can be established. These are the existence of large palatine teeth behind the choana (their different shape indicates considerable length of the tooth row) and the presence of shagreen teeth on the parasphenoid rostrum and at the bases of the quadrate rami of the pterygoid.

In the ontogeny of *M. exiguus*, presented in the collection by various age stages, the dental system shows a number of natural changes following the evolutionary transformations in the series of ancestral forms (Fig. 43).

In the smallest individuals with a skull less than 20 mm long (specimens PIN, nos. 3585/141, 204), the marginal teeth are unicuspid and usually have one small lateral projection on the anterior part of the cutting edge. The basal crown regions are not thickened; the bases are round in cross section.

In subsequent tooth generations, the lateral denticles appear and gradually increase in number; adults have four or a greater number of denticles on either side of the central apex. However, the denticles are small and arranged in serrated ridges; the latter are especially well developed in premaxillary teeth. The basal regions of the crowns are thickened, the bases become longer, and their plication is intensified. The average number of marginal teeth only slightly increases as compared to juveniles. The transformation of the initially sharp and not numerous ridges on the lingual side of the crowns into fine undulating threads is a particular adaptation aimed at the strengthening of the enamel cover to prevent frequently observed abrasion caused by hard food objects. Similar small ridges cover, for example, the crushing teeth of Recent *Ophysaurus*.

Similar changes of dentition are characteristic of *Microphon gracilis*. As the skull is 13 mm long (speci-

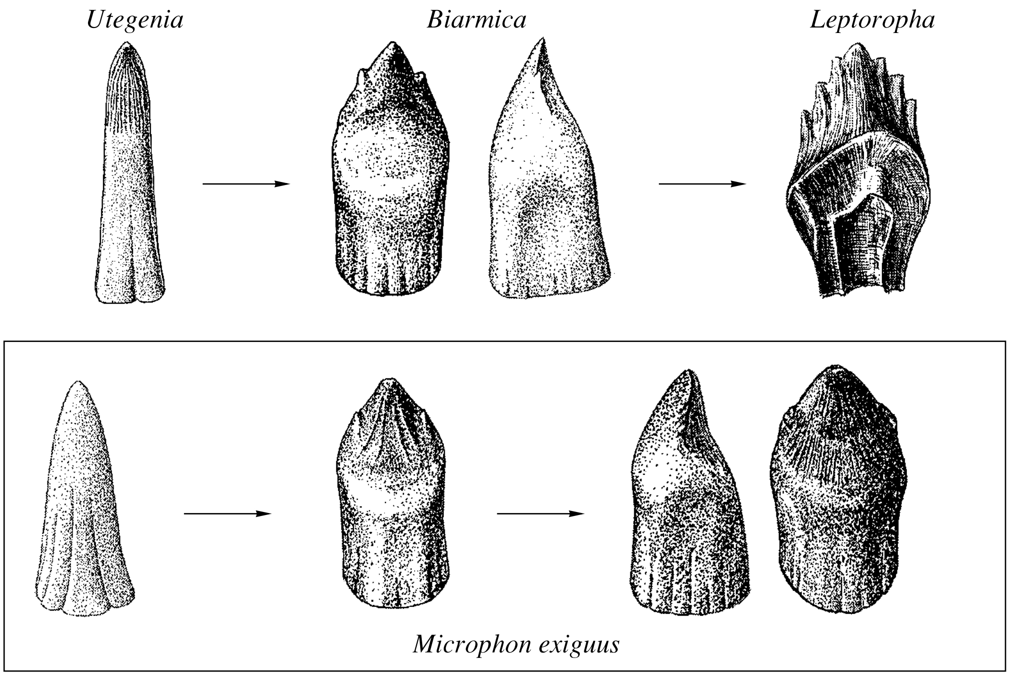


Fig. 43. Evolutionary and ontogenetic changes of marginal teeth in kotlassioids.

men PIN, no. 4617/110), there are only ten maxillary teeth with unicuspid crowns and weakly plicate bases round in cross section. The vomer of the holotype contains three caniniform teeth located along the greater part of the medial choanal edge. The palatine also bears two large teeth; however, the postchoanal row is not formed, its place is occupied by a longitudinal field of large shagreen teeth.

As the skull increases to 30–35 mm in length, the number of teeth in the maxilla increases to 13; their bases become longer, plication intensifies, and the proximal regions of crowns become notably thicker. Well-developed supplementary denticles appear on the cutting edge, ranging in number from one to three on each side of the high central apex.

The only kotlassiid genus retaining unicuspid crowns at the definitive stage is *Kotlassia*; however, the data on the structure of its dentition are incomplete. Unlike other kotlassiids, this genus is characterized by the absence of supplementary denticles on the cutting edge (shaped into a sharp border) and ridges on the lingual side of the crowns. Similar to all other members of the family, *Kotlassia* has a completely developed postchoanal row of at least 16 teeth extending from the posterior choanal end to the anterior edge of the adductor cavity. The data on the mediochoanal row are not available, but it was undoubtedly present in *Kotlassia*. It is remarkable that, similar to the marginal teeth, large palatal teeth have longitudinally elongated bases, which gradually become more round posteriorly.

It is also noteworthy that the large teeth in the isolated ectopterygoid of *Kotlassia prima* from the Gorokhovets locality (specimen PIN, no. 4818/614) have flattened rather than conical apices.

The number of marginal teeth is unknown. Amalitskii (1921) indicated the presence of at least 20 mandibular teeth in *Kotlassia*. However, these data could concern *Kotlassia secunda* (*Karpinskiosaurus secundus*); this inference is supported by the presence of longitudinal ridges on the crowns. Fragmentary material from the Gorokhovets locality permits only a rough estimate of this character. In particular, the posterior half of the dentary fragment (PIN, no. 4818/615) contains 20 alveoli. Consequently, the total number of teeth in the lower jaw of adults should reach 35 to 40. This agrees well with the condition of correlative characters, i.e., the simplified structure of crowns and the posteriorly displaced jaw joint as compared to the majority of the Kotlassiidae.

Undoubtedly, the simplification of the *Kotlassia* teeth is a secondary transformation induced by returning to predation. The presence of large teeth on the lateral elements of the palate indicates a close relationship between *Kotlassia* and other kotlassiids.

By analogy with *Microphon*, one can propose with confidence that Kazanian kotlassiids (Leptorophinae) were characterized by a complicated morphogenesis of dentition as well. The morphology of the palatal dentition in *Biarmica* and ontogenetic data on *Microphon gracilis* and *M. exiguus* are indicative of the priority of the mediochoanal row formation in kotlassiid evolution. This agrees well with the priority specialization of the premaxillary teeth. Unfortunately, available material gives no way of studying the character of abrasion in vomerine teeth of the Kotlassiidae. The main functional significance of the mediochoanal row was possibly the protection of the choanae against food fragments when animals changed feeding adaptations from predation to herbivory (see below); this was provided mainly by cutting movements of the premaxillary teeth. The functional significance of the postchoanal teeth is more obvious; together with the maxillary and mandibular teeth, they belonged to a complex structure that permitted cutting (*Leptoropha*) or crushing (*Microphon*) feeding objects depending on the trophic specialization.

A study of the marginal teeth in *Microphon gracilis* and *M. exiguus* enables one to conclude that the development of polycuspid teeth was preceded by the formation of lateral denticles on the cutting edge. In kotlassiids, the lateral denticles were not formed by the ends of the ridges of the lingual side reaching the crown edge, as was proposed earlier (Ivakhnenko, 1987). In ontogenetic development, additional denticles of the first polycuspid teeth lack ridges; they appear later and develop initially only close to the apices of the denticles.

The dental system of seymourioids is only slightly modified compared to utegeniids. At the adult stage, all members of the family, except for *Seymouria baylorensis*, have about 30 teeth in the maxilla and about 40 in the dentary. Some Lower Permian genera (*Ariekanerpeton* and *Seymouria*) show a well-pronounced size heterodonty in the anterior regions of the jaws, similar to that of *Utegenia*. Within the palate, large teeth present only on the vomer and palatine, and specialized teeth rows are not formed, i.e., each bone usually has at most two or three teeth. On the parasphenoid, shagreen is limited to the region of the basipterygoid articulation and entirely absent from the parasphenoid rostrum. Within the pterygoids, toothed fields do not expand onto the quadrate rami.

The dental system of *Ariekanerpeton* is in general similar to that of utegeniids, except for the absence of shagreen dentition from the parasphenoid rostrum and quadrate rami of the pterygoids, which is a characteristic feature of seymouroids. The number of marginal teeth is large and their bases are round in cross section over the entire extent of the tooth rows. Two or three palatine teeth are in the typical positions medial and posterior to the choana. Another common feature is the presence of enlarged caniniform teeth in the maxilla and premaxilla, which is one of the basic differences from the close genus *Discosauriscus.* In the largest individuals of the latter genus, the longitudinal grooves developed on the external surface of the tooth bases sometimes reach the very top of crown apex (Klembara, 1995a). Such intensive development of the grooves is occasionally observed in *Ariekanerpeton* of similar size but has never been registered in kotlassioids in which the external grooves always terminate short of reaching the boundary of the enamel cover.

The dental system of *Seymouria sanjuanensis* is similar to that of *Ariekanerpeton* (Vaughn, 1966; Laurin, 1995). The jaw dentition of *Seymouria baylorensis* is intriguing, since the size differentiation of the upper jaw teeth is combined with a considerable decrease in the number of maxillary teeth (to 16–21 instead of 24–30 in *S. sanjuanensis*). It is remarkable that similar changes are observed in nycteroleterine parareptiles of the *Bashkiroleter–Macroleter* series and show a similar adaptation to feeding on larger prey. The presence of large premaxillary teeth in a weakened zone at the contact between the premaxilla and maxilla of *S. baylorensis* (Laurin, 1996a) remains improperly explained. In other seymouriamorphs with strongly developed size heterodonty, large teeth are in a more medial position; therefore, the main load during feeding is applied to the ascending processes of the premaxillae attached to the nasals (in this case, the processes are tightly connected to each other).

Among seymourioids, the serrated (tricuspid) crown structure is registered in only juvenile *Karpinskiosaurus ultimus*, being a larval adaptation of this species (see below). During the metamorphosis, probably occurring at the skull length 20–25 mm, the teeth were replaced by the unicuspid ones; this was accompanied by a further increase in their number to a normative 30 instead of 22 in larvae. In Early Permian karpinskiosaurids (discosauriscines), the ontogeny of which was examined on the basis of representative material (Ivakhnenko, 1981, 1987; Klembara, 1997), the tooth crowns retain a unicuspid structure throughout the life cycle (Klembara, 1995a).

The bases of the marginal teeth of Late Permian karpinskiosaurids are longitudinally elongated, similar to those of kotlassioids, and form wide buttresses; however, they retain thin walls. Probably, these features explain the changes in the plication pattern; i.e., the first folds are formed late in ontogeny at the midline of the lateral sides of the teeth and strongly project into the pulp cavity toward each other. Secondary folds appear later and are small in amplitude. This type of plication is a distinctive feature of karpinskiosaurines and occurs already in Early Kazanian members of the subfamily from the Ust'-Koin locality (Karpinskiosaurinae gen. indet.).

The simplified structure of the marginal tooth crowns in seymouroids complicates somewhat the application of dental morphology for taxonomy and identification of isolated jaw fragments.

Species of *Karpinskiosarus* may be identified with confidence by the extent to which the tooth apices curve lingually (unlike *K. ultimus*, in *K. secundus*, the apices are hooked). However, this character varies along the tooth row; the apices of the posterior teeth of *K. secundus* are only weakly curved.

It is noteworthy that the collection includes jaws from different Late Tatarian localities that are tentatively

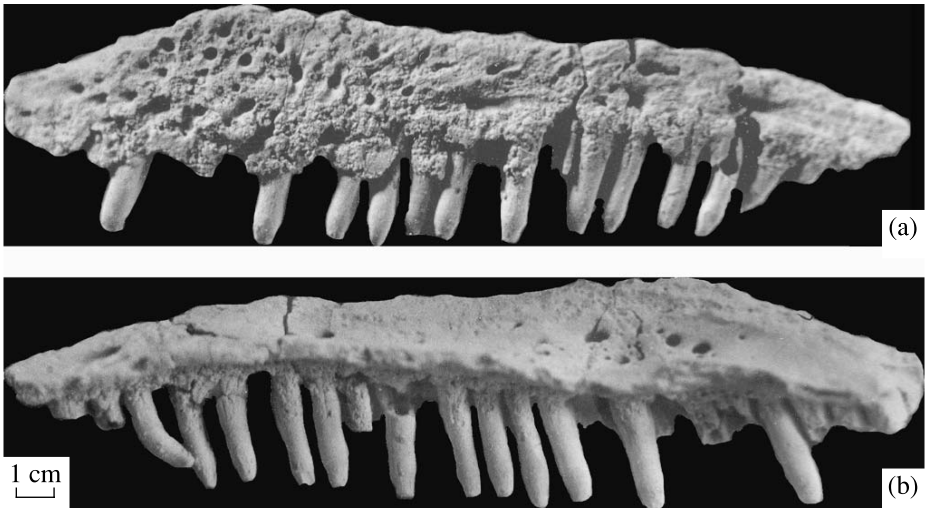


Fig. 44. *Karpinskiosaurus* cf. *ultimus*, left maxilla, specimen PIN, no. 3582/77: (a) labial and (b) lingual views.

attributed to *K. ultimus* on the basis of this character; however, they are distinguished by certain morphological features that are atypical of this species. Insufficient material and a lack of complete data on intraspecific and ontogenetic variability of the previously described *Karpinskiosaurus* species prevents description of new taxa.

A maxilla from the Aristovo locality (specimen PIN, no. 3582/77; Fig. 44) contains teeth with slightly inflated basal regions of the crowns having somewhat higher apices and covered lingually by numerous sharp ridges. On the contrary, in *Karpinskiosaurus* from the Sambullak locality (holotype *Kotlassia grandis*), the apical teeth parts are low and wide with widely spaced ridges and well-developed cutting edges (Fig. 45).

Fig. 45. *Karpinskiosaurus* cf. *ultimus*, rudimentary marginal tooth, specimen SGU, no. 104B/165 (holotype *Kotlassia grandis*), dorsal view.

The morphological analysis of the dental system of seymouriamorphs revealed that it is an integral, multicomponent, and well-adaptable mechanism. The processes responsible for the development of marginal and palatal dentition are undoubtedly closely interrelated in seymouriamorphs, especially in kotlassiids. This is manifested in simultaneous development of similar conditions in the marginal and palatal teeth of similar size. Thus, the crowns of the palatal teeth are thickened to the same extent as the nearest maxillary ones and have a similar distribution and shape of the ridges on the lingual side (or similarly lack such ridges, as in *Kotlassia*). As in the marginal teeth, in the postchoanal row, the tooth size gradually decreases posteriorly, sometimes changing in a similar way the shape of their bases from elongated oval to round in cross section (*Kotlassia*).

The complex morphogenesis of dentition in kotlassiids is based primarily on the larval adaptations. This is supported by a considerable divergence in morphology of the marginal teeth between different *Microphon* species even at early developmental stages, caused by the adaptation to rather different trophic factors. Ontogenetic changes in the marginal teeth of *Karpinskiosaurus ultimus* are also indicative of the high potentialities to reorganization of the marginal teeth in the larval period in seymouriamorphs.

The dental morphology of seymouriamorphs is of primary importance for the systematics of the group, especially taking into account the direct relationship between the morphology of the marginal teeth and certain structural features of the dermatocranium (the shape of the maxilla and its relations with adjacent elements, the presence or absence of the premaxillary fontanel, the degree of development of the coronoid process, the position of the jaw articulation, etc.). At the same time, a considerable ontogenetic modification of the dental system complicates its application for the identification of the taxa. In some cases, a comparison of individuals of similar size is required as well as the presence of necessary samples that permits one to ascertain the normative condition of a character and the range of its variability. The complete data on the variation pattern enables one to distinguish between closely related species and determine the forms represented by isolated specimens. This seems to be especially important for studying the fauna from the localities with an allochthonous burial type. The pronounced adaptive significance of dentition should be taken into account in phylogenetic elaboration, since many characters may develop independently in the course of adaptation to similar trophic niches or be a result of a recapitulation.

Surface Ornamentation

On the external side of membrane bones of the skull roof and lower jaw of seymouriamorphs, the surface ornamentation develops in the course of ontogeny. In general, it has much in common with that of anthracosauromorphs and tempospondyls. It is formed gradually and passes through a set of successive developmental stages. The bones substantially differ from each other in the moment of emergence and the rates of development of surface sculpturing; even at the definitive stage, these distinctions are rather prominent. Large bones characterized by high growth rates show clear trends in the changes of surface sculpturing from the central parts to the bone margins; therefore, differences in ornamentation are often observed even within the same bone.

Some bones remain only slightly ornamented throughout the entire ontogenetic cycle; in particular, this concerns the upper and lower jaw bones containing marginal teeth. On the lacrimal, the development of sculpturing is usually slowed down; among the lower jaw bones, the surangular lacks sculpturing or is only weakly sculptured.

