# Alpha Taxonomy of the Russian Permian Procolophonoid Reptiles

Author: Säilä, Laura K.

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# Alpha taxonomy of the Russian Permian procolophonoid reptiles

LAURA K. SÄILÄ

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European Russia has been the source of many procolophonoid taxa from both the Permian and Triassic, and a Permian origin for the procolophonoid family Procolophonidae has been based on the Russian taxon *Microphon exiguus.* Recently, this taxon was reclassified as a seymouriamorph and, in its place, the taxa *Nyctiphruretus*, *Suchonosaurus*, and *Kinelia* from the Middle and Upper Permian of Russia were suggested as "procolophons", using evolutionary-systematic classification methods. In recent phylogenies, however, *Nyctiphruretus* has been recovered as a non–procolophonoid parareptile, whereas *Kinelia* and *Suchonosaurus* have never been included in a phylogenetic study. Re-examination indicates that *Suchonosaurus* is a member of the procolophonoid subfamily Procolophonidae based on the shape of the maxillary bone and the external naris, the laterally visible maxillary depression, and the number and type of maxillary teeth. *Kinelia*, on the other hand, is excluded from the Procolophonoidea because of its subpleurodont dental attachment and lack of any procolophonoid features. Thus, *Suchonosaurus* is the only confirmed Permian procolophonid from the Permian of Russia. Additionally, re-examination of the holotype of *Microphon exiguus* confirms that it is identical to the seymouriamorph specimens recently included in the genus *Microphon* and that it lacks procolophonoid features. The earliest unequivocal record of the subfamily Procolophonidae is confirmed from the Late Permian of Russia, making Russia the only region where, with certainty, both Permian and Triassic procolophonids have been discovered.

Key words: Parareptilia, Procolophonoidea, Procolophonidae, origin, palaeobiogeography, Permian, Russia.

*Laura K. SäiIä [Laura.Saila@helsinki.fi], Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1JU, UK; current affiliation: Jernvall Evo-Devo Research Group, Institute of Biotechnology, Viikinkaari 9 (PL 56), 00014 University of Helsinki, Finland.*

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## Introduction

The Procolophonoidea is an important group of small- to medium-sized parareptiles that emerged in the Permian and had a global distribution during the Triassic. Procolophonoids have been proposed to be the sister group of turtles (Reisz and Laurin 1991; Laurin and Reisz 1995) and it has also been estimated that up to 80% of procolophonoid lineages survived the Permian–Triassic (P/Tr) extinction event (Modesto et al. 2001, 2003; Ketchum and Barrett 2004). European Russia is the only place outside southern Africa where a succession of procolophonoids from the Permian and the Triassic are found, but the Permian Russian procolophonoids are very poorly known, and their procolophonoid affinities are uncertain (Spencer and Benton 2000; Bulanov 2002; Cisneros 2008a). Most phylogenetic studies agree that the Procolophonoidea can be divided into two families, Owenettidae and Procolophonidae (deBraga 2003; Modesto and Damiani 2007; Cisneros 2008a, b; Säilä 2008) and a Permian origin for the Procolophonidae has been based on *Microphon exiguus* Ivakhnenko, 1983 from the Upper Permian of Russia. On the basis of the original description (Ivakhnenko 1983), Spencer and Benton (2000) and Modesto et al. (2001) recognized *Microphon* as a procolophonid but considered it a possible junior synonym of known Triassic procolophonids such as *Contritosaurus*. Bulanov (2002, 2003) subsequently excluded *Microphon* from Procolophonoidea after reidentifying it as a seymouriamorph. However, both the original description (Ivakhnenko 1983) and Bulanov (2002, 2003) provide only interpretive drawings, and their illustrations of the holotype specimen differ in some aspects.

