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New Data on Procolophons from the Permian of Eastern Europe

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Abstract—Procolophons from the Upper Permian of Eastern Europe are revised. The genus *Microphon* Ivachnenko, 1983 established on the basis of a maxilla from the Donguz 6 locality and earlier referred to procolophonids (Procolophonidae) is actually a seymouriamorph; the genera *Raphanodon* Ivachnenko, 1987 and *Raphaniscus* Bulanov, 2000 are its junior synonyms. The procolophons (Parareptilia) *Nyctiphruretus optabilis* sp. nov. (Nyctiphruretidae) and *Kinelia broomi* gen. et sp. nov. (Procolophonidae, Spondylolestinae) are described based on the jaws from the Upper Permian of European Russia.

INTRODUCTION

In this study, procolophons are treated after Ivachnenko (1987) as the order Procolophonomorpha of the class Parareptilia. Having appeared in the Permian, procolophons passed the Permian–Triassic boundary and demonstrated a peak of taxonomic diversity in the Early Triassic; in the deposits of this age, they are known from all continents, including Antarctica. This allows one to use this group for the interregional correlation. In spite of the wide geographical distribution, various trophic specializations (displayed in the variability of the dental system), and, consequently, diverse ecological adaptations, procolophons disappeared at the end of the Triassic. They were obviously superseded by the small-sized diapsid reptiles, lizards (Ivachnenko, 1979).

In the Permian, procolophons are scarce. To date, the following five monotypical genera have been described from the Upper Permian: *Nyctiphruretus* Efremov, 1938; *Microphon* Ivachnenko, 1983; *Suchonosaurus* Tverdochlebova et Ivachnenko, 1994; *Owenetta* Broom, 1939; and *Barasaurus* Piveteau, 1955. The first three genera occur in Eastern Europe, *Owenetta* comes from South Africa, and *Barasaurus* comes from Madagascar.

In the latest generalizing work devoted to the revision of this order (Ivachnenko, 1979), the least specialized members of the group, *Nyctiphruretus acudens*, *Owenetta rubidgei*, and *Barasaurus besairei*, which are characterized by the presence of surface sculpturing, superficial otic notch, and numerous weakly differentiated teeth, were combined in the family Nyctiphruretidae. *Microphon exiguus* and *Suchonosaurus minimus* described later on the basis of jaws were assigned to procolophonids (Spondylolestinae) based on the structural features of the dental system (Ivachnenko, 1983; Tverdokhlebova and Ivachnenko, 1994).

Among the European species, only *Nyctiphruretus acudens* is well characterized by the cranial material. About 70% of all finds from the localities in the basin of the Mezen River, having similar genesis and dated as the Upper Kazanian–Lower Tatarian Substages (Ivachnenko *et al.*, 1997), belong to this species (Ivachnenko, 1990). More than 100 *Nyctiphruretus* skulls and other skeletal fragments comprising a wide ontogenetic range are currently housed at the Paleontological Institute of the Russian Academy of Sciences (PIN). This allows one to judge the morphological features of primitive procolophons based on an extensive material.

Microphon exiguus is described from the Donguz 6 locality (Orenburg Region) based on several isolated maxillae (Ivachnenko, 1983). Our study of the type series has shown that all mentioned jaws, including the holotype of *M. exiguus* (PIN, no. 3585/31; Fig. 1), are comparable to the jaws of the juvenile seymouriamorph *Raphaniscus tverdochlebovae* (Ivachnenko, 1987) presented in the collection by complete skulls and numerous isolated jaws from the same locality.