At the larval stage, the external surface of membrane bones is almost smooth and complicated by only narrow radially oriented furrows for blood vessels that originate from the foramina accumulated mainly at the ossification centers. The initial stages of the relief formation are similar in all seymouriamorphs; the juveniles of which are present in the collections under study. Surface ornamentation first appears in the zone around the domed ossification center and looks like flattened ridges located in the spaces between furrows and, along with the latter, showing radial orientation. Within this zone, the foramina for blood vessels are located in superficial depressions.

This ornamentation pattern is observed in some large *Utegenia shpinari* (having 24-mm-long or longer skulls); however, it is especially well-pronounced in *Ariekanerpeton* where, at approximately the same size, the blood vessel furrows covering the bone are substantially more numerous and longer; the number and length of primary ridges are correspondingly increased. The ridges also appear in the marginal zones of relatively small bones forming the occipital edge and the orbital rim; in kotlassioids, these features are not observed.

In the course of kotlassiid evolution, the ornamentation pattern prevailing at the definitive stage gradually changed.

Thus, in the Leptorophinae (*Leptoropha* and *Biarmica*), the skull roof is predominantly covered by high radially oriented ridges (radial ridged pattern) developing by an increase in the height of primary ridges. The ridges are especially well developed in the marginal zones of large bones of the axial region of the skull (parietals, frontals, and nasals); in the central regions of these bones, the relief is mainly composed of separate tubercles (tuberculate pattern). The tubercles are formed by both the division of ridges (having a tuberculate surface) by transverse furrows and independently of the ridges (e.g., around the ossification centers and on small membrane bones where the true radial ridged relief is not formed). In the ossification centers of *Leptoropha*, adjacent tubercles sometimes fuse with each other (Pl. 5, fig. 2)

The development of surface ornamentation in the ontogeny of *Microphon exiguus* follows the evolutionary changes of earlier kotlassioids. In juveniles, the relief appears on membrane bones of skulls at least 23 mm in length and is generally identical to that of *Utegenia* of the same size. At this stage, the development of surface ornamentation is only slightly asynchronous; a weak relief is observed on the majority of bones of the skull roof.

The preservation of the radial ridged relief on the quadratojugal of adults (specimens PIN, nos. 3713/53, 75; Pl. 8, figs. 4, 5) and reduced ridges on the margins of the parietals (specimen PIN, no. 3713/61) and squamosal (specimen PIN, no. 3713/75; Pl. 8, fig. 6) are evidence for the presence of this stage in the ontogeny of *M. exiguus*. Apparently, this stage of relief formation was very short and ridges were divided into tubercles at a high rate. In the fragmentary skull roof of *Microphon* sp. (specimen PIN, no. 4620/1) from the Ust'-Elva locality, the final stage of this process is observed; isolated pectens cover all preserved membrane bones, including the marginal zones of the parietals (Fig. 46). However, the skull roof of adult *M. exiguus* is mainly covered by the relief of the joint tuberculate pattern composed of short ridges of irregular shape and random orientation and formed as a result of linkage between tubercles. The asynchrony of this process manifests itself in different rates of fusion between tubercles on different bones. In particular, on the bones forming the occipital edge, tubercles are only weakly fused, whereas on the parietals and supratemporals, the fusion results in places in the formation of cells (cellular pattern). This pattern undoubtedly prevails in *Kotlassia*, since it is observed on those elements of the skull roof

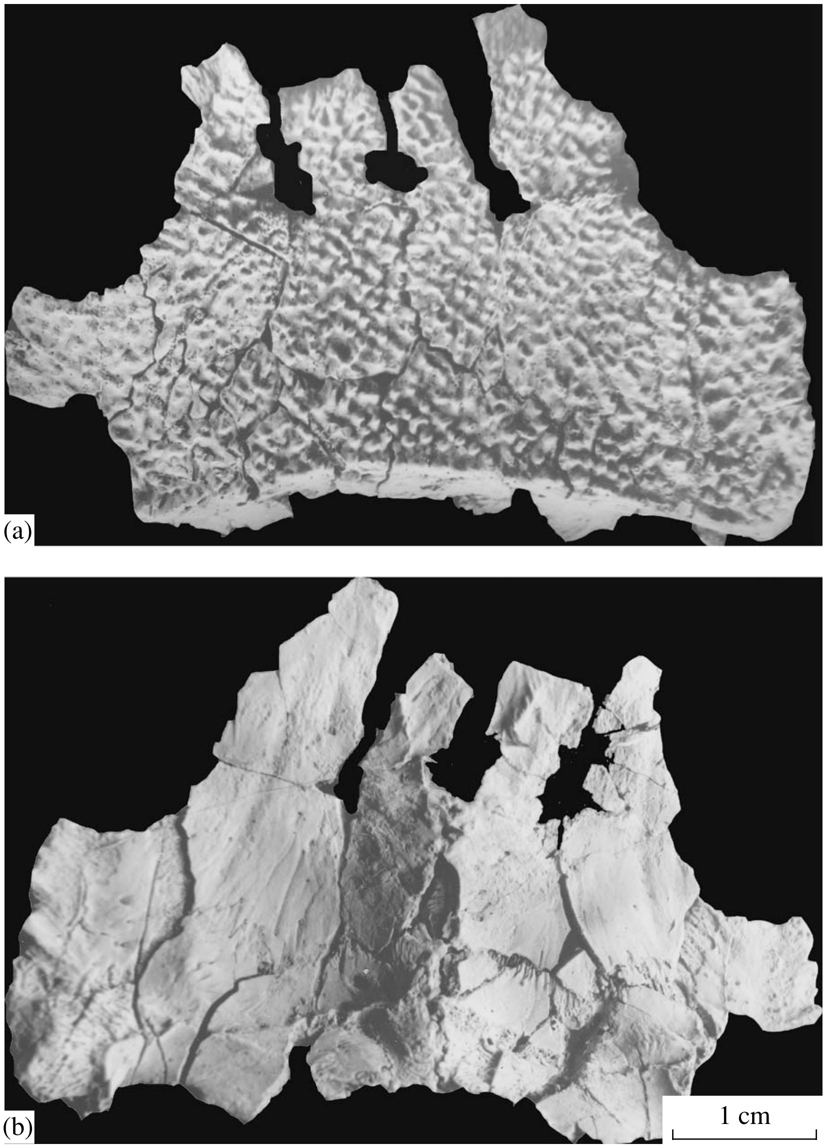


Fig. 46. *Microphon* sp., fragmentary skull roof, specimen PIN, no. 4620/1: (a) dorsal and (b) ventral views.

where, in *Microphon*, the changes of relief are slowed down (tabulars, prefrontals, and lacrimals).

Among seymourioids, the tuberculate stage of ornamentation is observed in only *Ariekanerpeton* (in the skulls at least 30 mm in length), in which this is the final stage of modification of the external surface of the skull roof. Since the tubercles are associated with reference to their positions with the radial ridges, they are isolated from each other to a lesser degree than in kotlassiids. In places, but only locally, the fusion between individual tubercles is observed. Even in the largest animals, the marginal zones of bones retain the radial ridged relief.

The features of the surface ornamentation of *Ariekanerpeton*, in particular, the presence of the tuberculate stage, are the basic distinctions between this genus and *Discosauriscus*; this indicates a greater primitiveness of *Ariekanerpeton*.

In *Discosauriscus*, the relief changed at an extremely high rate, bypassing the tuberculate stage; small depressions emerged near the exits of blood vessels between the primary radial ridges and subsequently became polygonal cells. Large members of the genus *Discosauriscus* show a well-pronounced cellular relief on the majority of cranial membrane bones (Klembara, 1995a).

The cellular pattern also prevails on the skull roof of other seymourioids. In *Karpinskiosaurus ultimus* which has 40-mm-long skull, the majority of membrane bones are already covered by well-pronounced small cells; in the peripheral zone of the bones, the cells become longer. Extended ridges are observed on only

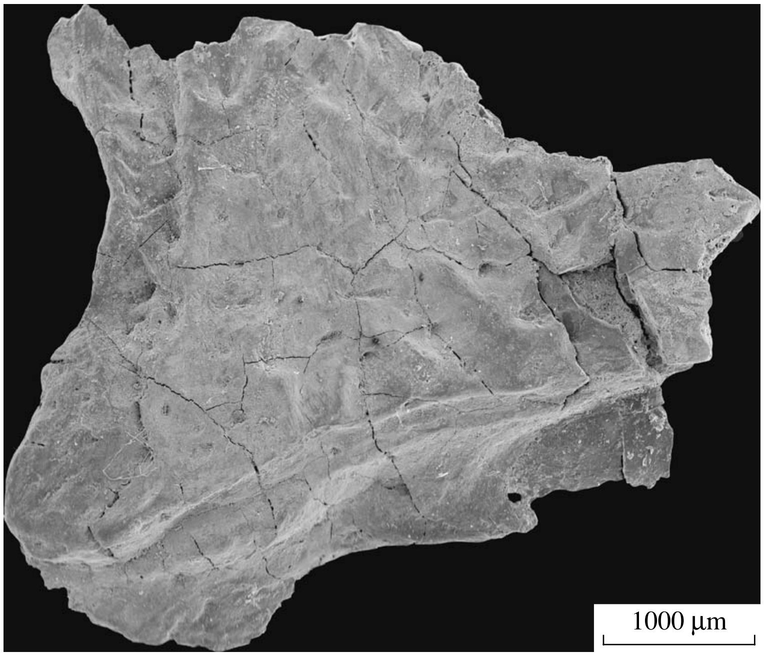


Fig. 47. *Karpinskiosaurus* sp., left tabular, specimen PIN, no. 4538/4, dorsal view.

the quadratojugal and angular. The data on *K. secundus* show that, in karpinskiosaurs, these regions retained the same pattern of sculpturing up to the definitive stage.

The membrane bones of adult *Seymouria baylorensis* are covered exclusively by the cellular relief. In the occipital region (postparietals and tabulars) and, to a lesser extent, in the temporal region (intertemporals and supratemporals), the cells are substantially larger (Laurin, 1996a). This is the only taxon in which the upper jaw arch and almost the entire external surface of the lower jaw are strongly sculptured; only the alveolar margin of the dentary, the upper part of the surangular, and a small area located ventral to the angular crest (attachment area for the pterygoid muscles) are free from surface sculpturing.

Thus, one can conclude that the final result of evolutionary changes of surface ornamentation in each seymouriamorph superfamily is the formation of cellular relief. In kotlassioids, this process is directional and gradual in both the evolution of the group and the ontogeny of its late members; this is clearly illustrated by a continuous series of transitional states that appear consecutively at appropriate evolutionary levels. When compared to batrachomorphs, kotlassioids show a great similarity in the development of surface ornamentation to the neotenic Dvinosauridae (Shishkin, 1973).

In seymourioids, the cellular relief is formed at a substantially higher rate; in the ontogeny, it develops without transitional stages in the majority of taxa, except for the most primitive forms, such as *Ariekanerpeton* lacking cellular sculpturing. In the course of evolution, the cellular relief appeared even in Early Permian dvinosauriscines and seymouriids; moreover, in the latter group, it is manifested to the maximum extent.

Seismosensory System

The presence of the seismosensory system is a character distinguishing seymouriamorphs from other parareptiles. The development of the lateral line organs demonstrates a close relationship with an aquatic environment and indicates the amphibian level of organization and the presence of a larval ontogenetic stage.

Every kotlassioid form (except for *M. arcanus* described on the basis of extremely fragmentary material) has been shown to retain the lateral line system at the definitive stage, i.e., is adapted to the aquatic mode of life. In this connection, it is worth noting that additional (newly formed) segments of the lateral line grooves are marked in members of this superfamily only (*Utegenia*, *Microphon*, and *Biarmica*). Among seymourioids, on the contrary, the lateral line system is usually partially [*Discosauriscus*, see Klembara (1997)] or completely (*Seymouria* and *Karpinskiosaurus*) reduced at the definitive stage. The presence of the seismosensory system at the early ontogenetic stages of *Seymouria* is evidenced by the preservation of rudimentary grooves below the orbit in some species of this genus (Vaughn, 1966; Laurin, 1996a). The absence of grooves on the skull roof of larval *Karpinskiosaurus ultimus* is most likely attributable to incomplete preservation of specimens and the underdevelopment of surface relief. This inference is corroborated by the presence of a seismosensory groove that is clearly visible against the background of well-developed relief on an isolated tabular of juvenile *Karpinskiosaurus* sp. from the Vozdvizhenka locality (PIN, no. 4538/4; Fig. 47). At the definitive stage, karpinskiosaurs lack a trace of seismosensory grooves on the surface of the skull roof.

The lateral line system is probably reduced in seymourioids in connection with the adaptation to the semiterrestrial mode of life and mastering of the near-water biotopes.

The preservation of the seismosensory system in Recent amphibians is marked in only resident aquatic urodelans, the seismosensory placodes of which are located in soft tissue and do not leave a trace on membrane bones. In the ontogeny of seymouriamorphs, as in many Paleozoic amphibians, the lateral line organs were gradually immersed in the bones of the skull roof; this process developed nonsynchronously in various regions of the dermatocranium.

The positions of seismosensory grooves on the skull roof usually follows the same standard, although certain variations are observed at the point of transition from the supraorbital groove to the postorbital commissure and in the position of the temporal branch of the supraorbital groove. In addition, a number of kotlassioids develop supplementary groove segments.

In the majority of forms, the supraorbital groove emerges at the contact between the nasal and the dorsal process of the premaxilla. *Discosauriscus* shows a short ethmoid commissure on the premaxillae (Klembara, 1997). It is highly plausible that a groove occurred in this position in other seymouriamorphs characterized by a well-developed seismosensory system. However, these elements are not preserved in some species (*Leptorophа* and *Kotlassia*); in others, they are well represented only at the early developmental stage (*Microphon*) when imprints of the commissure are probably not formed.

Within the nasal, the supraorbital groove extends along the upper wall of the naris slightly anterior to, or through, the ossification center. As the groove comes onto the prefrontal, it curves abruptly and forms a well-pronounced flexure whose size depends on the width and length of the preorbital region; the flexure is especially large in *Microphon* characterized by a short and broad skull at all ontogenetic stages. At the point of maximum curvature, the supraorbital groove usually comes onto the dorsally projecting region of the lacrimal.

In the prefrontal segment of the canal, a number of forms (*Utegenia, Microphon gracilis, M. exiguus*, and *Ariekanerpeton*) have a large foramen accompanied by an anteriorly oriented furrow that usually passes onto the nasal. This foramen provides passage for the superficial ramus of the ophthalmic nerve innervating the anterior region of the supraorbital groove.

When passing above the orbit, the supraorbital groove in all cases comes onto the external margin of the frontal. In *Utegenia*, it extends relatively far and covers a significant area on the lateral flank of this bone. As the main branch occupies such a position, an additional groove extending along the orbital rim close to its edge is occasionally presented in *Utegenia* as a form of individual variation. In *Microphon*, which has wider prefrontals and postfrontals, this groove comes onto the frontal as a small segment located in the region of the contact between these bones.

In *Utegenia* and discosauriscines, the supraorbital groove passes through the postorbital and intertemporal and continues without gaps to form the postorbital commissure. This is the primitive condition; as a form of individual variation, it occurs in *M. exiguus*. Normally, in *Microphon exiguus* and *M. gracilis*, the groove passes onto the parietal, where it is broken, and appears again only on the intertemporal. The infraorbital groove is also broken at the point where it passes onto the intertemporal (specimen PIN, no. 3585/92); in the lateral part of this bone, a groove connected to the postorbital commissure is clearly seen. This gives the impression that, in this case, deviation of the groove toward the parietal is associated with a break of the seismosensory canal so that its anterior and posterior parts have lost contact with each other.

The position of the temporal branch of the supraorbital groove is variable. The branch is usually connected to the occipital commissure in the upper (medial) part of the postorbital; however, in *Utegenia*, this contact is sometimes observed on the intertemporal. In *Utegenia* and *Microphon gracilis*, the groove sometimes occurs on the external margin of the intertemporal; in *Discosauriscus*, this is probably the normative position of this groove (Klembara, 1994b). However, the groove can deviate from this standard and pass onto the caudal process of the postorbital (*Utegenia*) or on the suture between the intertemporal and the squamosal (*M. gracilis* and *M exiguus*). On the supratemporal, the canal usually extends along the edge of the otic notch; only in *Utegenia*, does it curve medial to the central part of the bone because of the specific shape of the tabular.

The passage of the infraorbital groove is rather uniform. It emerges in the posterior part of the lacrimal and passes posteriorly below the orbit onto the jugal where it is always distinctly pronounced. It is particularly remarkable that, exactly in this area, rudimentary seismosensory structures are preserved in *Seymouria*. In juveniles, this area shows a system of deep lacunae associated with the passage of nerves and blood vessels; in the course of further development, they are enveloped by the bone, the surface of which retains a longitudinal groove. Within the squamosal, the infraorbital groove passes round the ossification center and, coming to the edge of the otic notch, extends toward the quadrate–articular articulation. In *Microphon exiguus*, the squamosal has an additional branch that passes lateral to the main branch and fuses with the latter in two points, in the posterior part of the squamosal and the postorbital region of the jugal.

The lower jaw has only one seismosensory canal varying in position. In *Discosauriscus*, it originates from the posterior margin of the angular and extends anteriorly immediately above the angular crest; subsequently, it passes onto the postsplenial and splenial. The dentary lacks lateral line grooves (Klembara, 1997). The mandibular groove of juvenile *Microphon exiguus* emerges near the border of the surangular and extends substantially above the angular crest; from the postsplenial, it passes onto the dentary; at the anterior end of the latter bone, it abruptly curves dorsally. The same position of grooves is observed within this area in *Biarmica*, *Leptoropha*, and large *M. exiguus*.