In addition to *Microphon*, other Permian fossils collected from Russia have been assigned to Procolophonidae. Bulanov (2002) considered the taxa *Nyctiphruretus*, *Suchonosaurus*, and *Kinelia* from the Middle and Upper Permian of Russia as "procolophons" (sensu the terminology of Bulanov 2002). *Suchonosaurus minimus* Tverdokhlebova and Ivakhnenko, 1994 was orinally assigned to the procolophonid subfamily Spondylolestinae (Tverdokhlebova and Ivakhnenko 1994) but this subfamily, erected by Ivakhnenko (1979), is not considered valid because its diagnosing characters are plesiomorphic for procolophonoids as a whole (Spencer and Benton 2000) and *Spondylolestes* itself is widely considered a nomen dubium (Spencer 2000; Spencer and Benton 2000; Modesto et al. 2002). However, Cisneros (2008a) went on to exclude *Suchonosaurus* from Procolophonoidea based on its

"pleurodont dentition", interpreted as such from the original descriptive drawings of Tverdokhlebova and Ivakhnenko (1994), which themselves are remarkably different from the line drawings of Bulanov (2002, 2003).

Of the other two Permian "procolophons", recent phylogenies (Lee 1995; Tsuji 2006; Müller and Tsuji 2007) recognize *Nyctiphruretus* as a non-procolophonoid parareptile and it has been used as an outgroup in studies of procolophonoid interrelationships (Cisneros et al. 2004; Cisneros 2008a, b; Säilä 2008). *Kinelia broomi* Bulanov, 2002 on the other hand, has never been included in a phylogenetic study, but was assigned to Spondylolestinae, the (now) invalid procolophonoid subfamily, by Bulanov (2002) and, conversely, based on the description of Bulanov (2002), Cisneros (2008a) considered *Kinelia* a member of the procolophonoid subfamily Procolophonidae. Thus, the affinities of *Suchonosaurus* and *Kinelia* remain debatable: they might be procolophonoids, belonging either to the Owenettidae or the Procolophonidae, or even fall outside Procolophonoidea. This cannot be inferred from the literature, however, because the previous descriptions differ from each other markedly. The objective of this paper is to provide a thorough redescription of *Kinelia* and *Suchonosaurus* from the original material, in order to affirm or dispute their procolophonoid affinities. The possibility of the Permian taxa being junior synonyms of one or more of the Triassic Russian procolophononids, as suggested for *Microphon* by Modesto et al. (2001) and Spencer and Benton (2000), is also explored. If one or both of the taxa were found to fall within Procolophonidae, this would be a confirmed first occurrence for the subfamily in the fossil record. Furthermore, if one or both of the taxa fell within Owenettidae, this would expand the geographical distribution of Owenettidae outside Gondwana, which is where all owenettid taxa have been found so far.

Additionally, photographs and accurate illustrations of the type material of *Microphon* are presented as these have not been provided in any previous publication, and are needed for confirming their (non-procolophonoid) status. The affinities of *Nyctiphruretus* also require further consideration, but because this taxon is represented by a high number of previously undescribed specimens, it is only briefly discussed here. More extensive osteological and phylogenetic studies, by Valery Bulanov and the author respectively, will appear in forthcoming papers.

*Institutional abbreviations*.—BMNH, Natural History Museum, London, UK; BPI, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; SGU, Saratov State University, Saratov, Russia.

# Systematic palaeontology

## Class Reptilia Laurenti, 1768

## Subclass Parareptilia Olson, 1947

## Superfamily Procolophonoidea Romer, 1956

## Family Procolophonidae Cope, 1889

## *Suchonosaurus minimus* Tverdokhlebova and Ivakhnenko, 1994

Figs. 1, 2.

*Holotype and only specimen*: SGU 104B/1326, an isolated right maxilla.

*Type locality*: Salarevo, Russia.

*Type horizon*: Sokolkovskii Subcomplex, Salarevskaya Svita, Vyatkian (uppermost Tatarian).

*Emended diagnosis*.—*Suchonosaurus* is distinguished from other procolophonids by the following three characters: (1) 11 or 12 conical, fairly large maxillary teeth that are taller anteriorly and have subcircular bases, (2) a bony lip that covers the entire lower half of the labial side of the maxillary dentition and (3) a distinctive, three-fold wear pattern of the maxillary tooth crowns.