The generic name *Raphaniscus* was introduced by Bulanov (2000) in exchange for *Raphanodon* Ivachnenko, 1987, since it was shown that the holotype of the type species (*R. ultimus*) of the later belonged to the genus *Karpinskiosaurus* Sushkin, 1925. The identity of the material on *Raphaniscus tverdochlebovae* and *Microphon exiguus* from the Donguz 6 locality (which is the type locality of both taxa) is presently undoubted. Therefore, *Microphon exiguus* Ivachnenko, 1983 should be accepted as the valid name for the Doguz seymouriamorph. *Raphanodon* Ivachnenko, 1987 and *Raphaniscus* Bulanov, 2000 are considered to be the junior synonyms of the genus *Microphon* Ivachnenko, 1983.

The structure of the seymouriamorph maxilla is rather peculiar and shows a number of morphological features atypical of procolophons. In particular, the ascending lamina of the maxilla in *Microphon exiguus* is weakly developed and only slightly overlaps the lachrymal. The lachrymal participates in the formation of the orbital rim and nares, as observed in all members of the order. The labial surface of the maxilla is pierced by numerous foramina, especially, in the postnasal area. A peculiar depression, which was probably the

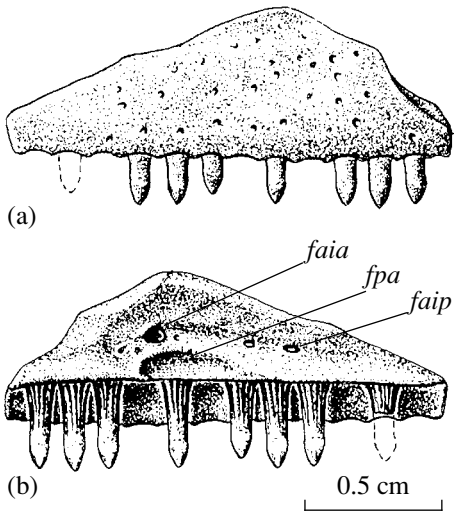

Fig. 1. *Microphon exiguus* Ivachnenko, 1983; holotype PIN, no. 3585/31, right maxilla: (a) external and (b) internal surfaces; Russia, Orenburg Region, Donguz 6 locality; Upper Permian, Upper Tatarian Substage, North Dvinian Regional Stage. Designations: (*faia*) and (*faip*) anterior and posterior foramina of the infraorbital artery, (*fpa*) depression for the preorbital process.

attachment area for the antorbital process of the cartilaginous olfactory capsule, is located on the lingual side under the anterior foramen of the infraorbital artery on a level with the posterior edge of the choana. The similar antorbital process is present in living anurans and urodelans and supports the maxilla at the early stages of ontogenetic development.

The *Microphon* jaw teeth have deep bases with well-pronounced folded structure. The folds are clearly seen on the external surface and inside the pulpar cavity. The teeth are attached to the jaws in a prothecodont manner; i.e., their bases are partly enclosed in the jaw bones. The crowns are monocuspid only in the specimens, the skulls of which are at most 23 mm long; in larger individuals, the replaceable teeth have additional denticles on the cutting edge. The number of the denticles gradually increased in the course of ontogeny and reached three or four on each side of the central tooth apex (Bulanov, 2000).

The tooth row is covered approximately to the middle of the tooth depth by a thin lamina formed as a result of the ventral growth of the maxillary alveolar margin. The teeth do not fuse with the lamina, and a free space is usually present between the lamina and the teeth.

The ascending lamina of procolophons is a high plate overlapping the anterior region of the lachrymal and widely articulated with the nasal. The absence of contact between the maxilla and the nasal is a primitive character; this is observed in only *Nyctiphruretus*, in which the lachrymal forms a narrow band extending onto the external surface of skull. The characteristic depression, which probably contained an analogue of the lateral nasal gland of extant lizards (Ivachnenko, 1979) is present around the nasal foramen at the external surface of the maxilla. The similar depression described and figured in the first description of *Microphon exiguus* is a result of the deformation of the holotype.