In ontogenetic development, the lateral line grooves on the skull surface of seymouriamorphs gradually form an integral system. The seismosensory placodes developed and differentiated within the thickness of the soft tissue, as in Recent amphibians. They immersed and reached the surface of membrane bones only after the canals were completely formed, and this process developed nonuniformly in different regions of the dermatocranium. This is evident from the study of juvenile *Microphon exiguus*; initially, only isolated segments of grooves are printed on the bones, whereas an integral network of grooves is formed later. This is closely associated with the development of surface ornamentation, the presence of which largely determines the possibility of detecting the positions of seismosensory structures.

In the absence of surface ornamentation, larvae show only weak imprints of the primary canals on membrane bones; since the rates of their immersion in different sites are nonuniform, the grooves initially appear as broken lines. As a weak surface relief appears, the network of grooves on the skull roof becomes distinct on almost all bones where it occurs; sometimes, this network is completed even at the stage preceding the formation of surface sculpturing (*Microphon*).

At later ontogenetic stages, elements of surface ornamentation appear inside the grooves; as a result, the grooves become less prominent; this complicates the identification of these structures in the specimens with strongly damaged membrane bone surfaces, in particular, in *Biarmica* and *Leptoropha*. At the definitive stage of *Leptoropha*, the positions of the primary grooves are occupied by high and partly fused tubercles. The preservation of seismosensory structures on these sites is evidenced by a considerable accumulation of foramina for nerves and blood vessels, since such accumulations are not observable in the sites where the seismosensory canals are absent in the normal state (specimen PIN, no. 161/105). In *Microphon exiguus*, the grooves are rather distinct because of relatively good preservation; they also contain separate high tubercles or are divided into separate cells by cross bonds arising between them (specimen PIN, no. 3713/60).

The features and arrangement of grooves on the skull roof of juveniles indicate that, initially, the seismosensory canals composed a morphologically and functionally integrated system. As the ornamentation developed on the surface of the grooves, the system should almost inevitably be divided into separate segments performing the registration of fluctuations independently of each other. Apparently, this decreased the ability of perception but increased the stereoscopic effect, which probably provided adaptation for existence in muddy waters. It is remarkable that Recent urodelans show essentially the same structure of seismosensory organs. Seymouriamorphs inherited such a structure from anthracosauromorph amphibians, the definitive state of which always shows well-developed relief on the surface of the lateral line grooves. On the contrary, in batrachomorphs, this feature occurred as a rare exception, e.g., in the Permian Melosauridae (Gubin, 1991), whereas in most cases, the seismosensory grooves were entirely smooth and contained continuous canals.

In addition to the grooves of seismosensory canals, the skull roof of seymouriamorphs often has special foraminate pits associated by some researchers with electrically sensitive organs (Klembara, 1992, 1994b). The system of these pits was examined in detail in *Discosauriscus austriacus* on the basis of extensive material from Moravian localities. In this species, the foraminate pits are observed on almost all membrane bones of the skull roof and the dentary (Klembara, 1994b). The presence of similar structures in similar positions was also marked in some other members of the order, in particular, in *Utegenia*. In this form, a large pit is almost always observed on the supratemporal at the transition point from the supraorbital groove to the occipital commissure. In addition, Malachov (2000a) marked the presence of similar pits on the frontal and postfrontal of *Utegenia*, where their positions are also associated with the lateral line grooves (using available material, I failed to register the presence of foraminate pits on these bones).

In *Ariekanerpeton*, the foraminate pits are observed on the postfrontal and tabular only; this is most likely attributable to incomplete preservation of the specimens under study. At the same time, it is highly plausible that these structures developed in *Ariekanerpeton* to the same extent as in *Discosauriscus*. They are also preserved in karpinskiosaurids, in particular, on the postfrontal of *Karpinskiosaurus ultimus* (PIN, no. 4617/158) and, in juvenile *Karpinskiosaurus* sp. from the Vozdvizhenka locality (PIN, no. 4538/4; Fig. 47), in the lateral part of the tabular at the transition from the temporal branch of the supraorbital groove to the occipital commissure (it is worth noting that, on the tabular of *Discosauriscus*, the pit is located in the central region of the bone). Among kotlassiids, similar structures have been marked in only adult *Microphon exiguus*; this is primarily associated with the poor preservation of specimens of the other genera of the family. In this case, pitted structures are present on the tabular and squamosal; on the squamosal, a pit (or, more precisely, an oblong depression) is located outside the seismosensory groove, adjoining it medially. In *Discosauriscus*, the absence of contacts between the foraminate pits and the seismosensory grooves is often marked on membrane bones of the axial skull region, in particular, on the parietals where the grooves are absent in the standard state.

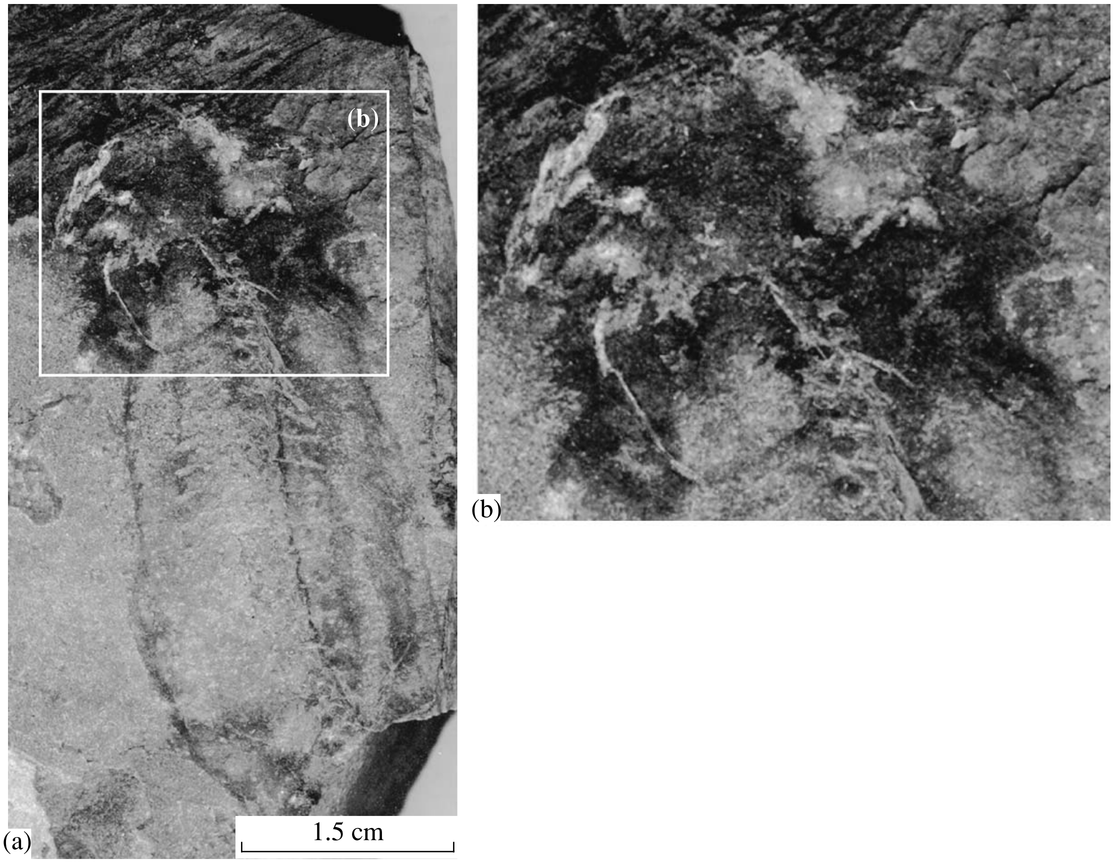


Fig. 48. *Ariekanerpeton sigalovi*, imprint of larva, specimen PIN, no. 2079/755: (a) general appearance and (b) area with imprints of branchiomeres, magnified.

CHAPTER 6. ECOLOGY

Physiologically, seymouriamorphs are amphibians, since their reproduction and mode of life are closely related to the aquatic environment. The presence of the larval stage in these animals is supported by the finds of discosauriscines with clear imprints of external gills. By analogy with living amphibians, one can propose that seymouriamorphs had three branchial pairs. The skull of the largest individual of *Discosauriscus austriacus* with branchiomeres is a little larger than 30 mm in length (Klembara, 1995a). In the collection under study, distinct imprints of external gills are observed in some larval *Ariekanerpeton* with the skull at most 15 mm long (Figs. 48, 49). Larger animals lack clear traces of these structures; nevertheless, it is quite possible that the bituminous elements in the cervical region of large individuals (e.g., the holotype, PIN, no. 2079/1) are imprints of the opercular fold, the presence of which suggests breathing with the use of the branchial apparatus. Ivakhnenko (1981) indicated that the external gills and traces of nonossified branchial arches are observed in *Utegenia shpinari* and other seymouriamorphs. It is now known beyond doubt that *Utegenia* had a gill-breathing larval stage; however, I failed to detect clear imprints of branchiomeres in the available material.

The fact that seymouriamorphs had a larval stage is corroborated by the presence of grooves of the lateral line system on the skull roof surface of the majority of these animals. In the course of seymourioid ontogeny, the lateral line organs are partially or completely reduced. On the *Seymouria* skull, only rudimentary seismosensory grooves are sometimes preserved under the orbit. In almost all known karpinskiosaurs, these grooves are completely absent; an exception is provided by juvenile *Karpinskiosaurus* sp. from the Vozdvizhenka locality (Fig. 47); this suggests the transition to a facultative terrestrial mode of life.

The analysis of dental morphology, using the data on the extant analogues, allows one to discover trophic relationships of seymouriamorphs and to show their position in the communities of terrestrial vertebrates. The peculiarity of the dental system *in toto*, consisting in specific marginal and palatal dentition, a multicomponent composition, and a wide ontogenetic variability, gives no way of finding direct equivalents in the Recent faunas, including living amphibians. The data on lizards are mainly used for reconstruction, because their considerable ecological diversity greatly simplifies the problem and shows certain similarities in particular

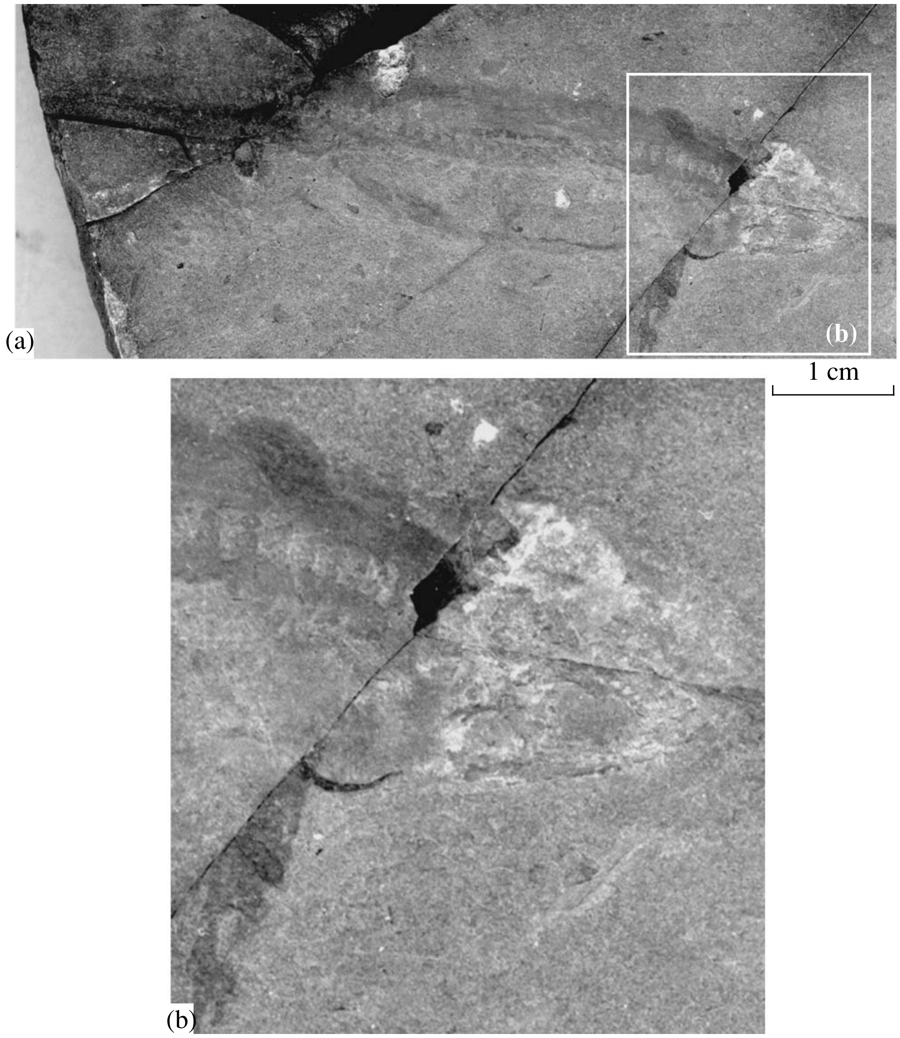


Fig. 49. *Ariekanerpeton sigalovi*, imprint of larva, specimen PIN, no. 2079/719: (a) general appearance and (b) area with imprints of branchiomeres, magnified.

components of the jaw apparatus if not in the entire apparatus as an integral functional system.

The results obtained by such comparison may only be of a qualitative character, considering the characteristic features of either group. The reconstruction of particular trophic connections necessitates additional analysis of all fossils from localities, which is hardly practical because of selective nature of fossilization.

The dental morphology of the most primitive Early Permian seymouriamorphs shows that they led a predatory mode of life, as did all other Carboniferous anthracosauromorphs, displaying similar marginal and palatal dentition. Usually, *Utegenia shpinary* and *Ariekanerpeton sigalovi* do not co-occur with other faunal elements; this is evidence for feeding of these animals on soft or chitinized invertebrates, which agrees with the relatively small sizes of these animals. Insects occur in the oryctocoenoses from the Moravian beds including *Discosauriscus austriacus* (Kochov); in these localities, they are confined to the layers most abundant in tetrapods. The Holosteimorpha similar to *Paramblypterus* are registered in the same layers (Klembara and Meszaros, 1992); however, they show a wider range in the section and are comparable in size to *Discosauriscus*; therefore, they are excluded from the list of the main food objects. Undoubtedly, fish young could serve as an additional food source for large *Discosauriscus* for which cannibalism was theorized (Klembara and Meszaros, 1992), but its presence in the ration of larvae is unlikely. In general, the dentition of Moravian forms looks substantially less specialized than that of *Ariekanerpeton* owing to the absence of pronounced size differentiation of the maxillary teeth. Feeding on fish should be excluded for *Ariekanerpeton* by virtue of the taphonomic data, i.e., the complete absence of fish remains in the type locality. Late Permian karpinskiosaurids were mainly invertebrate-eaters as well. The morphology of the marginal teeth in *Karpinskiosaurus ultimus* indicates the inability of capturing relatively large prey; consequently, aquatic invertebrates were the principal food objects for this form. The teeth of postmetamorphic *K. ultimus*, with flattened unicuspid crowns and transversely widened bases, resemble in appearance those of certain living geckos (such as *Gekko* and *Coleonyx*), which are mainly insectivorous lizards. Similar to the Karpinskiosauridae, geckos, with small forms in particular, possess isodont dentition with a large number of marginal teeth (up to 40 in the maxilla and 46 in the dentary of *Coleonyx variegatus*; however, the majority of other species have a smaller number of teeth) and a high replacement rate, to judge from the presence of numerous rudimentary replacement teeth (Vorob'eva and Chugunova, 1995).

The hooked marginal teeth of *Karpinskiosaurus secundus* show the necessity of holding active prey. Possibly, unlike *K. ultimus*, one of the main feeding objects of this animal was small fish (remains of the Paleoniscidae are registered together with this form in all localities: Sokolki, Adamovka Blumental 3, and Gorokhovets). A generally weak specialization implies a wide range of potential prey. By the shape of crowns and homodont dentition, *K. secundus* resembles Recent *Cryptobranchus* (*Megalobatrachus*), feeding mostly on river invertebrates.

The dentition of *Seymouria sanjuanensis* is almost identical to that of *Ariekanerpeton.* The excessively developed teeth in the preorbital section of the maxilla of *Seymouria baylorensis* is undoubtedly an adaptation for capturing relatively large prey, fish or small terrestrial vertebrates. The latter seems more probable, because the marginal teeth of this form are analogues of those of the nycteroleterine parareptile *Macroleter poezicus* from the Mezen Faunal Assemblage of Eastern Europe, the main feeding object of which is evident, primitive procolophons of the family Nyctypruretidae (*Nyctypruretus acudens*). A curious feature of all Mezen localities, despite the fact that they are well understood, is the absence of fish remains. This is very unusual for the Permian beds of European Russia and accounts for the entire lack of specialized fish-eaters in the Mezen Fauna. The specific character of the oryctocoenosis permits the exclusion of vertebrates from the preferred food objects of small nycteroleterine parareptiles from the same localities, *Nycteroleter ineptus* and *Bashkiroleter mesensis*, which are basically similar in marginal dentition to *Seymouria sanjuanensis*; they feed mainly on invertebrates.