*Description*.—The holotype, and only specimen, of *Suchonosaurus minimus* is a nearly complete right maxilla, free of surrounding matrix, and thus all sides can be seen (Figs. 1, 2). The porous surface of the specimen, however, might have obscured some details. The overall shape of the maxilla is very similar to that of basal procolophonid *Coletta seca* Gow, 2000 (see Modesto et al. 2002) but is slightly less tall. In lateral view, a depression can be seen behind the circular external

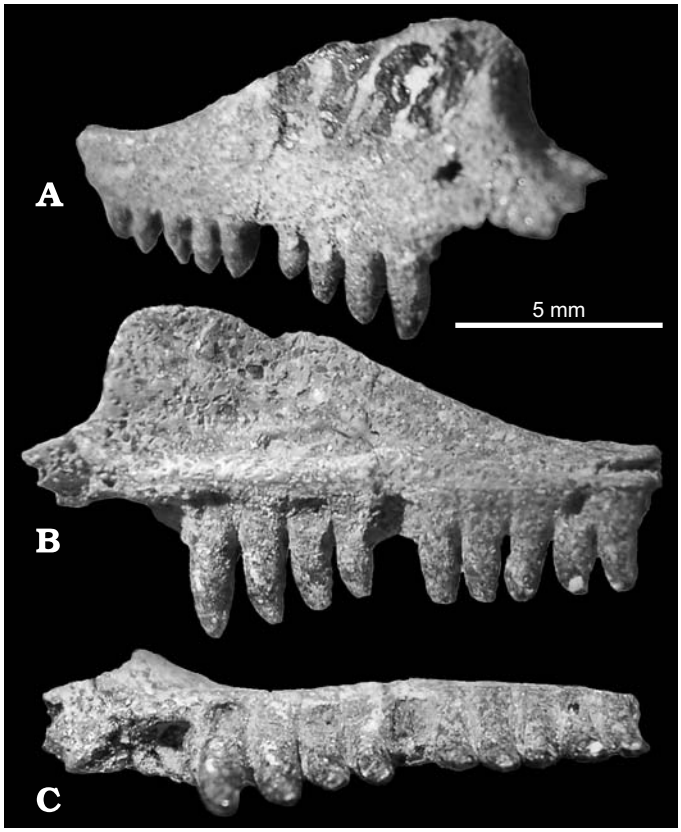


Fig. 1. Procolophonid reptile *Suchonosaurus minimus* Tverdokhlebova and Ivakhnenko, 1994, Salarevskaya Svita, uppermost Tatarian; SGU 104B/1326 (holotype), right maxilla. In anterolateral (**A**), medial (**B**), and medio-occlusal (**C**) views.

naris (Fig. 2A) and its considerable depth is revealed in anterolateral view (Fig. 1A). A large foramen, identified as the "labial foramen of the infraorbital artery" by Bulanov (2002: 527), is situated behind the depression. The equivalent foramen in other reptilian taxa has also been called the "anterolateral maxillary foramen" (Laurin and Reisz 1995: 186; Modesto et al. 2002: 885). Because of the erosion of the lateral surface, it is unclear how many other foramina opened on this surface but another, smaller, foramen can be seen near the posterior end of the maxilla (Fig. 2A). In lateral view, the teeth appear quite short and peg-like but this is because the lower half of the dentition is covered by a bony "lip". This is not evident in lateral view, but can be seen clearly from the medial side where the tooth apices are exposed in their entire length and the lip is exposed where a tooth is missing (Fig. 2B). There is a two-fold facet on the anterior process of the maxilla, exposed medially. The two halves of the facet face dorsomedially and ventromedially (Fig. 2B), thus indicating either that the premaxilla had a maxillary process that fitted both of the facets or, more likely, that the dorsomedial facet was contacted by a septomaxilla. The anterior facets cannot be seen on the maxillae of *Coletta* but the shape of the anterior process in lateral view (Modesto et al. 2002: fig. 1) is very similar to that of *Suchonosaurus* (Fig. 2A). In *Coletta* the process is contacted by both the premaxilla and the septomaxilla. Other notable features on the medial side of the maxilla of *Suchonosaurus* are a large foramen and a shelf (Fig. 2B) that were interpreted, respectively, as the "anterior foramen of the infraorbital artery" and a facet for the palatine attachment by Bulanov (2002: 527). However, a similar shelf or groove above the anterior maxillary dentition has been interpreted as an opening that carried nerves and/or blood vessels from the interior of the snout in pelycosaurs and the parareptile *Colobomyter* (Vaughn 1958; Modesto 1999), making this an alternative hypothesis for the function of the shelf.