The infraorbital artery of procolophons passed to the labial surface through a large foramen. The latter faces anteriorly and is located under the nares. In addition to this foramen, the external surface of the bone has only a small number of the upper labial foramina arranged strictly in a line. These foramina provided passage for the blood vessels and accompanying nerves from the alveolar canal to the soft tissue of the mouth margin. A pit for the articulation with the antorbital process is absent, and the entire arterial groove located on the internal surface of the maxilla extends along the dorsal surface of the dental area.

Among procolophons, I registered weak folding of the tooth bases only in some nyctiphrurets (specimen PIN, no. 4659/1), additional denticles are absent at all ontogenetic stages. The teeth are attached to the jaws in subacrodont manner, i.e., the tooth bases cover the ridge of the alveolar margin, which weakly projects relative to the surface of the dental area.

In contrast to *M. exiguus*, there is no doubt about the assignment of *Suchonosaurus minimus*, which was described based on an incomplete maxilla from the Salarevo locality (Vologda Region) (Tverdokhlebova and Ivachnenko, 1994), to procolophons. The shape and height of the ascending lamina; the patterns of the passage of the infraorbital artery and, in particular, its passage on the labial surface; the absence of depression for the antorbital process; and the presence of a depression in the nasal area unequivocally indicate the taxonomic position of the specimen. Available jaw (holotype SSU (Saratov State University), no. 104B/1326; Fig. 2) contains 12 alveoli; however, the actual number of teeth in the *Suchonosaurus* maxilla was much larger. Three alveoli lack teeth; teeth 2, 4, and 10 bears traces of resorption manifested by the presence of rounded depressions in the basal part of the tooth bases.

Suchonosaurus is characterized by a well-pronounced size differentiation of teeth. This allows one to refer this genus to procolophonids. Remarkably, the large teeth are located in the anterior division of the bone, while, in the other members of the family, they are located in the posterior part of the tooth row. The second tooth is the largest in the maxilla (the first alveolus is also large). The tooth height decreases posteriorly, the third tooth is smaller than the second, and the fourth is smaller than the third; other teeth are approximately equal in size beginning with teeth. The crowns are flattened and chisel-shaped; they are high and narrow in the anterior teeth and become wider and lower in the posterior teeth. The lingual surface of the crowns bears two facets covered by short longitudinal ridges and converging to the center; the anterior facet is relatively wide and the posterior facet is somewhat smaller.

Since procolophons are scarce in the Permian deposits, jaw bones of these animals found in different localities and currently housed at the PIN deserve special consideration. These specimens are isolated finds of fragmentary dentaries. Based on the presence of the characteristic dentition, the majority of these bones are assigned to the least specialized procolophons of the family *Nyctiphruretidae*.

An exception is an incomplete dentary (PIN, no. 4548/3; Fig. 3) from the Vozdvizhenka locality (Orenburg Region). The teeth preserved on this bone display a well-pronounced size heterodonty in the anterior division of the jaws, as in *Suchonosaurus*. This allows one to assign this specimen to spondylolestines and establish a new genus and species, *Kinelia broomi* gen. et sp. nov., based on the tooth shape.

The second specimen, PIN, no. 4544/4, a fragmentary dentary (Fig. 4) from the Pokrovka locality (Orenburg Region), belongs to a nyctiphruretid. In the structure of the jaw teeth, this form demonstrates some nuances, which do not fit into the intraspecific and ontogenetic variabilities of *Nyctiphruretus acudens.* This form is established as a new species of the same genus, *N. optabilis* sp. nov.

A dentary (specimen PIN, no. 3713/87; Fig. 5) from the Poteryakha 2 locality (Vologda Region) is referred to the genus *Nyctiphruretus*. The structure of the teeth is similar to that of nyctiphrurets from Mezen, and the only indirect indication on differences between these forms is the different ages of the localities. A dentary from the Aristovo locality (Vologda Region) probably also belongs to a nyctiphruretid. This specimen is poorly preserved and contains only damaged teeth; however, the subacrodont type of their attachment, the absence of the folding of the bases, and the arrangement of the foramina for blood vessels on the external surface of the dentary clearly distinguish this specimen from the jaws of other Late Permian terrestrial vertebrates.