The diverse dental morphology of the Kotlassiidae indicates a wide range of consumed food. The presence of symmetrically serrated crowns in the Leptorophinae is an adaptation to phytophagy; this feature is characteristic of the marginal teeth of the majority of herbivorous lizards, most of which belong to the family Iguanidae. The presence of supplementary denticles in the Lacertilia is a widespread feature registered in many insectivorous forms, feeding on plants only occasionally. However, the morphology of their teeth differs from that of herbivores by the narrow crowns and their pronounced asymmetry manifested in either the development of the denticles on only the anterior side of the crown or the different extent of their development on the anterior and posterior sides (*Lacerta strigata, L. pratocola, Eremias arguta*, and *E. grammica*). It is remarkable that, even in this case, vegetable fragments are regularly met in the gastric content of some lacertids; in *E. grammica*, they compose up to 15% (Vorob'eva and Chugunova, 1995). There are also data on the obligate herbivory of some lacertids, in particular, *Gallotia simonyi*; however, tricuspid crowns of this form are widened and symmetric.

The development of polycuspid teeth in specialized phytophagous lizards was undoubtedly based on the crown of the advanced insectivorous type with one or two (mainly large) supplementary apices aimed to assist in crushing chitinous fragments. On the other hand, the realized structure appears suitable for seizing and cutting plants. This is supported by the universal character of such teeth: tricuspid crowns are used by both insectivorous (*Cyclura macleayi* and *Basiliscus*) and herbivorous (*Leiocephalus, Gallotia simonyi*, and *Amblyrhynchus cristatus*) lizards (Vorob'eva and Chugunova, 1995). The acquisition of polycuspid teeth undoubtedly took place independently in different lacertilian families, but further specialization, i.e., the development of wide and flat crowns with numerous denticles, is observed only among the Iguanidae (Queiros, 1987). It should be remarked that a principally similar morphology of the marginal teeth develops independently in the evolution of very different groups and is observed in animals who were not assumed to have a predatory mode of life, such as the Pareiasauridae, many of the Pelycosauria, Ornitischia, etc. (Ivakhnenko, 1987; Reisz and Suez, 2000; Weishampel and Jianu, 2000).

It is noteworthy that the optional utilization of animal food by lizards cannot be an obstacle to the development of the fundamental adaptation, determined by the main feeding object. Heterodonty, well pronounced in all lizards, implies differentiation of the teeth in conformity with their function and the ability to consume different food. Hence, a full assortment of possible food objects is defined by the morphology of dentition as a whole, while a group of properly specialized teeth is responsible for the consumption of particular types of food. This allows one to draw analogues between the extant and extinct forms.

Among the Kotlassiidae, *Leptoropha* exhibits the most pronounced adaptations for herbivory. The marginal teeth of this form have symmetrically enlarged crowns provided with flat apical parts and large supplementary denticles. A strong lingual inclination of apices is connected with the holding of a vegetable mass and practically excludes the effective use of teeth for other purposes. A total absence of any wear signs indicates consumption of very soft food, possibly, certain groups of algae, together with which different invertebrates were caught, serving as a source of necessary animal proteins. Evidently, this explains the development of the additional (postchoanal) tooth row in the course of Kotlassiidae evolution, permitting the rational utilization of this resource as well.

Biarmica is an initial step of specialization in this direction. The dental morphology suggests the domination of vegetable food in its diet. Although the proportion of animal food seems to be relatively large as compared to *Leptoropha*, the absence of a well-developed postchoanal row of palatine teeth prevented the utilization of organisms with sufficiently hard integument.

The ontogenetic reorganization of dentition discovered in the *Microphon* species shows the changes in the nature of the main consumed food during the life cycle.

Larval *M. exiguus* was a predator; this is obvious from the morphology of the marginal tooth crowns, which are simple conical like those of the Utegeniidae, or, more frequently, are equipped with projections on the cutting edge; in the subsequent generations, these projections become lateral denticles. In the latter case, the crown is asymmetrical because of the stronger development of the anterior cutting edge and larger dimensions of the denticle on the anterior side. The same structural pattern is characteristic of entomophagous lacertids (Vorob’eva and Chugunova, 1995). It was acquired by the Kotlassiidae because of the need for an increase in the efficiency of dentition at early ontogenetic stages, when the number of marginal teeth was small. This was especially important for the Kotlassiidae because of the underdevelopment of the marginal teeth characterized by a low rate of the increase in tooth number. The presence of such stage indicates that the dentition of specialized phytophagous seymouriamorphs developed as a result of absolutely definite modification of dentition of the predatory type, similar to that of lizards.

The heterodonty, well developed in adult *M. exiguus*, allowed these animals to use a wide range of food objects. Thus, the premaxillary teeth with their high and wide crowns equipped with serrated cutting edge were used primarily for seizing and cutting aquatic vegetation. The maxillary teeth and the opposed teeth in the dentary with weakly developed supplementary denticles as well as large palatal teeth of the postchoanal row with conical apices constituted the integral functional mechanism, which permitted effective holding and crushing of such objects as insects with hard integument, conchostracans, thin-shelled mollusks, etc. This is supported by frequently observed wear marks on the tooth crowns in juveniles and adults, which are expressed in blunt central apices, smoothed supplementary denticles, and wear of ridges on the lingual tooth sides. A tendency of *M. exiguus* to sclerophagy at late developmental stages is especially evident in large individuals from the type locality, especially in the dentary PIN, no. 3585/26, in which the teeth formed a part of crushing mechanism and the tooth apices became flattened and rounded as a result of wear. Similarly worn crowns were found in the Poteryakha locality as well.

The data on the jaw morphology in *Microphon gracilis* at late developmental stages are not available. In juveniles, the marginal teeth differ from those of *M. exiguus* of the same size by thickened basal regions of tooth crowns, more strongly developed lateral denticles, and only slightly thickened but higher central apices. In the majority of completely developed teeth, the apex is blunted by wear (sometimes, strongly worn), and its participation in crushing hard objects is almost beyond question. A large amount of thin conchostracan shells that could be the main prey were found together with tetrapods in the Babintsevo locality. There is no doubt that large teeth from the lateral palatal elements participated in this process; however, the data on their morphology and distribution are not yet complete. It is necessary to remember the presence of very large coronoid teeth in *Microphon gracilis*, which, being antagonistic to the postchoanal teeth, could perfectly assist in the fixation of crushed objects.

Vegetation was the second important component of the *M. gracilis* diet at early stages. This is evident from the good development of lateral denticles, which are more pronounced than those of *M. exiguus* of similar size.

The dentition of *Kotlassia* is close to the initial morphotype because of its secondary simplification. This is accounted for by the return to predation, and the large size of this animal suggests that it was most likely ichthyophagous. Indirect evidence of this is the large number of *Kotlassia* specimens found in the Gorokhovets locality (isolated teeth, vertebrae, and jaw fragments), where the bone beds are rich in fish scales. However, the incompleteness of available material together with the absence of data on the development of the marginal and palatal dentition casts some doubt on the adduced interpretation.

It is reasonable to describe the composition of oryctocoenosis of the main deposits in order to assess the position of seymouriamorphs within the communities of terrestrial vertebrates. Recently, Ivakhnenko (2001) performed a general study on this subject with reference to East European tetrapods. Collections from the Late Permian beds housed at the PIN differ in representativeness, preservation of material, and degree of investigation. They may reflect only a qualitative correlation between the taxa composing the reconstructed communities; however, this is quite enough to solve the problem posed in this study (Table 1).

The Lower Permian localities containing seymouriamorphs in Central Europe and Asia, with rare exception, are distinguished by the complete absence of other terrestrial vertebrates. This reflects the very specific and poorly understood conditions of their life in shallow lentic basins subjected to seasonal fluctuations and lacking active water flows. It is evident that the burials

Table 1. Composition of the oryctocoenoses from the Late Permian localities of Eastern Europe

Locality	Seymouri-amorpha	Chronio-suchidae	Dvinosau-ridae	Pareiasau-ridae	Dicinodontia	Gorgonopidae	Other taxa
Babintsevo	30.3	58.4	1.1	9.2	0.5		0.5
Donguz 6	31.4	66.7		0.6		1.3	
Mutovino	1.2	65.1	32.5			1.2	
Poteryakha 1	38.5	53.9	7.7				
Kochevala 1	58.4	23.2	0.9	8.5			
Poteryakha 2	36.2	34.3	4.1			6.9	1.4
Ust’e Strel’ny	9.1	27.3	40.9			13.6	9.1
Navoloki	29.7	8.1	29.7			2.7	
Sokolki	3.6	2.3	15.3	49.7	12.3	12	4.9
Pron’kino	46.3	47.8	3.7				2.2
Aristovo	0.9	21.3	24.1	43.5	1.9	6.5	1.9
Sambullak	9.7	89.5					0.8
Blumental 3	7	83.7	1.2	3	1.2	2.3	2.3
Adamovka	12.5	83.9		3.6			
Gorokhovets	26.6	48.2	20.8	1.8	0.6	0.2	1.8

rich in seymouriamorphs were formed as a result of geologically instantaneous mass mortality caused by abrupt environmental changes rather than gradual formation of oryctocoenoses. It is highly probable that episodic stagnation accompanied by oxygen depletion were the main factors responsible for the fatal consequences for the gill-breathing fauna (see below). The anoxic condition could be caused by the decay of vegetable remains (found in all localities) or (and) development of winter kills. A detailed study of the deposits and distribution of organic remains within particular sections is required to gain better insight into this question. For example, a fish kill was suggested for explaining the formation of oryctocoenosis with *Utegenia shpinary* in the Kurty locality (Kuznetsov and Ivakhnenko, 1981).

In the Moravian localities, *Discosauriscus* is mainly limited to thin bituminous interlayers, which is direct evidence of anoxic conditions. More light-colored layers, where animal remains are much scarcer, most likely correspond to the time intervals when the oryctocoenoses were formed according to the standard mode. These events seem to be interconnected, testifying against the supposed allochthonous burial of *Discosauriscus* beyond the area of their habitats as a result of posthumous redeposition (Klembara and Meszaros, 1992). This is supported by the completeness of remains as well as by the thin-intermittent structure of the enclosing rocks, indicating the absence of water currents able to provide transport (which would result in burials within coarser facies). The latter implies that river floods could not influence the hydrodynamics of basins, which would change the sedimentation pattern. Apparently, these basins were filled up primarily by precipitation.

The scarcity of larvae in the localities is undoubtedly caused by the delimitation of ecotopes, similar to what is observed in a number of Recent amphibians and fish. In the Late Paleozoic, this was especially topical, taking into account the composition of aquatic faunas, composed predominantly of large predatory amphibians. In the Babintsevo and Donguz 6 localities, juvenile kotlassiids are accompanied by young chroniosaurs and karpinskiosaurs; in the oryctocoenosis, large animals are either absent or extremely scarce. The fossils are more or less disintegrated, especially so in the Donguz 6 locality, where only a small proportion of skulls are morphologically complete (Tverdokhlebova, 1969); the percent of such finds is substantially lower (Babintsevo) than in the Early Permian localities containing seymouriamorphs. The other distinctive feature is the fact that, in the sections under consideration, the tetrapod faunas consist of many components, i.e., the structure of the aquatic community remains the same as in the other Late Permian localities, where the co-occurrence of large and juvenile animals is virtually not registered.

The pattern of enclosing rocks is also different, they never form thin rhythmic interbedding; entire sections are also specific, showing a more active hydrodynamic regime and the absence of stagnation. The entire set of taphonomic data suggests that such localities were formed within the seasonally flooded bottomland.

The Kotlassiidae are one of the aquatic components of terrestrial vertebrate communities from the Late Permian of Eastern Europe (Ivakhnenko *et al.*, 1997; Golubev, 2000).

In the Kazanian sections, the Leptorophinae were observed in association with labyrinthodonts. The presence of batrachomorphs together with *Biarmica* in the

Vyshka locality was indicated by N.M. Shomysov (identification by A.P. Hartmann-Weinberg). In the type locality (Shikhovo-Chirki) *Leptoropha* was accompanied by numerous remains of the archegosaurid *Platyoposaurus watsoni*, melosaurid *Melosaurus platyrhinus*, and the gephyrostegid *Nyctiboetus kassini*.

In the localities of the Il'inskoe Faunal Subassemblage of terrestrial vertebrates[2] (Poteryakha 1, Poteryakha 2, Navoloki, Kochevala 1, Mikulino, Mutovino, Donguz 6, Babintsevo, and Ust'e Strel'ny), the Kotlassiidae constitute a considerable part of specimens and always co-occur with relict anthracosauromorph amphibians, chroniosuchians. Sometimes, neotenic batrachomorphs, the Dvinosauridae, are an important component; this looks quite reasonable, taking into account the fetalized appearance of the Kotlassiidae. Ichthyophagous chroniosuchians clearly dominate in the majority of localities, even taking into account that their percentage could be overestimated because of the presence of numerous easily identified plates, as was mentioned earlier (Ivakhnenko, 2001). The domination of the Kotlassiidae in certain localities (e.g., Navoloki) is most likely a result of small sample sizes, distorting the proportions of particular forms in the localities. The proportion of other taxa, including gorgonopians, pareiasaurids, dicynodonts, galeopids, and burnetiids, in the localities listed above is very low, only isolated scarce finds (Table 1).

The proportions of aquatic organisms in the localities containing the Sokolki Subassemblage range widely. Thus, in the Sokolki locality, the proportion of terrestrial and tentatively terrestrial groups (dicynodontids, annatherapsids, inostranceviids, and pareiasaurids) is notably higher than the proportion of typical aquatic tetrapods of the Tatarian Time, such as chroniosuchians, seymouriamorphs, and batrachomorphs (Dvinosauridae). Sokolki belongs exactly to such localities where, in spite of a large sample size, seymouriamorphs compose an extremely small proportion of specimens.

The Gorokhovets locality shows an inverse picture; in the presence of the same taxa, aquatic animals, including seymouriamorphs, obviously predominate. At least three seymouriamorph species, *Karpinskiosaurus secundus*, *Kotlassia prima*, and a previously unknown kotlassiid species similar to *Leptoropha* in the shape of its tooth crowns, occur there. The locality is characterized by the allochthonous burial type; the remains are numerous but fragmentary, with domination of postcranial elements. The identification of the above taxa on the basis of isolated cranial bones and teeth, a large amount of which was washed from the bone beds, is beyond question.

The analysis of oryctocoenoses and trophic specialization of the Kotlassiidae allows one to determine their role in the aquatic community of terrestrial vertebrates from the Late Permian of Eastern Europe, represented mainly by predatory amphibians, batrachomorph, and anthracosauromorph labyrinthodonts. They adapted to a wide ecological zone of plant-eaters and invertebrate-eaters, permitting them to avoid direct competition with predators and realized in many respects owing to the complexity and evolutionary plasticity of their dental system. The absence in the majority of cases of a strictly determined direction of trophic specialization implies a wider ecological and taxonomic diversity of seymouriamorph parareptiles than that of typical ichthyophagous predators. At the initial stage of studying, this may complicate stratification in the absence of sufficient data (a large variety of forms would reflect not so much age differences, as a consequence of ecological differentiation); at the same time, this is of great importance for reconstruction of the Permian communities.

Unlike the Kotlassiidae, karpinskiosaurids are scarcely represented in the Late Permian deposits by mass material; however, they are also members of the aquatic block of the vertebrate communities, where fish-eaters predominate. The role they played in aquatic communities was insignificant, which may be connected with the deficiency of ecological niches for a weakly specialized predator, whose main food objects, invertebrates, were actively consumed by other aquatic animals, including fish. The ability for amphibious existence (beyond the aquatic environment) could not offer any advantage providing a high diversity and evolutionary success of the group in the presence of chroniosuchians, which were secondarily aquatic animals (Golubev, 2000) and, hence, perfectly adapted to the facultative terrestrial mode of life.

The adaptation of certain seymouriamorphs to herbivory restricts their ability to cutaneous–pulmonary respiration, which dominates in Recent amphibians. The oxygenated blood of the latter from lungs and skin capillaries arrives to the auricles through the pulmonary and large cutaneous veins (v. pulmonalis and v. cutanea magna) and mixes with the venous blood in the heart. Hence, the arteries receive and distribute mixed blood, which is the reason for the low metabolic level in amphibians, preventing them from effective utilization of vegetable food. Such an imperfect structure of the blood circulation is a result of the development of a system using atmospheric oxygen for breathing and intended to replace the gills, it is an inevitable consequence of adaptation to the terrestrial environment (Kalandadze and Rautian, 1983).

In fish with internal gills as the main organ for gas exchange, the arterial and venous blood flows do not mix; therefore, the herbivory is widespread, especially in freshwater forms (for example, in cyprinids). Many actinopterygians possess different adaptations for breathing with air, such as special pouches in the anterior region of the esophagus or the ability to ventilate

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[2] The Tatarian Stage, upper part of the Northern Dvina Horizon; for the division into particular faunal assemblages and their zonation, see Ivakhnenko *et al.* (1997) and Ivakhnenko *et al.* (2003) (amended English version).

the air bladder. However, they are always only additional structures, which are used primarily under anoxic conditions (Schmalhausen, 1964), and do not significantly influence the metabolic intensity.