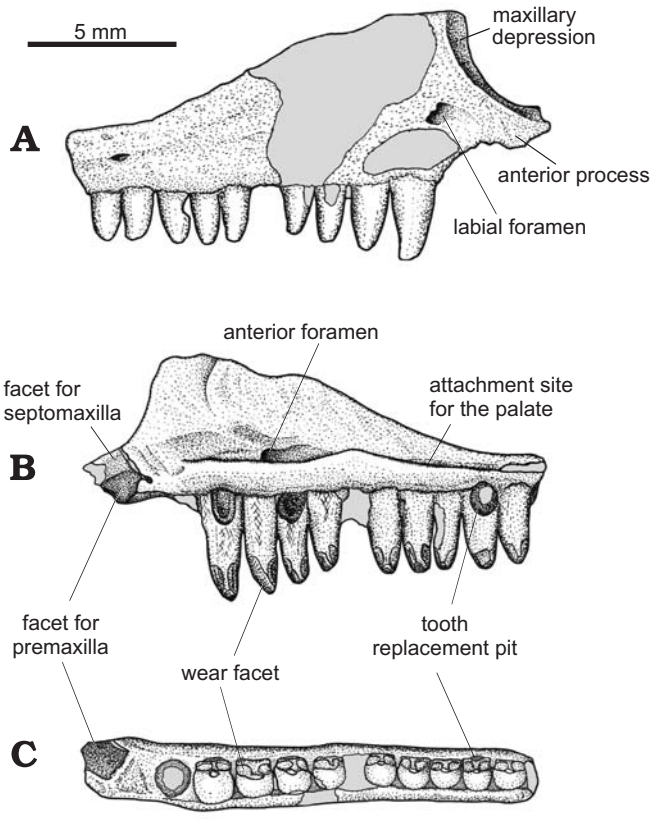


Fig. 2. Procolophonid reptile *Suchonosaurus minimus* Tverdokhlebova and Ivakhnenko, 1994, Salarevskaya Svita, uppermost Tatarian; SGU 104B/1326 (holotype), right maxilla. In lateral (**A**), medial (**B**), and occlusal (**C**) views.