The new finds of procolophons come from different stratigraphic levels. In the Vozdvizhenka locality, *Kinelia broomi* is accompanied by nycteroleteriins (Nycteroleteromorpha), karpinskiosaurs (Seymouriamorpha), labyrinthodonts, and *Syodon* sp.; this indicates the Lower Tatarian Age of this locality and, consequently, an earlier appearance of procolophonid. The Pokrovka locality, where pareiasaurids were found, is dated as the Upper Tatarian Substage. Nyctiphruretid remains were also found in Poteryakha 2 (North Dvinian Regional Stage) and Aristovo (Vyatka Regional Stage) assigned to the same substage. Thus, primitive procolophons from Eastern Europe occurred in a wide age range from the Upper Kazanian Substage to the upper part of the Upper Tatarian. Nyctiphruretids were probably adapted to feeding on small-sized invertebrates and were widespread; the fact that they are rather scarce is attributable to the small sizes and terrestrial mode of live caused by the dominance of large amphibians in the Late Permian basins: anthracosauromorphs,

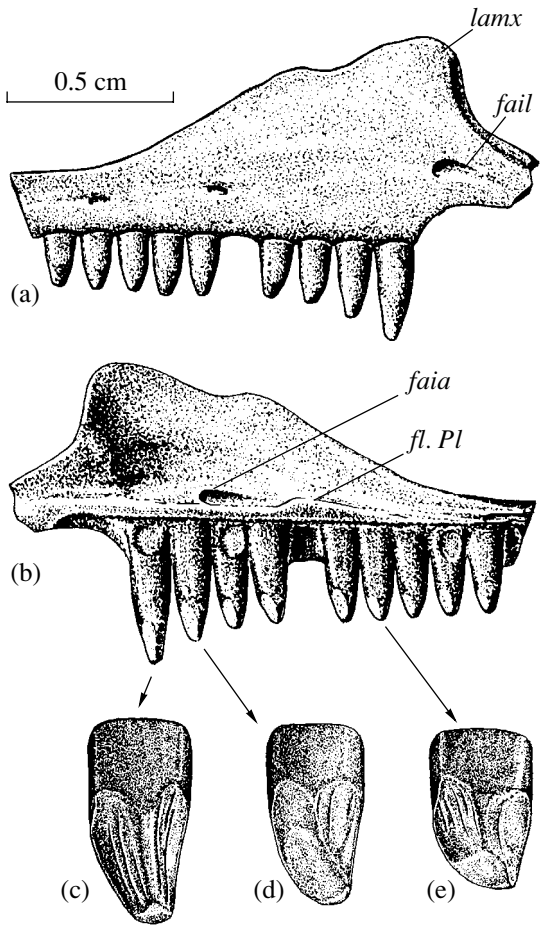

Fig. 2. *Suchonosaurus minimus* Tverdochlebova et Ivachnenko, 1994; holotype SSU (Saratov State University), no. 104B/1326, right maxilla: (a) external and (b) internal surfaces; (c), (d), and (e) crowns of the maxillary teeth, lingual view: (c) second, (d) third, and (e) eighth; Russia, Vologda Region, Salarevo locality; Upper Permian, Upper Tatarian Substage, Vyatkian Regional Stage. Designations: (*faia*) anterior foramen for the infraorbital artery, (*fail*) labial foramen of the infraorbital artery; (*fl.Pl*) facet for the palatine attachment, and (*lamx*) ascending lamina of the maxilla.

seymouriamorphs, and batrachomorph labyrinthodonts. Spondylolestines emerged in the course of adaptation to new feed object, which was accompanied by the reorganizations of the dental system and jaws.