After the transition of vertebrates to the terrestrial mode of life, only reptiles, owing to the reorganization of their circulatory system, in which the arterial and venous blood flows are secondarily separated, have an opportunity to use vegetation as their main food.

Examples of obligatory herbivory are known in Recent lizards and were undoubtedly widespread among large Paleozoic and Mesozoic amniotes (Reisz and Sues, 2000; Weishampel and Jianu, 2000; Ivakhnenko, 2001). It is remarkable that, even among lacertids, vegetable food is used comparatively rarely, and mainly flowers and fruits, full of nutrients, are used in this case (Vorob'eva and Chugunova, 1995). To all appearances, small sizes prevent Recent diapsids from a wider utilization of vegetable food (Szarski, 1962; Kalandadze and Rautian, 1983). This inference is supported by the comparatively large size of the majority of herbivorous lacertids (Vorob'eva and Chugunova, 1995). Some authors regard the presence of symbiotic organisms, facilitating cellulose decomposition, as a necessary condition for herbivory in this group (Ostrom, 1963).

Very diverse Recent amphibians are obligatory predators throughout their postlarval existence, and only larval anurans with functioning gills and nonfunctioning lungs can exclusively use vegetable food (Schmalhausen, 1964). During the metamorphosis and transition from branchial breathing to cutaneous–pulmonary respiration, this ability is lost and animals change their feeding habits.

It is evident from the aforesaid that the only possible mechanism of gas exchange for seymouriamorphs adapted to herbivory is branchial respiration providing a metabolic level high enough for effective utilization of vegetable food. The presence of a larval stage with branchial respiration may be taken for granted for all members of the order. However, the use of external gills is only possible in relatively small animals. A further increase in size requires a disproportionate increase in branchiomere surface, since, in the course of growing, the body surface increases according to an arithmetical progression, whereas the volume increases according to a geometric progression. For the Kotlassiidae, this implies a substitution of external gills by the internal gills at late ontogenetic stages.

The homology of external amphibian gills and the internal gills of fish was definitely established by Schmalhausen (1953, 1954, 1955, 1964). In both cases branchiomeres are similarly arranged with reference to the gill septa, blood vessels, and visceral muscles. External gills, functioning together with the internal gills, may be found in some fish young, such as *Acipenser* and larval dipneumone dipnoans (Schmalhausen, 1964). Their main adaptive significance is to segregate respiration from feeding. In young fish lacking a well-developed gill cover, the pumping of water through the gill slits is performed by the movements of the gular apparatus, which cannot work during feeding. Freely washed external gills provide permanent gas exchange during the swallowing of relatively large prey. After the formation of the operculum, the gular breathing in fish is substituted by opercular respiration and the need for external gills disappears (Schmalhausen, 1964).

In the Recent Anura, there is a larval stage with secondary internal gills; as a result of expansion of the opercular fold, the external edges of the gill septa, supporting typical external gills, become covered from the outside. Passive washing of the branchiomeres is replaced by active water pumping with the help of movements of the hypoglossal apparatus (Schmalhausen, 1955).

Apparently, the branchial apparatus was similarly modified in the course of kotlassiid ontogeny; the external gills were substituted by either the internal gills, similar to what occurs in fish (there was no need for any fundamental transformation owing to the homology of all structures involved), or secondarily internal gills similar to those of the Recent Anura. This enabled them to substantially improve the efficiency of gas exchange as compared to passive respiration with external gills and, in this manner, to solve the problem of herbivory acquisition despite a considerable increase in size.

The above discussion does not preclude the presence of rudimentary lungs in the Kotlassiidae; however, they could only be used as an accessory apparatus lacking principal significance in respiration. The role of cutaneous respiration was minimized if not completely blocked by the development of squamation.

The remains of scales are frequently preserved in the fossil record and were registered in Moravian discosauriscines (Shpinar, 1953; Klembara and Meszaros, 1992; Klembara and Bartik, 2000), juvenile *Ariekanerpeton sigalovi* (Ivakhnenko, 1981, 1987), and *Microphon gracilis* (SGU, no. 104B/2023, fragmentary larval skeleton, Babintsevo locality). Weakly ossified thin plates, the possible fragments of external epidermal structures, were repeatedly met during preparation of medium-sized *Karpinskiosaurus ultimus* (PIN, no. 4617/158). Perfectly preserved scales were found together with skeletons of seymouriamorphs of uncertain taxonomic position from the Mikhailovskii Mine locality, mentioned in the literature as *Discosauriscus netschajevi* (Fig. 50, an internal view of the integument; this explains the inverse overlapping of scales). In this form, the scales are slightly polygonal (as is seen in their free edges not covered by other scales) and show distinct growth rings. *Discosauriscus austriacus* has round scales covered by numerous fine concentric rings joined in four into the rings of the second order (Shpinar, 1953; Klembara and Batik, 2000), which most likely reflect seasonal fluctuations.

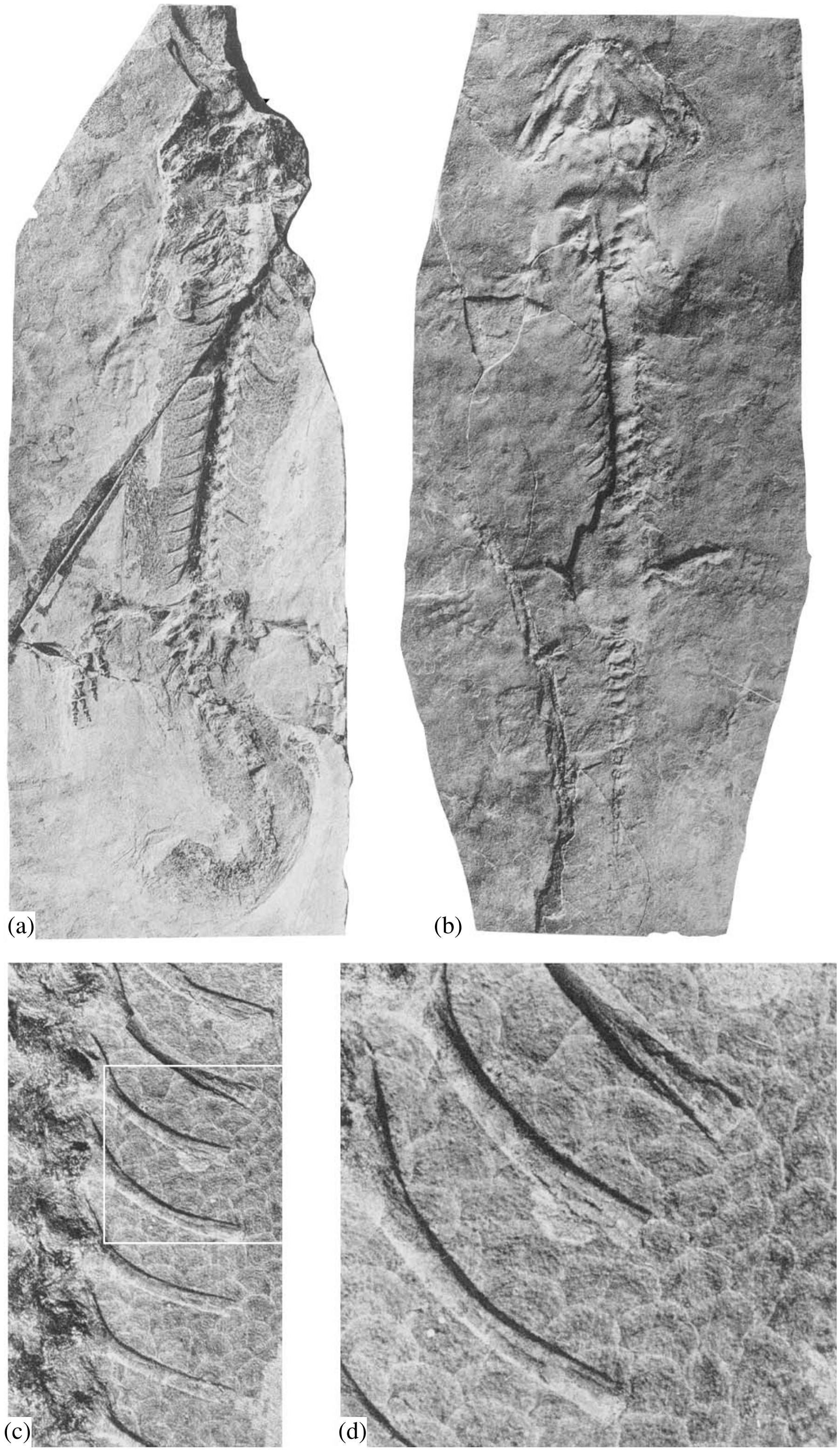

Fig. 50. *“Discosauriscus netschajevi,”* after Ryabinin (1911): (a, b) juvenile skeletons and (c, d) imprints of scales.

Shpinar (1953) indicated the presence of squamation on the entire body surface of *Discosauriscus*, whereas Klembara and Bartik (2000) believed that scales covered only the ventral side, but did not exclude the possibility of complete pholidosis. Ivakhnenko (1981, 1987) indicated that squamation disappeared in *Ariekanerpeton* after metamorphosis, which, judging by the disappearance of imprints of external gills,

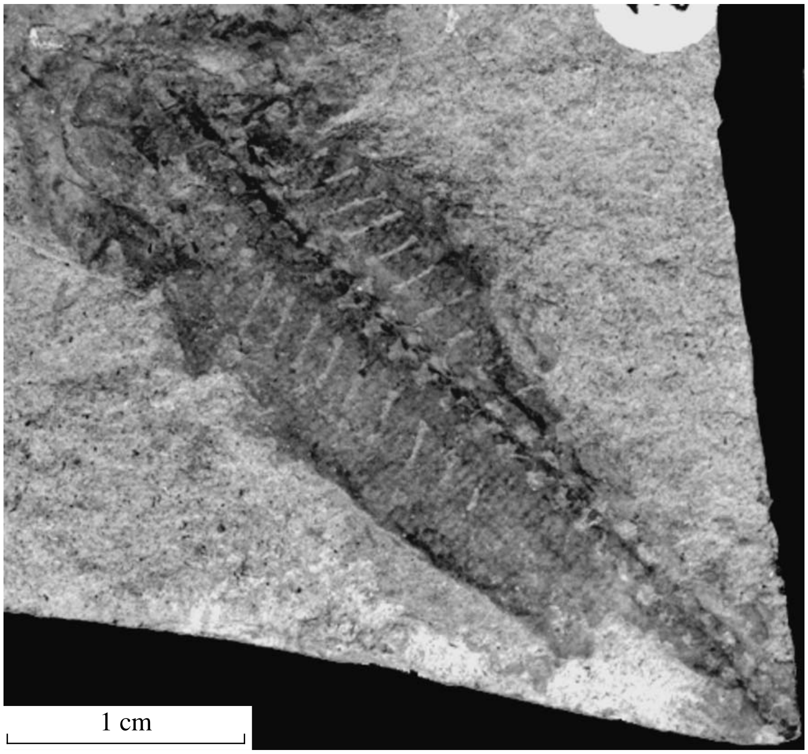

Fig. 51. *Ariekanerpeton sigalovi*, imprint of juvenile with the traces of scales, specimen PIN, no. 2079/465.

occurred in the animals with a skull about 15 mm long. The largest individual *Ariekanerpeton* that possesses squamation (it is notable that scales cover the body entirely) has a 30-mm-long skull (specimen PIN, no. 2079/252). This suggests *Ariekanerpeton* either passed through metamorphosis at the same size as *Discosauriscus* from Moravia or retained *squamation* at postlarval stages; it is not unlikely that the same was characteristic of the forms from Moravia.

The reconstruction of the seymourioid physiology meets with certain contradictions.

Discosauriscines of late ontogenetic stages, after the reduction of external gills, retain a wide set of sensory structures, the functioning of which is associated with existence in an aquatic environment, such as the seismosensory organs, pit-lines, and foraminate pits (*Discosauriscus*). In the largest *Discosauriscus*, the seismosensory grooves are preserved in the preorbital region, whereas they are virtually indiscernible in the postorbital region (Klembara, 1997). This allowed one to propose that all currently known specimens of *Discosauriscus* belong to the "larval" and "early juvenile" ontogenetic stages (Klembara, 1997). The absence of larger individuals in the same localities is probably attributable to the transition to a terrestrial mode of life, i.e., dwelling beyond the area where aquatic oryctocenoses were formed. This conclusion was subsequently extended to other seymouriamorphs showing a similar pattern of burial, i.e., *Utegenia* and *Ariekanerpeton*, where numerous individuals are accumulated (Laurin, 1996b, 1996c).

These conclusions, however, disagree with available taphonomic data. Notwithstanding a large number of European localities, the long history of their study, and extensive material coming from these localities (many hundreds of specimens), adults (or, more precisely, fossils of animals corresponding to the idea of how adults of these species should look like) have not yet been found. This is rather surprising, since these adults should be closely associated with aquatic conditions with reference to both trophic adaptations and reproduction. If this is the case, the transition to a terrestrial mode of life occurred in *Discosauriscus* at relatively late ontogenetic stages (when the animals became twice as large as the largest larvae) rather than at the end of the metamorphosis; using mass material, the boundary of metamorphosis is reliably enough determined by the disappearance of branchiomere imprints.

The statement that postlarval seymourioids, including permanently aquatic discosauriscines, did not breath by internal gills is substantiated by the absence of specialized herbivores within this superfamily. Judging by the dental structure, the only example of obligatory consumption of vegetable food among seymourioids is larval *Karpinskiosaurus ultimus.* Having a small body size (skull at most 17 mm long), it was undoubtedly a gill-breathing animal. Only the development of cutaneous–pulmonary respiration, imposing for amphibians a restriction on the phytophagy, offers an explanation of the profound change in food objects resulting in an essential transformation of the dental system (a similar change in the feeding pattern, associated with the metamorphosis, is observed in extant anurans).

In contrast to kotlassioids, discosauriscs, retaining an aquatic mode of life after metamorphosis, most likely used mainly pulmonary respiration, which was undoubtedly characteristic of adult seymouriids and karpinskiosaurs. This could be caused by the presence of a nonaquatic stage in the evolution of the superfamily. The presence of such a stage is evidenced, among other things, by the presence of large otic notches most likely formed in the course of development of the terrestrial sound-transmitting apparatus. If this is the case, one could expect that, in discosauriscines, external squamation reduced; this occurred, for example, in *Ariekanerpeton*, but was not shown with certainty for *Discosauriscus*.

The material from the Bromacker locality shows that, in contrast to discosauriscines, seymouriids, the main evolutionary trend of which allowed for the adaptation to semiaquatic biotopes, passed the metamorphosis and lost seismosensory organs at rather early developmental stages (Berman and Martens, 1993). The same is observed in Late Permian karpinskiosaurs (*K. ultimus*).

It is worth noting that, contrary to a widespread belief, seymouriids most likely predominantly inhabited semiaquatic ecotopes and retained adaptation to a facultatively aquatic existence. This is corroborated by the finding of six complete *Seymouria sanjuanensis* in their natural position in a block of enclosing rock (Berman *et al.*, 1987). Such burial pattern is primarily characteristic of aquatic vertebrates (among seymouriamorphs, this concerns utegeniids and discosauriscines) and entirely atypical of the essentially terrestrial amniotes. As follows from the analysis performed in the present study, karpinskiosaurines are also a component of the aquatic block of the terrestrial vertebrate community of Eastern Europe (see above).

CHAPTER 7. STRATIGRAPHIC DISTRIBUTION

Seymouriaomorphs are known from the basal horizons of the Lower Permian up to the terminal Upper Permian deposits. The origin of the group can be confidently dated to the Upper Carboniferous. This is corroborated by a significant morphological divergence of kotlassioid and seymourioid lineages and by the presence of the evolutionary advanced Seymouriidae already in the middle part of the Wolfkampian (Berman *et al.*, 1987). As early as the Early Permian, the group had a wide geographical distribution (China, Central Asia, Central Europe, and North America) and was represented by both known superfamilies. No younger deposits are preserved in the territory of the specified regions. The main data on the final stages of historical development of seymouriaomorphs are based on the finds in the Russian Upper Permian.

The Lower Permian age of the Kurty locality is grounded on the paleobotanic data (determined by S.V. Meyen). The lack of faunal remains hampers a more precise biostratigraphic dating. Li and Cheng (1995) assigned *Urumqia* to the dinocephalian–labyrinthodont complex zone characterized by intasuchids, bolosaurids, and brithopodids from a number of localities dated to the lower part of the Upper Permian. This assemblage is similar in composition and probably synchronous to the Inta Assemblage of terrestrial vertebrates from Eastern Europe. However, this conclusion is merely a speculation and open to question due to a primitive appearance of the Utegeniidae. In the proposed phylogenetic tree, the range of the vertical distribution of this family is given somewhat provisionally because of a lack of sound data on the age of either taxon.

The stratigraphic position of Late Permian seymouriaomorphs can be considered within the context of the Regional Zonal Scale for Terrestrial Vertebrates of Eastern Europe, elaborated by a team of researchers, and the coordinated scheme of successive faunal assemblages from this region (Ivakhnenko *et al.*, 1997; Golubev, 2000; Fig. 52).