There are 11 tooth positions on the maxilla but the first and fifth teeth are missing. The first preserved tooth is the tallest, with the second to fourth becoming progressively shorter and the rest being of similar size to the fourth. A shallow, large pit, indicating a short root, can be seen where the first tooth should be (Figs. 1C, 2C). Based on the diameter of the pit, the first tooth was most likely shorter than the second. Because the bony lip continues behind the last tooth (Fig. 2B), it has been considered a sign of more teeth being present in an unbroken maxilla (Tverdokhlebova and Ivakhnenko 1994; Bulanov 2002). The maxilla has, however, broken off very near the eleventh tooth (Figs. 1, 2), unlike Bulanov (2002: fig. 2) depicts. Additionally, the maxilla becomes very shallow towards the end of the row (Fig. 2B), indicating that it was nearing its posterior extent. The posterior tip of the maxilla is devoid of dentition in procolophonoids with similar maxillary shape (Modesto et al. 2002; Reisz and Scott 2002; Modesto and Damiani 2007). Thus the tooth number of *Suchonosaurus* is considered as no more than 11 or 12 at most. A similar number of maxillary teeth is present in the basal procolophonids *Coletta* and in *Pintosaurus magnidentis* Piñeiro, Rojas, and Ubilla, 2004. The teeth of *Suchonosaurus* were described as recurved by Tverdokhlebova and Ivakhnenko (1994) and depicted as totally straight by Bulanov (2002). In reality, the teeth are more or less straight, but the amount of wear on the mesial side of the tooth crowns has made some of them appear to be distally recurved (Fig. 2B). Most of the preserved teeth have three separate wear facets: the first on the mesolingual side of the tip, the second on the tip and the third on the distolingual side of the tip of the tooth crown (Fig. 2B, C). However, on the second and fourth preserved teeth the first two wear facets have fused together, making one large, mesolingually sloping facet that also touches the distal, third facet (Fig. 2B). The mesial wear facet is always the largest, except on the seventh preserved tooth where the distal wear facet is slightly larger. There are also distinct striations on the wear surfaces of some of the teeth (Fig. 2B). Similar, distinctive wear facets have not been previously reported on procolophonoids with conical dentition. There are also tooth replacement pits on the lingual sides of some teeth (Fig. 2B, C).

*Comments*.—*Suchonosaurus* was excluded from Procolophonoidea by Cisneros (2008a) because he regarded this genus as exhibiting "pleurodont dentition", a mode of implantation that is unknown in procolophonoids. Cisneros (2008a) drew his conclusions on the basis of the illustrations of Tverdokhlebova and Ivakhnenko (1994), which show the maxilla in medial and lateral views. Bulanov (2002) also il-

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lustrates only these views. However, the assessment of pleurodont dentition for *Suchonosaurus* is mistaken. Pleurodont dentition is characterized by (1) no sockets/alveoli or roots, (2) the teeth sitting in a dental groove with a high labial wall (and possibly a low lingual wall), and (3) attachment mainly to the lingual side of the labial wall (Motani 1997: fig. 1). The dentition of *Suchonosaurus* looks superficially pleurodont because it has a high labial wall or a bony "lip". However, *Suchonosaurus* does not have a dental groove, and instead has individual alveoli and shallow roots for each tooth, even if the teeth are tightly packed. This is evident from the missing first tooth, which reveals the empty alveolus and no dental groove (Figs. 1C, 2C). Additionally, the labial "lip" of bone is very shallow next to the first, missing tooth, indicating it was not the primary attachment surface for the tooth. The pattern of tooth implantation of procolophonoids is poorly documented, but it is generally agreed that they have teeth that are firmly ankylosed to the bone, a condition labelled "protothecodont" by Cisneros (2008a: 17) and Small (1997: 676). However, the use of the term protothecodont is variable in the literature. A definition by Small (1997), modified from Benton (1984) and Bolt and DeMar (1975), states "protothecodont (= subthecodont) teeth have shallow or fairly deep roots, and are ankylosed into the socket by bone of attachment, with no space for a periodontal ligament or other soft tissue between the socket and the base of the tooth. A typical reptilian tooth replacement or a variation thereof occurs" (Small 1997: 76). Other authors understand proto/subthecodonty to be comparable to pleurothecodonty, a condition where shallow sockets are within a dental groove that has low lingual and high labial walls (Motani 1997; Romer 1956; Wild 1973). There is also an implantation type called "ankylosed thecodonty", characterised by shallow roots that are ankylosed to the surrounding bone which is the same height on both sides of the teeth (Edmund 1969; Motani 1997), and this definition has been applied to procolophonids by Sues and Olsen (1993). Small (1997) points out, however, that ankylosed thecodonty is also linked with non-reptilian or totally absent tooth replacement in rhynchosaurs (Benton 1984; Chatterjee 1974), and while tooth replacement type is unknown in most procolophonoids, *Libognathus* (Small 1997) displays the normal reptilian type with replacement pits on the lingual side of the teeth. *Suchonosaurus* has the same method of tooth attachment, by shallow roots ankylosed firmly to the bone, as do other procolophonoids, regardless of what the method of attachment is called. It also has the normal reptilian tooth replacement, indicated by the pits next to its second, fourth and tenth teeth (Fig. 2B).