In conclusion, the numerous small upper and lower jaws (more than 150 specimens) described by Bolt (1980) from the Lower Permian of North America (Fort Sill locality) and presumably referred to the microsaurs or reptiles should be mentioned. The detailed figures in this work allow one to assign this form, which has no Latin binomial name, to the Nyctiphruretidae. The deep ascending lamina of the maxilla, a deep depression in the nasal area, a large foramen of the infraorbital artery located below this depression, the presence of a high dorsal process and a well-developed palatine process of the premaxilla, the pattern of attachment and the num-

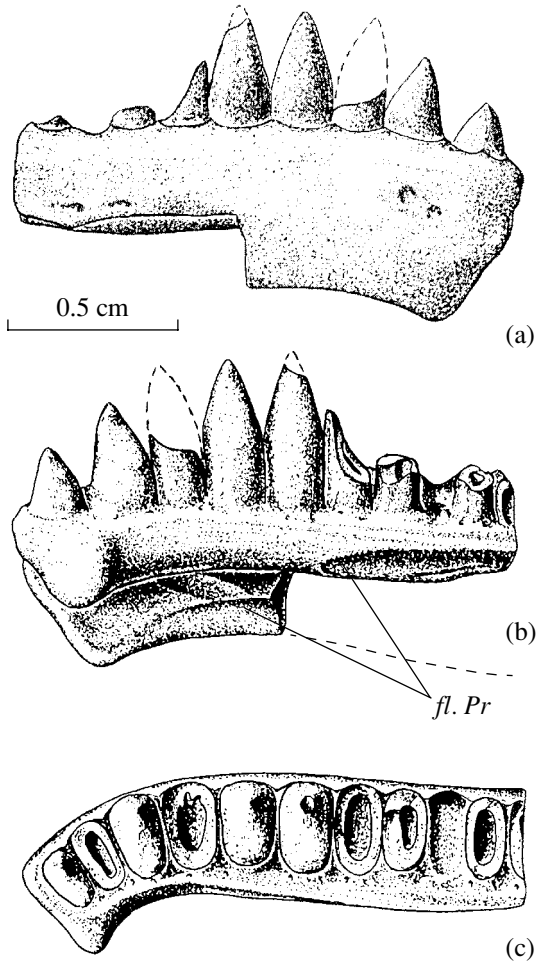

Fig. 3. *Kinelia broomi*, sp. nov.; holotype PIN, no. 4538/3, right dentary: (a) external, (b) internal, and (c) dorsal views. Designations: (*fl.Pr*) area for the prearticular.

ber of jaw teeth, the shape of tooth crowns, and certain other characters suggest formal identity of this form with *Nyctiphruretus acudens*. An exception is one feature, i.e., a greater number of premaxillary teeth (five or six up to seven in normal cases versus, four or five in *Nyctiphruretus* from Mezen). This most likely indicates that the American procolophon is more primitive. Possibly, the cosmopolitan distribution in the Triassic, various specialization patterns, and the presence of parallelisms in the development are a result of the wide geographical distribution of this group as early as the Permian.

SYSTEMATIC PALEONTOLOGY

Order Procolophonomorpha

Family Nyctiphruretidae Efremov, 1938

Genus *Nyctiphruretus* Efremov, 1938

***Nyctiphruretus optabilis* Bulanov, sp. nov.**

Etymology. From the Latin *optabilis* (desirable).