The principal evolutionary sequence of kotlassiids established on the basis of morphological analysis decently fits the data on regional stratigraphy. The finds of the Leptorophinae are confined to the Kazanian Stage, with *Biarmica* characterizing the Lower Kazanian Substage (Vyshka locality, *Parabradysaurus silantjevi* Zone). The remains of *Leptoropha* are confined to the middle part of the Upper Kazanian, the Shikhovo-Chirki locality, the terminal part of the Verkhnii Uslon Beds in the stratotype section of the Tatarian Stage, the *Estemmenosuchus uralensis* Zone (Golubev, 2001).

The Kotlassiinae are typical representatives of the Late Tatarian faunas of terrestrial vertebrates. Their first occurrence is recorded in the Kotelnich Time (*Deltavjatia vjatkensis* Zone) based on a single find in the Ust'-Elva locality. A fragmentary parietal shield with the intermediate type of surface ornament (specimen PIN, no. 4620/1; Fig. 46) is determined as *Microphon* sp.

The other localities are later in geological age. Most of them are located within the reference section of the Tatarian Stage exposed along the Sukhona and Malaya Northern Dvina rivers. Well exposed outcrops and monoclinal bedding enable a visual correlation of almost the entire complex of the Upper Tatarian deposits, a unique situation for Eastern Europe. It is thus possible to get precise data on the relative age of terrestrial vertebrates occurring there (Fig. 53).

The Upper Tatarian Substage in the studied area is represented by the following sequence of formations upsection: the Sukhona Formation with its lower part corresponding to the Urzhum Horizon of the Lower

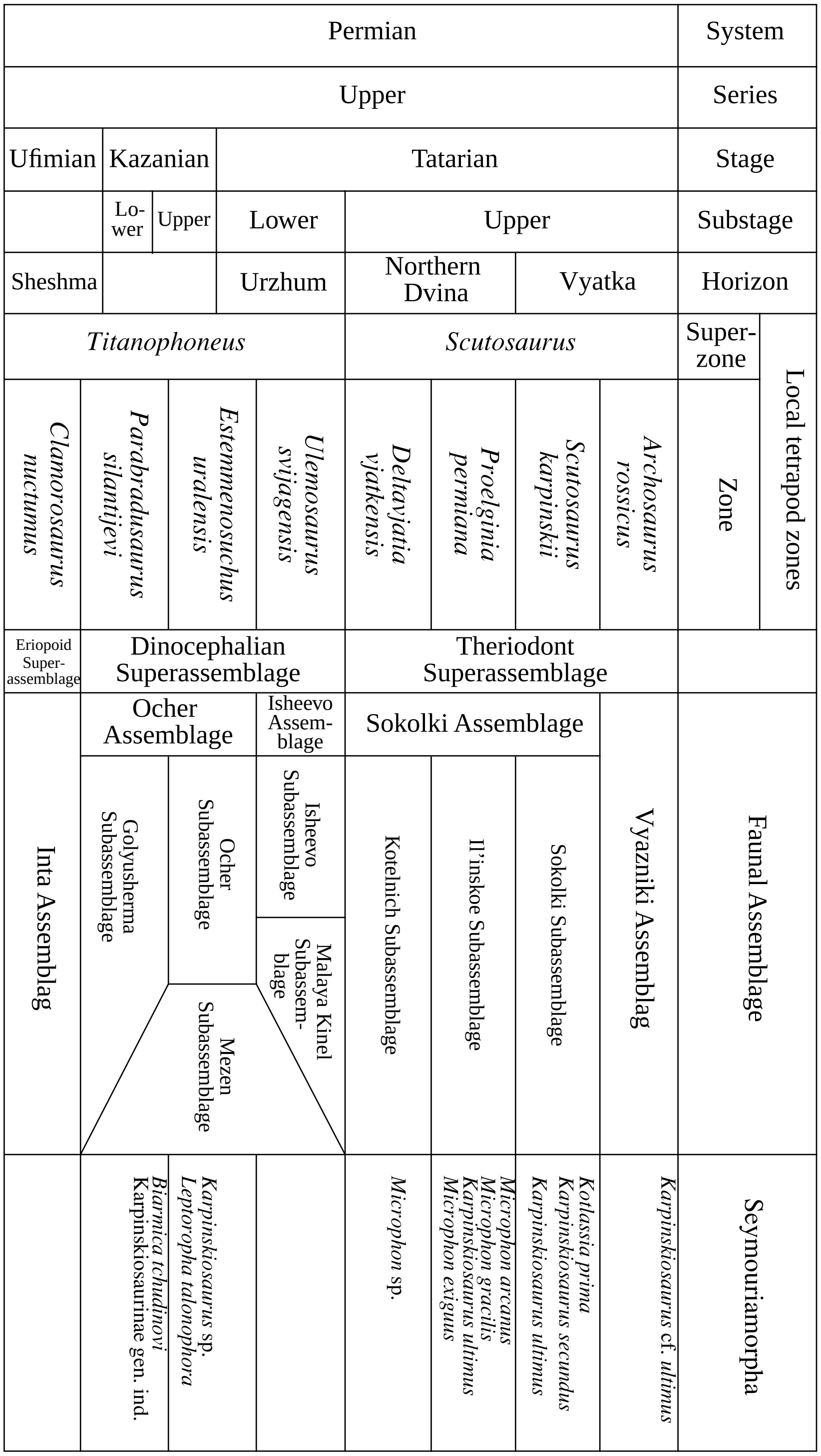

Fig. 52. Stratigraphic position of seymouriamorphs in the Late Permian of Eastern Europe and their place in the faunal assemblages.

Tatarian Substage; the Poldarsa Formation correlated with the upper part of the Northern Dvina Horizon; and the Salarevo Formation. In this section, the lower border of the latter formation coincides with the border between the Northern Dvina and Vyatka horizons (Golubev, 2000).

The occurrence of *Microphon exiguus* is confined to the lower part of the Poldarsa Formation. This form occurs in both the eastern (Ust'e Strel'ny, Strel'na Member) and western (Poteryakha 1, Poteryakha 2, Kochevala 2, and Navoloki) limbs of the anticlinal structure of the Sukhona Elevation. This record

System	Series	Substage	Horizon	Zone	Subzone	Formation	Member	Seymouriamorphs
Permian	Upper	Upper Tatarian	Vyatka	*Archosaurus rossicus* *Scutosaurus karpinskii*	*Chroniosuchus paradoxus*	Salarevo	Komaritsy	*Kotlassia prima* *Karpinskiosaurus secundus*
							Nizhnyaya Fedosa	
							Salarevo	*Karpinskiosaurus* cf. *ultimus*
					Jarilinus mirabilis		Rovdino	Kotlassiidae gen. ind.
			Northern Dvina	*Proelginia permiana*	*Chroniosaurus levis*	Poldarsa	Erogoda	
							Kalikino	
							Kichuga	*Microphon arcanus*
							Purtovino	*Microphon* sp.
					Chroniosaurus dongusensis		Isada	
							Strelna	*Microphon exiguus*
				Deltavjatia vjatkensis			Mikulino	
						Sukhona	Nyukseno	

Fig. 53. Distribution of seymouriamorphs within the Sukhona–Northern Dvina reference section of the Tatarian Stage of Eastern Europe.

strengthens the stratigraphic correlation within this complex structure the core of which contains outcrops of Urzhum terrigenous rocks with poor faunal characteristics (Golubev, 2000).

The upper part of the same formation (Mutovino locality, Kichuga Memeber) yielded remains of *Microphon arcanus*. The type locality of *Kotlassia prima*, Sokolki, is the latest site with kotlassiids. It has a much higher stratigraphic position in the upper part of the Salarevo Formation (the Komaritsa Member). In Late Vyatka Time (*Archosaurus rossicus* Zone), the group has not been found.

In the Sukhona–Northern Dvina section, the Kotlassiidae occur at other levels as well. In particular, they are known from the middle part of the Poldarsa Formation (Mikulino locality) and the lower part of the Salarevo Formation (Klimovo and Myakolitsa 1 localities). The high fragmentation of the material does not allow any exact determinations. It is not improbable that we are dealing with unknown taxa here.

The Tatarian strata in southeastern European Russia (Orenburg Region) are difficult to correlate because of their isolated position and the poorly outcropped deposits of most sections. Nevertheless, when ade-

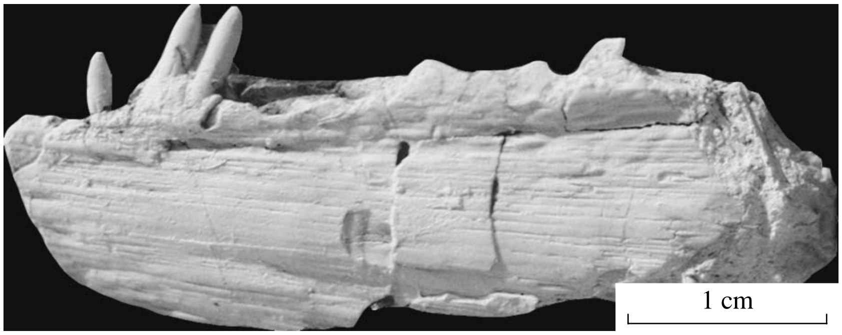

Fig. 54. Karpinskiosaurinae gen. indet., fragmentary dentary, specimen PIN, no. 4416/14, labial view.

quately characterized by tetrapods, they can have a reliable stratigraphic position and the enclosed taxa may be correlated to the faunal assemblages from Eastern Europe (Ivakhnenko *et al.*, 1987; Golubev, 2000).

Thus, the presence of *Microphon exiguus* and the chroniosuchid *Chroniosaurus dongusensis* in the Donguz 6 locality enables its confident correlation with the Il'inkoe stage in the development of terrestrial vertebrates and the synchronous localities of northeastern European Russia (Ust'e Strel'ny, Poteryakha 2, etc.). The association of the same zonal species, *C. dongusensis*, and *Microphon gracilis* in the Babintsevo locality allows one to date it to the middle part of the Northern Dvina Horizon as well. A more advanced condition of some cranial characters of *M. gracilis* is evidence of the younger age of this form compared to the type species of the genus. In the Sukhona–Northern Dvina reference section, the distribution of this form should fit the interval of the Isady and Purtovino members.

According to available stratigraphic charts, Moravian localities with *Discosauriscus* are dated to the basal Upper Rotliegend. The rests assigned to this genus (or to the synonymous genus *Letoverpeton*) were also recorded from stratigraphically lower deposits, namely, the terminal Lower Rotliegend of Poland, Germany, and France (Werneburg and Kiersnowski, 1996). It is remarkable that the Polish form is reconstructed with a wide, completely dentate parasphenoid rostrum, never observed in seimourioids, whereas *Letoverpeton thuringiacum* from Germany shows a contact of the supratemporal and postorbital, a shallow otic notch, and large teeth on the ectopterygoid (Werneburg and Kiersnowski, 1996; Werneburg, 1988). If this morphological account is correct, it can be an indication of the different taxonomic position of these taxa.

Sarytaipan, the type locality of *Ariekanerpeton sigalovi*, lacks other faunal remains. In this situation, it is aged on the basis of comparison with the European sections containing a close genus, *Discosauriscus*. Taking into account a slightly more archaic appearance of *Ariekanerpeton*, the upper limit of its tentative age is the basal Upper Rotliegend. If the similarity of this form in some cranial characters to *Seymouria* (Laurin, 1996c) shows an actual phylogenetic sequence (or proximity to the divergence point of karpinskiosaurid and seymourid lineages), the time of existence of *Ariekanerpeton* should not overlap the biozone of typical seymouriids. In Central Europe, the genus *Seymouria* is present in the Bromaker locality (Tambach Formation, Germany), which is also assigned to the basal Upper Rotliegend (Sumida *et al.*, 1996). This allows for a correlation of the deposits with *Ariekanerpeton* to the Lower Rotliegend.

The North American Seymouriidae are known upsection from the middle of the Wolfcampian Group. This is *Seymouria sanjuanensis* from the Cutler Formaton, New Mexico (Berman *et al.*, 1987). The latest datum is represented by *S. grandis*. There are, however, doubts in its taxonomic assignment (Sillivan and Reisz, 1999). In this situation, the upper limit of the family chronological distribution is preferably associated with the Arroyo Formation (Clear Fork Group, Leonardian; Texas). Its deposits yielded the type material of *S. baylorensis*. According to available data (Berman *et al.*, 1987), the biozones of the two *Seymouria* species do not overlap. They occurred in succession at the boundary between the Wolfcampian and the Leonardian.

Finds in Germany of the rich tetrapod association of typical North American appearance, including *S. sanjuanensis*, allowed us to correlate the basal Upper Rotliegend (Tambach Formation) with the middle part of the Wolfcampian Group of North America (Sumida *et al.*, 1996). The data on terrestrial vertebrates of the Bromaker locality most likely indicate a closer genetic affinity of the Late Permian faunal assemblages of Eastern Europe with the Early Permian faunas of Central and Western Europe rather than those of North America, as was believed earlier (Kalandadze and Rautian, 1993; Golubev, 2000).

The first occurrence of the Karpinskiosauridae in East European sections is recorded in the Lower Kazanian Ust'-Koin locality; a fragmentary dentary of a large individual with the characteristic pattern of vascular imprints on the labial side and weakly folded teeth (specimen PIN, no. 4416/14; Fig. 54) co-occurs with melosaurids, dissorophids, bolosaurids, captorhinids, and certain other groups composing the core of the Golyusherma Faunal Assemblage, which corresponds to the *Parabradysaurus silantjevi* Zone (Ivakhnenko *et al.*, 1997).

The material still under study from the Vozdvizhenka locality (isolated cranial bones and jaws of juveniles) likely belongs to a new species of the genus *Karpinskiosaurus*. This is the only record so far known of a karpinskiosaurine in the Lower Tatarian.[3]

Finds in the Upper Tatarian sections are more frequent. According to available data, Pron'kino, the type locality of *Karpinskiosaurus ultimus*, and the Babintsevo locality, with a more complete record of this form, are considerably diachronous. The first is dated to the Vyatka Horizon (*Scutosaurus karpinskii* Zone); the second, to the Northern Dvina Horizon (*Proelginia permiana* Zone). This age difference of the sites is mainly inferred from the occurrence of *Chroniosuchus paradoxus* in Pron'kino and *Chroniosaurus dongusensis* in Babintsevo. The succession of chroniosuchids is used for a detailed division of the Upper Tatarian Substage into subzones (Golubev, 2000). This conclusion is likely reliable because, contrary to kotlassiids, karpinskiosaurines are rather conservative morphologically. Thus, an isolated maxilla of *Karpinskiosaurus* cf. *ultimus* was found in the Aristovo locality (Vyatka Horizon, *Scutosaurus karpinskii* Zone) of the reference section. A fragmentary skull from the Sambullak locality originally described as *Kotlassia grandis* (Tverdokhlebova and Ivakhnenko, 1994) does not clearly differ from *K. ultimus.* This find comes from the even later uppermost beds of the Upper Tatarian (Vyatka Horizon, *Archosaurus rossicus* Zone).

It is worth noting that these finds, in spite of their similar taxonomic determinations, differ in some morphological features. In the absence of sufficient data on already known taxa, they may alternatively indicate a real species-level distinction, intraspecific (size independent), or ontogenetic variability.

Dating of the sites with *Karpinskiosaurus secundus* (Sokolki, Adamovka, Blumental 3, and Gorokhovets) is more definite. They all correspond to the *Scutosaurus karpinskii* Zone (*Chroniosuchus paradoxus* Subzone) of the Vyatka Horizon. This confirms the concept of the later origin of this species compared to *K. ultimus.*

CHAPTER 8. DIFFERENTIATION OF SEYMOURIAMORPHS AND THEIR POSITION IN THE PHYLOGENY OF TERRESTRIAL VERTEBRATES

Seymouriamorphs are tentatively divided by cranial structure into two well-defined groups which evolved independently for a long time. The most similar to the archetype condition are Early Permian kotlassioids, i.e., the family Utegeniidae. Although this family shows certain specific apomorphies, e.g., a wide toothed rostrum, it can be regarded as the ancestral taxon which provides the initial adaptive radiation.

As the skull of primitive kotlassioids is compared with that of anthracosauromorphs, it displays especially great similarities to certain embolomere anthracosaurs, in particular, *Proterogyrinus scheelei* (Holmes, 1984). *Proterogyrinus* shows a well-pronounced contact between the supratemporal and postorbital, which is preserved in *Utegenia* and Kazanian kotlassiids. The tabulars are substantially smaller than the postparietals, become narrower toward the otic notches, and have long paroccipital processes; the posterior flanks of the postparietals project posteriorly to form a curving occipital edge similar to that of larval *Utegenia*. The articular region of the lower jaw is located posterior to the occipital plane. The anterior edge of the otic notches of *Proterogyrinus* terminates short of reaching the ossification centers of the supratemporals. The frontals are longer than the parietals and project deep into the preorbital region. In the zygomatic region, of special note is the jugal strongly extended caudally and covered posteriorly, and partly dorsally, by a high quadratojugal. The latter bone is located far from the maxilla. The maxilla is low over the entire extent. The maxillary teeth are simple, conical, and numerous; the number of teeth is greater than in the Utegeniidae because the preorbital region is lengthened. In the anterior region of the maxilla, the teeth are differentiated in size in the same manner as in *Utegenia*. The premaxilla contains only five teeth.