In addition, however, *Suchonosaurus* has a bony "lip" covering approximately half of the tooth crown on the labial side. This feature has not been reported in any other procolophonoid, but a paratype maxilla of the Triassic Russian procolophonid *Contritosaurus convector* Ivakhnenko, 1974, PIN 3357/2, appears to have an expansion of bone covering part of the labial side of its dentition (Fig. 3A, B), although

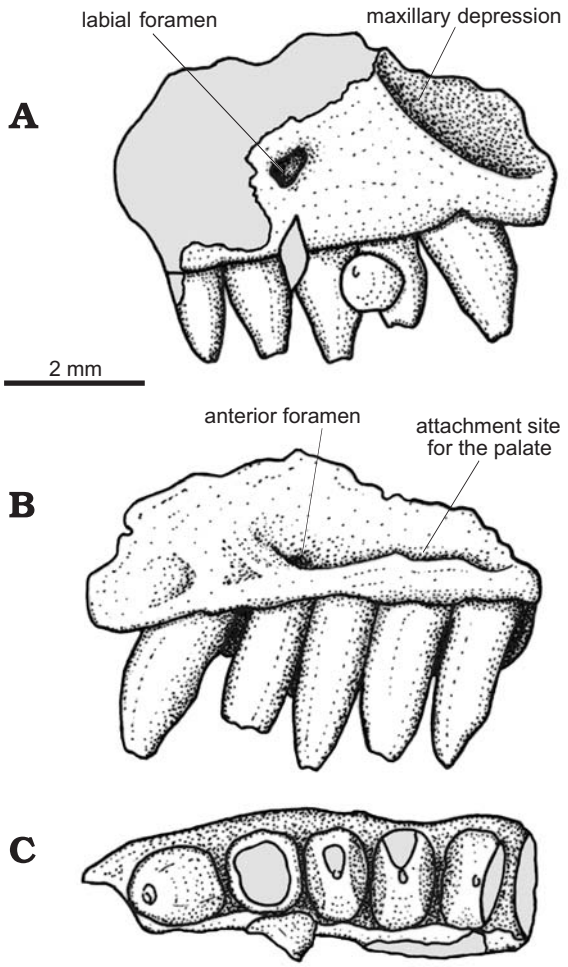


Fig. 3. Procolophonid reptile *Contritosaurus convector* Ivakhnenko 1974, Vokhmian Gorizont, Induan, earliest Triassic; PIN 3357/2, partial right maxilla. In lateral (**A**), medial (**B**), and occlusal (**C**) views.

the "lip" is not quite as extensive as in *Suchonosaurus*. The tooth attachment and features of the medial side of the maxillary bone are also very similar in *Suchonosaurus* (Fig. 2B) and *C. convector* (Fig. 3B). However, *C. convector* has transversely expanded tooth bases (Fig. 3C) and the maxillary depression is extensive (Fig. 3A), whereas the teeth of *Suchonosaurus* retain the more rudimentary conical shape with subcircular bases and the maxillary depression is restricted to the immediate border of the external naris (Fig. 2). Of other procolophonoids with conical dentition, tooth implantation is not specifically discussed (Modesto et al. 2001, 2002, 2003; Reisz and Scott 2002; Cisneros et al. 2004; Piñeiro et al. 2004; Modesto and Damiani 2007). This is largely because most taxa are represented by skulls that are preserved in occlusion with the mandible. No "lip" has been reported on *Coletta seca*, which is most similar to *Suchonosaurus* with respect to the shape of the maxillary bone and tooth number. Additionally, the tooth bases of the conical dentition of *Coletta* (and also *Pintosaurus*, which shares some features with *Suchonosaurus*) have been described as somewhat transversely expanded (Cisneros 2008a), whereas