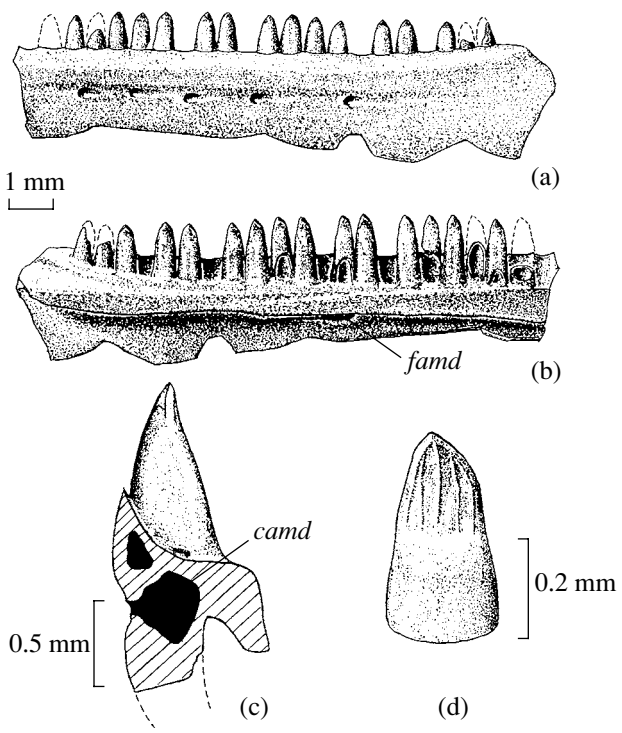

Fig. 4. *Nyctiphruretus optabilis*, sp. nov.; holotype PIN, no. 4544/4, left dentary: (a) external and (b) internal surfaces, (c) cross section of the bone at tooth 13 from the end of the lower jaw, and (d) tooth 10 from the end of the lower jaw, lingual view. Designations: (*camd*) alveolar canal of the lower jaw and (*famd*) foramen for the mandibular artery.

Holotype. PIN (Paleontological Institute of the Russian Academy of Sciences), no. 4544/4, fragmentary dentary; Russia, Orenburg Region, Grachevka District, Pokrovka locality (quarry southwest of the village of Pokrovka); Upper Permian, Upper Tatarian Substage.

Diagnosis. Jaw teeth with narrowed and asymmetrical crowns, narrower than tooth bases; tooth apices displaced caudally with reference to central position.

Description (Fig. 4). The holotype is a fragmentary dentary containing 21 alveoli of the posterior half of the tooth row. Five alveoli lack teeth; the bases of four teeth in the basal part are resorbed. The ventral edge of the dentary is damaged; the external surface of the bone has five foramina facing posteriorly and forming a row lengthways the alveolar edge, which is somewhat raised above the dental area. The foramen of the mandibular artery in the depression of the Meckel's groove is located at tooth 13 from the posterior end of the lower jaw.

The teeth are low and have small crowns, which are narrower than the upper part of the bases. The tooth apices are weakly flattened and displaced caudally from the central position; on the lingual surface, the crowns bear apically converging crests. The thin-walled bases