The posterior region of the parasphenoid has only short lateral projections isolated from each other by a slightly sloping notch in the posterior margin of the bone. A small shagreen field completely covers the anterior and quadrate rami of the pterygoids and reaches the jaw joint. It is particularly remarkable that *Proterogyrinus* has large teeth on the ectopterygoid; this suggests that, in kotlassiids, the postchoanal tooth row could develop by the recapitulation of the ancestral condition. The skull roof retains discontinuous seismosensory grooves at the definitive stage.

However, the palatal structure shows clear differences. This is primarily the absence of well-developed pterygoid flanges. Laterally, the pterygoid is connected to the alar process of the jugal and isolates the ectopterygoid from the adductor cavity. The narrow rostral region of the parasphenoid lacks shagreen teeth. Small teeth are also absent from the lateral elements of the palate (Holmes, 1984).

Apparently, the establishment of seymouriamorphs as a special morphotype was largely provided by the specialization of the jaw apparatus (especially, the jaw

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[3] The locality was initially dated to the Upper Tatarian (Ivakhnenko *et al.*, 1997). This age was, however, reconsidered on the basis of newly collected remains of Melosauridae gen. indet., Nycteroleteriinae gen. indet., and Procolophonidae (*Kinelia broomi*), *Syodon* sp., Microuraniidae gen. indet.).

muscles) of primitive reptiliomorphs at early ontogenetic stages. This evolutionary trend associated with the primary adaptation of larvae was clearly pronounced in kotlassioids, the basic morphogenetic changes in the cranial structure of which developed against the background of general fetalization accompanied by the preservation of an obligatory aquatic mode of life.

The changes in the jaw apparatus could result in a stronger attachment of the zygomatic regions to the parietal shield, which changed the general kinetic model of the skull, and the development of the synpareial cranial pattern. On this basis, in the course of subsequent Kotlassioidea evolution, a complex multicomponent and polyfunctional dental system developed and substantially influenced the other cranial features, in particular, the structure of the dermatocranium.

The above inference is corroborated by the fact that the first changes in the jaw and palatal dentition of kotlassiids are already noted at the larval stage. The formation of a wide toothed rostrum of the parasphenoid is most likely accounted for by the significant role of shagreen teeth in larval feeding; in larval seymouriamorphs, the marginal teeth are at the initial developmental stage, whereas the shagreen teeth are always larger in size. The expansion of small teeth on the lateral elements of the palate are attributable to the same reason.

Apparently, inverse dependence also took place, i.e., as the trophic conditions changed, the mechanism providing gradual modification of teeth allowed the dental system to get rid of adaptations that had lost their significance primarily by means of underdevelopment, stopping at a certain morphogenetic stage followed by the transition to a new trend of specialization. Being limited by their adaptations to the aquatic ecotopes and escaping direct competition with large specialized predators (anthracosauromorph and batrachomorph labyrinthodonts), Late Permian kotlassioids mastered a wide adaptive zone of aquatic invertebrate-eaters and plant-eaters. This was accompanied by certain morphophysiological changes, the greatest of which was the transition to breathing using internal gills.

The Seymourioidea are rather conservative in terms of cranial structure. Various aberrations discovered among extremely extensive materials on discosauriscines (the presence of contact between the intertemporal and the postorbital, the occurrence of superficial otic notches, and relatively small postparietals at early ontogenetic stages) indicate close relationships between this superfamily and primitive kotlassioids.

The most peculiar forms are seymouriids, the key distinction of which is the different pattern of articulation between the parietal shield and the zygomatic region. Apparently, this pattern gave rise to a complex construction developed at the boundary between these regions in nycteroleteromorph parareptiles. The latter group undoubtedly had a well-developed sound-transmitting system provided with the tympanic membrane. This is evidenced by the size of the otic notches and the presence of fossae for the parotid glands at the edges of these notches (Ivakhnenko, 1987). The space for the middle ear cavity was released by spreading the otic plate of the squamosal under the parietal shield (see *Macroleter* and *Emeroleter*), which is associated with a complex articulation between the membrane bones in the otic region of nycteroleteromorphs.

Apparently, the development of the sound-transmitting apparatus was initiated even in primitive seymourioids; this is evidenced by the presence of deep otic notches (a principal distinctive character of the superfamilies). This process could occur only in a terrestrial environment and most likely determined the main evolutionary trend of the seymourioid lineage, i.e., a decrease in the relationship to the aquatic environment and adaptation to the semiaquatic ecotopes. The first and subsequent stages of this process could lead to numerous secondary returns to the aquatic environment by the prolongation of the larval stage; apparently, an example of such a return is discosauriscines. The Seymouriidae and Karpinskiosauridae, characterized by the early metamorphosis and the loss of the seismosensory system, were better adapted to a facultative terrestrial mode of life.

Regarding the general morphological pattern, discosauriscines could be the ancestral group of seymouriids. The Karpinskiosaurinae are generally less specialized than the Seymouriidae; therefore, the conclusion that they gave rise to the Seymouriidae is hampered only by data on the stratigraphic occurrence of the two groups. The similarity between these groups is a result of parallel development caused by common evolutionary potentialities.

The entire set of morphological and stratigraphic data enable one to propose the phylogenetic tree of seymouriamorph parareptiles shown in Fig. 55.

The main difference of seymouriamorphs from other parareptiles is an enlarged set of dermatocranial membrane bones. However, the majority of these elements (tabulars, postparietals, intertemporals, and postsplenials) are the canal bones, i.e., their development is closely associated with the seismosensory placodes. Because of their small sizes, these bones do not play a significant role in the mechanical skull design. As higher parareptiles acquired direct development (i.e., lost the larval stage) and completely lost the lateral line organs, the rudiments of these bones could remain undeveloped or fused with the rudiments of adjacent bones at early ontogenetic stages. The same factors are probably partially responsible for the break of contact between the prefrontal and the postfrontal marked in procolophonomorphs and nycteroleteromorphs.

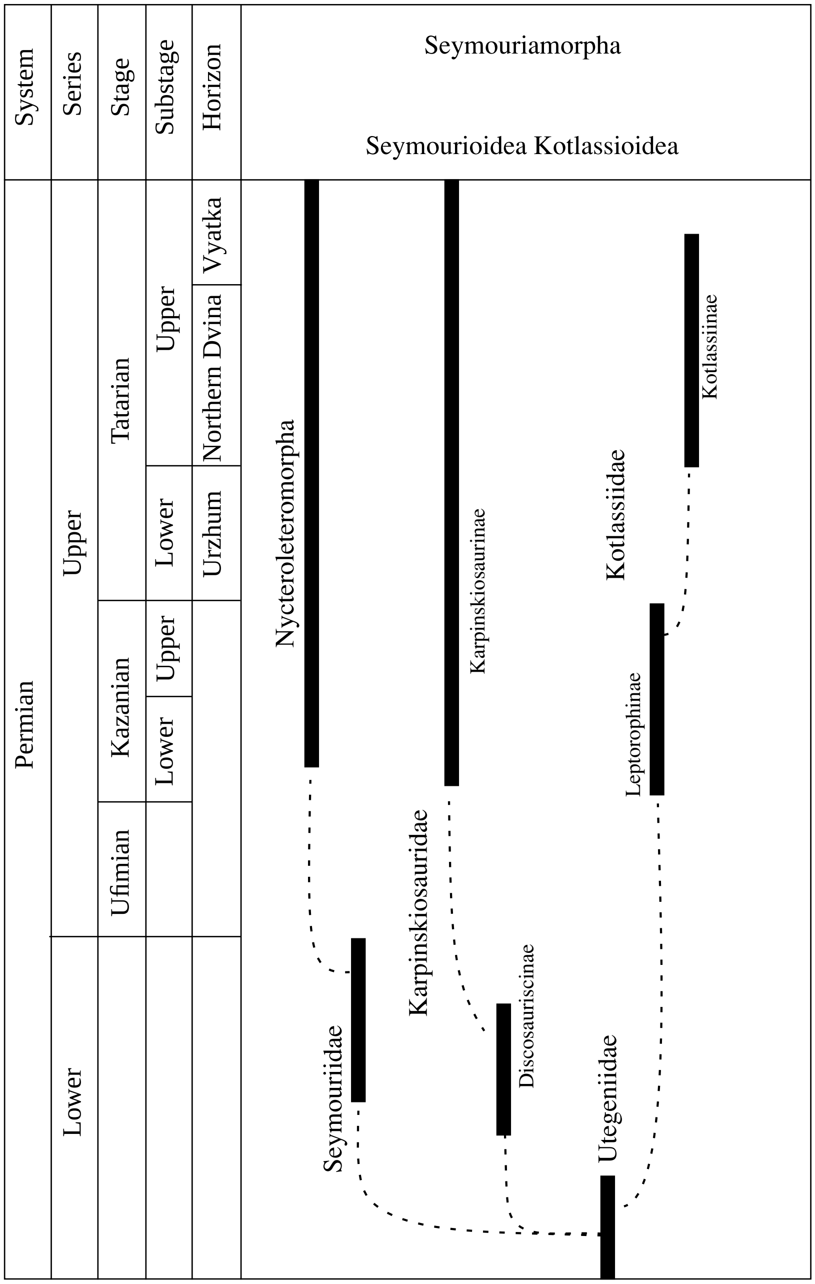

Fig. 55. Phylogeny of seymouriamorph parareptiles.

The loss of the anterior and middle coronoids, disappearance of large palatal teeth, appearance of specialized rows of shagreen teeth, and consolidation of the nasomaxillary region (i.e., a strong development of the ascending lamina of the maxilla and appearance of the palatine processes of the premaxillae, which strengthened the attachment of the upper jaw arch to the bones of the palatal complex) in higher parareptiles are likely a result of further evolutionary changes of the jaw apparatus associated with the improvement of the skull that has the temporal fenestrae or their analogues.

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REFERENCES

Amalitzky, V.P., *Severo-Dvinskie raskopki professora V.P. Amalitskogo. II. Seymouriidae* (Excavation of Prof. V.P. Amalitzky in the Northern Dvina Region: 2. Seymouriidae), Petrograd: Ros. Gos. Akad., 1921.

Berman, D.S. and Martens, T., First Occurrence of *Seymouria* (Amphibia: Batrachosauria) in the Lower Permian Rotliegend of Central Germany, *Ann. Carneg. Mus.*, 1993, vol. 62, no. 1, pp. 63–79.

Berman, D.S., Reisz, R.R., and Eberth, D.A., *Seymouria sanjuanensis* (Batrachosauria) from the Lower Permian Culter Formation of North–Central New Mexico and the Occurrence of Sexual Dimorphism in That Genus Questioned, *Can. J. Earth Sci.*, 1987, vol. 24, pp. 1769–1784.

Boy, J. and Martens, T., Ein neues captorhinomorphes Reptil aus dem thüringischen Rotliegend (Unter-Perm; Ost-Deutschland), *Paläontol. Z.*, 1991, vol. 65, no. 3, pp. 363–389.

Broili, F., Permische Stegocephalen und Reptilien aus Texas, *Paleontographica A*, 1904, vol. 51, pp. 80–84.

Broili, F., Über den Zahnbau von *Seymouria*, *Anat. Anz.*, 1927, vol. 63, pp. 185–188.

Bulanov, V.V., Seymouriamorphs from the Late Permian of Eastern Europe, *Cand. Sci. (Biol.) Dissertation*, Moscow: Paleontol. Inst. Ross. Akad. Nauk, 1999.

Bulanov, V.V., A New Genus of the Leptorophidae (Batrachosauria) from the Upper Tatarian Beds of Eastern Europe, *Paleontol. Zh.*, 2000, no. 3, pp. 82–89.

Bulanov, V.V., *Karpinskiosaurus ultimus* (Seymouriamorpha, Parareptilia) from the Upper Permian of European Russia, *Paleontol. Zh.*, 2002a, no. 1, pp. 77–84.

Bulanov, V.V., New Data on the Procolophonidae from the Permian of Eastern Europe, *Paleontol. Zh.*, 2002b, no. 5, pp. 77–84.

Bystrow, A.P., Microstructure of the Armor Elements of *Kotlassia prima* Amal., *Izv. Akad. Nauk SSSR, Otd. Biol.*, 1940, no. 1, pp. 125–127.

Bystrow, A.P., *Kotlassia prima* Amalitzky, *Bull. Geol. Soc. Am.*, 1944, vol. 55, pp. 379–416.

Credner, H., Die Stegocephalen aus dem Rothliegenden des Plauen'sehen Grundes bei Dresden, *Zaitsch. Deut. Geol. Gesellsch.*, 1883, vol. 4, no. 35, pp. 275–300.

Credner, H., Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen'sehen Grundes bei Dresden, *Zaitsch. Deut. Geol. Gesellsch.*, 1890, vol. 11, pp. 240–277.

Eberth, B.A., Berman, D.S., Sumida, S.S., and Hopf, H., Lower Permian Terrestrial Paleoenvironment and Vertebrate Paleoecology of the Tambach Basin (Thuringia, Central Germany): The Upland Holy Grail, *Palaios*, 2000, vol. 15, pp. 293–313.

Efremov, I.A., Übersicht die Formen der Perm- und Trias Tetrapoden Fauna der UdSSR, *Zbl. Mineral. Geol. Paläontol., Abt. B*, 1940, no. 12, pp. 372–383.

Efremov, I.A., On the Subclass Batrachosauria, a Group of Forms Intermediate between Amphibians and Reptiles, *Izv. Akad. Nauk SSSR, Otd. Biol.* (Moscow), 1946, no. 6, pp. 615–638.

Efremov, I.A. and Vjuschkov, B.P., Catalogue of Localities of Permian and Triassic Terrestrial Vertebrates from the USSR, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1955, vol. 46, pp. 1–185.

Fischer von Waldheim, G., Notice sur quelques Sauriens d I'Oolithe du Gouverment du Simbirsk, *Bull. Soc. Imp. Nat. Moscou*, 1847, vol. 20, no. 102, pp. 362–370.

Golubev, V.K., Permian and Triassic Chroniosuchians and Biostratigraphy of Upper Tatarian Beds of European Russia Based on Tetrapods, *Tr. Paleontol. Inst. Ross. Akad. Nauk* (Moscow), 2000, vol. 276, pp. 1–174.

Gubin, Yu.M., Permian Archegosaurid Amphibians, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1991, vol. 249, pp. 1–141.

Hartmann-Weinberg, A.P., Membrane Bones of Russian Seymouriids, *Tr. Paleozool. Inst.*, 1935, vol. 4, pp. 53–68.

Heaton, M.J., The Cotylosauria: The Reconsideration of a Group of Archaic Tetrapods, *System. Ass.* (London–New York), 1980, spec. vol. 15 (The Terrestrial Environment and the Origin of Land Vertebrates, Panchen, A.L., Ed.), pp. 497–551.

Holmes, R., The Carboniferous Amphibian *Proterogyrinus scheelei* Romer, and Early Evolution of Tetrapods, *Phil. Trans. Roy. Soc. London*, 1984, vol. 306, pp. 431–524.

Ivakhnenko, M.F., Permian and Triassic Procolophons from the Russian Platform, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1979, vol. 164, pp. 1–80.

Ivakhnenko, M.F., Discosauriscines from the Permian of Tajikistan, *Paleontol. Zh.*, 1981, no. 1, pp. 114–128.

Ivakhnenko, M.F., New Procolophons from Eastern Europe, *Paleontol. Zh.*, 1983, no. 2, pp. 130–133.

Ivakhnenko, M.F., Permian Parareptiles from the USSR, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1987, vol. 223, pp. 1–160.

Ivakhnenko, M.F., Early Permian Elements of Faunal Tetrapod Assemblages from Eastern Europe, *Paleontol. Zh.*, 1990a, no. 2, pp. 102–111.

Ivakhnenko, M.F., Faunal Tetrapod Assemblages from the Late Permian of Eastern Europe, *Byull. Mosk. O–va Ispyt. Prir., Otd. Geol.*, 1990b, vol. 65, no. 6, pp. 55–60.

Ivakhnenko, M.F., Taphonomy of the Late Paleozoic Localities of Tetrapods from Central Asia and Kazakhstan, in *Materialy po metodam tafonomicheskikh issledovanii* (Materials on the Methods of Taphonomic Studies), 1992, pp. 120–128.

Ivakhnenko, M.F., *Tetrapody Vostochno-Evropeiskogo plakkata—pozdnepaleozoiskogo territorial'no-prirodnogo kompleksa* (Tetrapods from the East European Placket, a Late Paleozoic Territorial Natural Assemblage), Perm: Perm. Obl. Kraeved. Muz., 2001.

Ivakhnenko, M.F., Golubev, V.K., Gubin, Yu.M., *et al.*, Permian and Triassic Tetrapods from Eastern Europe, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1997, vol. 268, pp. 1–216.

Kalandadze, N.N., Ochev, V.G., Tatarinov, L.P., *et al.*, Catalogue of Permian and Triassic Tetrapods from the USSR, in *Verkhnepaleozoiskie i mezozoiskie zemnovodnye i presmykayushchiesya SSSR* (Upper Paleozoic and Mesozoic Amphibians and Reptiles from the USSR), Moscow: Nauka, 1968, pp. 72–91.

Kalandadze, N.N. and Rautian, A.S., The Position of Central Asia in the Zoogeographic History of the Mesozoic, *Tr. Sovm. Sovet.–Mongol. Paleontol. Eksped.* (Moscow), 1983, vol. 24 (Extinct Reptiles from Mongolia), pp. 6–44.

Kalandadze, N.N. and Rautian, A.S., Comments on the Geochronological Schedule (Calendar) of the Most Important Events in the Phylogeny of Community (Taxocoene) of Terrestrial Vertebrates: Part 3, in *Ekosistemnye perestroiki i evolyutsiya biosfery* (Ecosystem Transformations and the Biosphere Evolution), Moscow: Paleontol. Inst. Ross. Akad. Nauk, 1998, pp. 38–41.

Klembara, J., The First Record of Pit-lines and Foraminal Pits in Tetrapods and the Problem of the Skull Roof Bones Homology between Tetrapods and Fishes, *Geol. Carpathica*, 1992, vol. 42, no. 4, pp. 249–252.

Klembara, J., The Subdivision and Fusions of the Exoskeletal Skull Bones of *Discosauriscus austriacus* (Makowsky, 1876) and Their Possible Homologues in Rhipidistians, *Paläontol. Z.*, 1993, vol. 67, pp. 145–168.

Klembara, J., The Sutural Pattern of Skull-Roof Bones in Lower Permian *Discosauriscus austriacus* from Moravia, *Lethaia*, 1994a, vol. 27, pp. 85–95.

Klembara, J., Electroreceptors in the Lower Permian Tetrapod *Discosauriscus austriacus, Paleontology*, 1994b, vol. 37, part 3, pp. 609–626.

Klembara, J., The External Gills and Ornamentation of Skull Roof Bones of the Lower Permian Tetrapod *Discosauriscus* (Kuhn, 1933) with Remarks to Its Ontogeny, *Paläontol. Z.*, 1995a, vol. 69, pp. 265–281.

Klembara, J., Some Cases of Fused and Concrescent Exocranial Bones in the Lower Permian Seymouriamorph Tetrapod *Discosauriscus* Kuhn, 1933, *Geobios*, 1995b, no. 19, pp. 263–267.

Klembara, J., The Lateral Line System of *Discosauriscus austriacus* (Makowsky, 1876) and the Homologisation of Skull Roof Bones between Tetrapods and Fishes, *Palaeontographica*, 1996, vol. 240, pp. 1–27.

Klembara, J., The Cranial Anatomy of *Discosauriscus* Kuhn, a Seymouriamorph Tetrapod from the Lower Permian of the Boskovice Furrow (Czech Republic), *Phil. Trans. Roy. Soc. London*, 1997, vol. 352, pp. 257–302.

Klembara, J. and Bartik, I., The Postcranial Skeleton of *Discosauriscus* Kuhn, a Seymouriamorph Tetrapod from the Lower Permian of the Boskovice Furrow (Czech Republic), *Trans. R. Soc. Edinburg Earth Sci.*, 2000, vol. 90, pp. 287–316.

Klembara, J. and Janiga, M., Variation in *Discosauriscus austriacus* (Makowsky, 1876) from the Lower Permian of Boskovice Furrow (Czech Republic), *Zool. J. Linn. Soc.*, 1993, vol. 108, pp. 247–270.

Klembara, J. and Meszaros, S., New Finds of *Discosauriscus austriacus* (Makowsky, 1876) from the Lower Permian of Boskovice Furrow (Czecho-Slovakia), *Geol. Carpathica*, 1992, vol. 43, no. 5, pp. 305–312.

Klembara, J., Martens, T., and Bartik, I., The Postcranial Remains of a Juvenile Seymouriamorph Tetrapod from the Lower Permian Rotliegend of the Tambach Formation of Central Germany, *J. Vertebr. Paleontol.*, 2001, vol. 21, no. 3, pp. 521–527.

Konzhukova, E.D., The First Find of Phyllospondyle Amphibians in the Upper Paleozoic of Kazakhstan, *Paleontol. Zh.*, 1963, no. 4, p. 141.

Konzhukova, E.D., The Suborder Seymouriamorpha, in *Osnovy paleontologii: zemnovodnye, presmykayushchiesya, ptitsy* (Fundamentals of Paleontology: Amphibian, Reptiles, and Birds), Moscow: Akad. Nauk SSSR, 1964, pp. 138–144.

Kuhn, O., *Fossilium catalogus. Animalia, Amphibia*, Westfal, F., Ed., 1933, vol. 61.

Kuhn, O., Die Grossliederung der Amphibien und Reptilien, *Neues Jahrb. Geol. Paläontol. Monatsh.*, 1968, no. 9, pp. 513–521.

Kuhn, O., Seymourida, *Handb. Paläoherpetol.*, 1972, vol. 5, no. 5, pp. 20–69.

Kuznetsov, V.V. and Ivakhnenko, M.F., Discosauriscids from the Upper Paleozoic of Southern Kazakhstan, *Paleontol. Zh.*, 1981, no. 3, pp. 102–110.

Laurin, M., Comparative Cranial Anatomy of *Seymouria sanjuanensis* (Tetrapoda: Batrachosauria) from the Lower Permian of Utah and New Mexico, *Paleobios*, 1995, vol. 16, no. 4, pp. 1–8.

Laurin, M., A Redescription of the Cranial Anatomy of *Seymouria baylorensis*, the Best Known Seymouriamorph (Vertebrata: Seymouriamorpha), *Paleobios*, 1996a, vol. 17, no. 1, pp. 1–16.

Laurin, M., A Reappraisal of *Utegenia*, a Permo-Carboniferous Seymouriamorph (Tetrapoda: Batrachosauria) from Kazakhstan, *J. Vertebr. Paleontol.*, 1996b, vol. 16, no. 3, pp. 374–383.

Laurin, M., A Reevaluation of *Ariekanerpeton*, a Lower Permian Seymouriamorph (Vertebrata: Seymouriamorpha) from Tadzhikistan, *J. Vertebr. Paleontol.*, 1996c, vol. 16, no. 4, pp. 653–665.

Laurin, M. and Reisz, R., A Reevaluation of Early Amniote Phylogeny, *Zool. J. Linn. Soc.*, 1995, vol. 113, pp. 165–223.

Lebedkina, N.S., *Evolyutsiya cherepa amfibii* (Evolution of Amphibian Skull), Moscow: Nauka, 1979.

Li, J.-L. and Cheng, Z.-W., A New Late Permian Vertebrate Fauna from Dashankou, Gansu with Comments on Permian and Triassic Vertebrate Assemblage Zones of China, in *Short Papers of Sixth Symposium on Mesozoic Terrestrial Ecosystem and Biota*, Beijing: China Ocean Press, 1995, pp. 33–37.

Malachov, D.V., The Topography of the Lateral Line Organs on the Skull of *Utegenia shpinari, Biota*, 2000a, vol. 1, no. 2, pp. 77–82.

Malachov, D.V., Some Speculations on the Life Style of Permo-Carboniferous Seymouriamorph Tetrapods (Discosauriscidae): Immaturity or Paedomorphosis? *Russ. J. Herpetol.*, 2000b, vol. 7, no. 3, pp. 227–231.

Medvedeva, I.M., The Nasolacrimal Duct and Its Relationship with the Membrane Bones *lacrimale* and *septomaxillare* in *Ranodon sibiricus*, *Dokl. Akad. Nauk SSSR* (Moscow), 1959, vol. 128, no. 2, pp. 425–428.

Medvedeva, I.M., *Organ obonyaniya amfibii i ego filogeneticheskoe znachenie* (The Olfactory Organ in Amphibians and Its Phylogenetic Significance), Leningrad: Nauka, 1975.

Olson, E.C., The family Diadectidae and Its Bearing on the Classification of Reptiles, *Fieldiana. Geol.*, 1947, vol. 11, no. 1, pp. 3–53.

Olson, E.C., Relationships of *Seymouria*, *Diadectes* and Chelonia, *Am. Zool.*, 1965, no. 5, pp. 295–307.

Olson, E.C., *Seymouria grandis* n. sp. (Batrachosauria: Amphibia) from the Middle Clear Fork (Permian) of Oklahoma and Texas, *J. Paleontol.*, 1979, vol. 53, no. 3, pp. 720–728.

Olson, E.C., The North American Seymouridae, in *Aspects of Vertebrate History*, Jacobs, L.L., Ed., Flagstaff: Mus. North Press, 1980, pp. 137–152.

Ostrom, J.H., Further Comments on Herbivorous Lizards, *Evolution*, 1963, vol. 17, no. 3, pp. 368–369.

Panchen, A.L., The Skull and Skeleton of *Eogyrinus attheyi* Watson (Amphibia: Labyrinthodontia), *Paleontol. Trans. R. Soc. London*, 1972, vol. 263, no. 851, pp. 279–326.

Panchen, A.L., A New Genus and Species of Anthracosaur Amphibian from the Lower Carboniferous of Scotland and the Status of *Pholidogaster pisciformis* Huxley, *Paleontol. Trans. R. Soc. London*, 1975, vol. 269, no. 900, pp. 681–540.

Queiros, K., *Phylogenetic Systematics of Iguanine Lizards*, Moyle, P.B. and Patton, G.L., Ed., Berkeley: Univ. California Publ. (vol. 118), 1987.

Ryabinin, A.N., On the Fossils of Stegocephals from the Kargalinskii Mines of the Orenburg Region, *Izv. Geol. Kom.*, 1911, vol. 30, no. 1, pp. 25–37.

Reisz, R.R. and Laurin, M., The Reptile *Macroleter:* First Vertebrae Evidence for Correlation of Upper Permian Continental Strata of North America and Russia, *GSA Bill.*, 2001, vol. 113, no. 9, pp. 1229–1233.

Reis, R.R. and Sues, H.D., Herbivory in Late Paleozoic and Triassic Terrestrial Vertebrates, in *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record*, Sues, H.D., Ed., Cambridge, 2000, pp. 1–41.

Romer, A.S., Review of the Labyrinthodontia, *Bull. Mus. Compar. Zool.* (Harvard), 1947, vol. 99, pp. 1–368.

Schmalhausen, I.I., Development of the Arterial System of Head of Urodelans, *Zool. Zh.* (Moscow), 1953, vol. 32, no. 5, pp. 937–954.

Schmalhausen, I.I., Development of Gills, Their Blood Vessels, and Muscles in Amphibians, *Zool. Zh.* (Moscow), 1954, vol. 33, no. 4, pp. 848–868.

Schmalhausen, I.I., Gills and Interbranchial Septa of Amphibians, *Zool. Zh.* (Moscow), 1955, vol. 34, no. 2, pp. 383–398.

Schmalhausen, I.I., *Proiskhozhdenie nazemnykh pozvonochnykh* (The Origin of Terrestrial Vertebrates), Moscow: Nauka, 1964.

Shishkin, M.A., The Morphology of Early Amphibians and the Problem of Evolution of Lower Tetrapods, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1973, vol. 137, pp. 1–257.

Shomysov, N.M., On the Geological and Petrological Characteristics of a New Locality Containing a Permian Terrestrial Vertebrate Fauna, Vyshka, from Molotov Mountain, *Uchen. Zap. Gor'k. Gos. Univ.* (Gorki), 1954, no. 25, pp. 267–273.

Shpinar, Z.V., *Reviziya nekotorykh moravskikh diskozavristsidov (Labyrinthodontia)* [Revision of Some Moravian Discosauriscids (Labyrinthodontia)], Prague: Chekhosl. Akad. Nauk, 1953.

Sullivan, C. and Reisz, R.R., First Record of *Seymouria* (Vertebrata: Seymouriamorpha) from Early Permian Fissure Fills at Richards Spur, Oklahoma, *Can. J. Earth Sci.*, 1999, vol. 36, pp. 1257–1266.

Sumida, S.S., Lombard, R.E., and Berman, D.S., Morphology of the Atlas–Axis Complex of the Late Palaeozoic Tetrapod Suborders Diadectomorpha and Seymouriamorpha, *Phil. Trans. Roy. Soc. London*, 1992, vol. 36, pp. 259–273.

Sumida, S.S., Berman, D.S., and Martens, T., Biostratigraphic Correlation between the Lower Permian of North America and Central Europe Using the First Record of an Assemblage of Terrestrial Tetrapods from Germany, *Paleobios*, 1996, vol. 17, nos. 2–4, pp. 1–12.

Sushkin, P.P., On the Representatives of the Seymouriamorpha, Supposed Primitive Reptiles, from the Upper Permian of Russia, and on Their Phylogenetic Relations, *Occas. Pap. Boston Soc. Nat. Hist.*, 1925, vol. 5, pp. 179–181.

Sushkin, P.P., Notes on the Pre-Jurassic Tetrapoda from Russia: 3. On Seymouriamorpha from the Upper Permian of North Dvina, *Repr. Palaeontol. Hungarica*, 1926, vol. 1, pp. 337–342.

Sushkin, P.P., On the Modifications of the Mandibular and Hyoid Arches and Their Relations to the Brain-case in the Early Tetrapoda, *Paleontol. Z.* (Sonderabdruck), 1927, vol. 8, no. 4, pp. 263–321.

Szarski, H., Some Remarks on Herbivorous Lizard, *Evolution*, 1962, vol. 16, pp. 1–529.

Tatarinov, L.P., A New Locality of Permian Seymouriamorphs in the USSR, *Paleontol. Zh.*, 1964, no. 1, pp. 139–141.

Tatarinov, L.P., Seymouriamorphen aus der Fauna der USSR, *Handb. Paläoherpetol.*, 1972, vol. 5, no. 5, pp. 70–80.

Tchudinov, P.K., Cotylosaurs from the Shikhovo-Chirki Locality, *Dokl. Akad. Nauk SSSR* (Moscow), 1955, vol. 103, no. 3, pp. 913–916.

Tchudinov, P.K., Cotylosaurs from the Upper Permian Red Beds of the Fore-Urals, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1957, vol. 68 (Cotylosaurs and Batrachosaurs from the Upper Permian of the USSR), pp. 19–88.

Tchudinov, P.K. and Vjuschkov, B.P., New Data on Small Cotylosaurs from the Permian and Triassic of the USSR, *Dokl. Akad. Nauk SSSR* (Moscow), 1956, vol. 8, no. 3, pp. 547–550.

Tverdokhlebova, G.I., On a New Find of Small Cotylosaurs in the Upper Tatarian Beds of the Orenburg Fore-Urals, *Vopr. Geol. Yuzhn. Urala Povolzh.*, 1972, no. 8, pp. 45–49.

Tverdokhlebova, G.I. and Ivakhnenko, M.F., New Tetrapods from the Tatarian Stage of Eastern Europe, *Paleontol. Zh.*, 1984, no. 2, pp. 122–126.

Vaughn, P.P., *Seymouria* from the Lower Permian of Southeastern Utah, and Possible Sexual Dimorphism in That Genus, *J. Paleontol.*, 1966, vol. 40, no. 3, pp. 603–612.

Vjuschkov, B.P., New Kotlassiomorphs from the Tatarian Beds of European Russia, *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Moscow), 1957, vol. 68, pp. 89–107.

Vorob'eva, E.I. and Chugunova, T.Yu., *Zubnaya sistema yashcherits: Taksonomicheskoe i ekologicheskoe raznoobra-*

zie (Dental System of Lizards: A Taxonomic and Ecological Diversity), Moscow: Nauka, 1995.

Watson, D.M.S., A Sketch Classification of the Pre-Jurassic Tetrapod Vertebrates, *Proc. Zool. Soc. London*, 1917, pp. 167–186.

Watson, D.M.S., On *Bolosaurus* and the Origin and Classification of Reptiles, *Bull. Mus. Compar. Zool.*, 1954, vol. 111, no. 9, pp. 295–450.

Weishampel, D.B. and Jianu, C.M., Plant Eaters and Ghost Lineages: Dinosaurian Herbivory Revisited, in *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record*, Sues, H.D., Ed., Cambridge, 2000, pp. 123–143.

Werneburg, R. and Kiersnowsky, H., A Discosauriscid Amphibian from the Rotliegend of the Intrasudetic Basin in Poland and Its Biostratigraphic Importance, *Acta Univ. Wratislaviensis*, 1996, no. 1795, pp. 117–122.

Werneburg, R., Zur Taxonomie der jungpaläozoichen Familie Discosauriscidae Romer, 1947 (Batrachosauria, Amphibia), *Freib. Forsch.*, 1985, vol. C400, pp. 117–133.

Werneburg, R., Some Notes to Systematic, Phylogeny, and Biostratigraphy of Labyrinthodont Amphibians from the Upper Carboniferous and Lower Permian in Central Europe, *Acta Mus. Reginaerhadecensis, Ser. A: Sci. Naturales*, 1989, vol. 22, pp. 117–129.

White, T.E., Osteology of *Seymouria baylorensis* Broili, *Bull. Mus. Compar. Zool.*, 1939, vol. 85, no. 5, pp. 325–409.

Williston, S.W., A New Family of Reptiles of the Permian of New Mexico, *Am. J. Sci.*, 1911, vol. 31, pp. 378–398.

Zhang, F., Li, Y., and Wan, X., A New Occurrence of Permian Seymouriamorphs in Xinjiang, China, *Vertebr. Palasiat.*, 1984, vol. 22, no. 4, pp. 294–304.