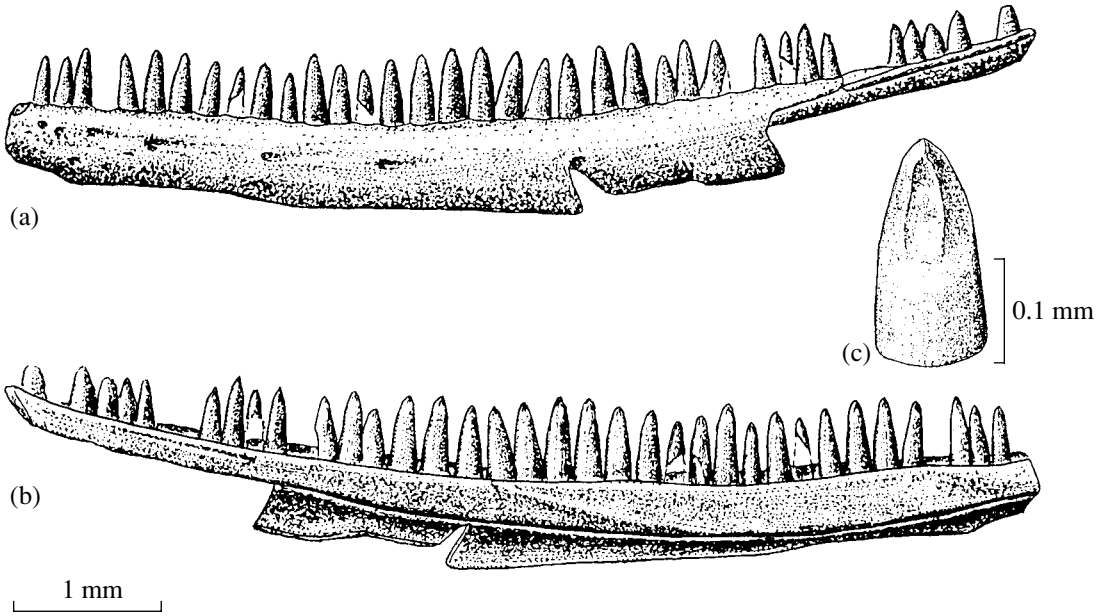

Fig. 5. *Nyctiphruretus* sp.; PIN, no. 3713/87: (a) and (b) left dentary: (a) external and (b) internal surfaces, and (c) crown of a lower jaw tooth, lingual view. Vologda Region, Poteryakha 2 locality; Upper Permian, Upper Tatarian Substage.

are weakly lengthened ovals in cross section, lack folding, and widely envelop the ridge of the alveolar edge.

Comparison. The new species differs from *N. acudens* by the asymmetrical and narrow crowns, which are narrower than the upper part of the tooth bases.

Material. Holotype.

Family Procolophonidae Seeley, 1888

Subfamily Spondylolestinae Ivachnenko, 1979

Genus *Kinelia* Bulanov, gen. nov.

Etymology. From the Malaya Kinel River.

Type species. *Kinelia broomi* Bulanov, sp. nov.

Diagnosis. Dentary with at least ten teeth. Tooth bases longitudinally extended and tooth crowns conical.

Species composition. Type species.

Comparison. The new genus differs from the genera *Contritosaurus* Ivachnenko, 1974 and *Procolophonoides* Ivachnenko, 1979 by a larger number of the lower jaw teeth. It differs from the genera *Spondylolestes* Broom, 1937, *Phaantosaurus* Tchudinov et Vjuschkov, 1956, and *Contritosaurus* by the more expressed heterodonty of the lower jaw teeth; it differs from the genera *Suchonosaurus* Tverdochlebova et Ivachnenko, 1994, *Neoprocolophon* Young, 1957, and *Phaantosaurus* by the shape of the tooth crowns; it differs from the genera *Suchonosaurus, Contritosaurus,* and *Spondylolestes* by the longitudinally extended tooth bases; and it differs from the genus *Contritosaurus* by the absence of the jaw teeth inclination.

Kinelia broomi Bulanov, sp. nov.

Etymology. In honor of the South African palaeontologist R.L. Broom.

Holotype. PIN, no. 4538/3, anterior division of the dentary; Russia, Orenburg Region, Vozdvizhenka locality; Upper Permian, Lower Tatarian Substage.

Description (Fig. 3). The dentary is massive and contains at least ten teeth. The symphysial surface is increased by a peculiar expansion at the anterior edge of the dental lamina. The position of the facets for the prearticular indicates the presence of an extended notch between the prearticular and the symphysis. A notch is present in the same position in other procolophonids (*Phaantosaurus, Contritosaurus*, etc.). A pair of small foramina is located on the external surface of the anterior margin of the bone. A foramen accompanied by a posteroventrally directed groove is located just posterior to the symphysis in the depression of the Meckel's groove.

The bases of the completely developed teeth are thick-walled, lack folding (dentin is folded only inside the pulpar cavities of the fourth tooth), and substantially compressed laterally; they are lengthened and oval in cross section. The crowns are conical, their apices lack flattening and slightly displaced caudally from the central position; this is especially clear in dorsal view; the lingual surface lacks ridges. The first tooth is smaller than the others; the other teeth increase in size to tooth 6, which is the largest tooth of the jaw.

Material. Holotype.

ACKNOWLEDGMENTS

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