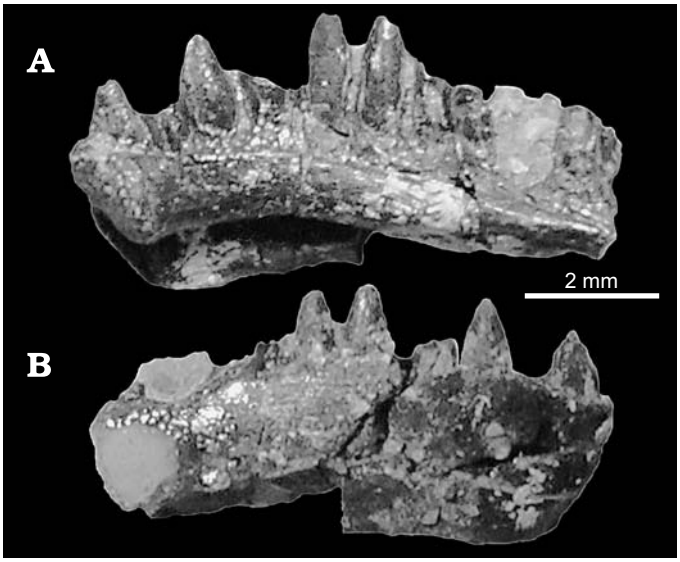


Fig. 4. Tetrapod *Kinelia broomi* Novikov 2002, Kutlukskaya Svita, uppermost Tatarian; PIN 4538/3 (holotype), partial right dentary. In medial (**A**) and lateral (**B**) views.

in *Suchonosaurus* the tooth bases are subcircular. Conical teeth with subcircular bases are also present in all owenettids and the basal procolophonid *Sauropareion anoplus* Modesto, Sues, and Damiani, 2001 (Modesto and Damiani 2007). *Sauropareion*, however, differs from *Suchonosaurus* in tooth number and the shape of the maxillary bone, and owenettids have a much higher number of much smaller teeth than *Suchonosaurus*. Additionally, *Suchonosaurus* is the only procolophonoid taxon that has straight, conical maxillary theet that is noticeably taller anteriorly.

Thus, *Suchonosaurus* does not possess pleurodont dentition or any other characters that would exclude it from Procolophonoidea. Furthermore, the circular shape of its external naris, the laterally visible maxillary depression, tooth number of 11 or 12, and size of its teeth support its inclusion in the procolophonoid family Procolophonidae. It is also not identical with any other known procolophonid, as evidenced by its several unique autapomorphies, and thus its status as a separate genus and species is upheld here.

*Stratigraphic and geographic range*.—Vyatkian (uppermost Tatarian) of European Russia.

## Order Tetrapoda Goodrich, 1930
## Class ?Reptilia Laurenti, 1768
## Subclass ?Parareptilia Olson, 1947
## *Kinelia broomi* Bulanov, 2002

Figs. 4, 5.

*Holotype and only specimen*: PIN 4538/3, a fragmentary right dentary.

*Type locality*: Vozdvizehnka, Russia.

*Type horizon*: Kutlukskaya Svita, Vyatkian Gorizont (uppermost Tatarian).

*Diagnosis*.—Extremely small tetrapod, possibly a parareptile, *Kinelia* is differentiated from other known tetrapod taxa by: (1) tightly packed teeth with labiolingually expanded tooth bases and labially situated tooth apices, set within a dental groove by subpleurodont tooth attachment, and (2) an oval symphyseal facet.

*Remarks*.—In the original description of *Kinelia*, Bulanov (2002) indicated that the length of the dentary was approximately 15 mm, which is almost double its actual length.

*Description*.—The dentary of *Kinelia* is minuscule, only 8.2 mm long, but because it is broken at its distal end, it must have been somewhat longer in life (Fig. 4). Bulanov (2002) called the dentary "massive" but it is in fact quite narrow, with the teeth being about the same height as the dentary bone in medial view (Figs. 4A, 5A). A deep Meckelian

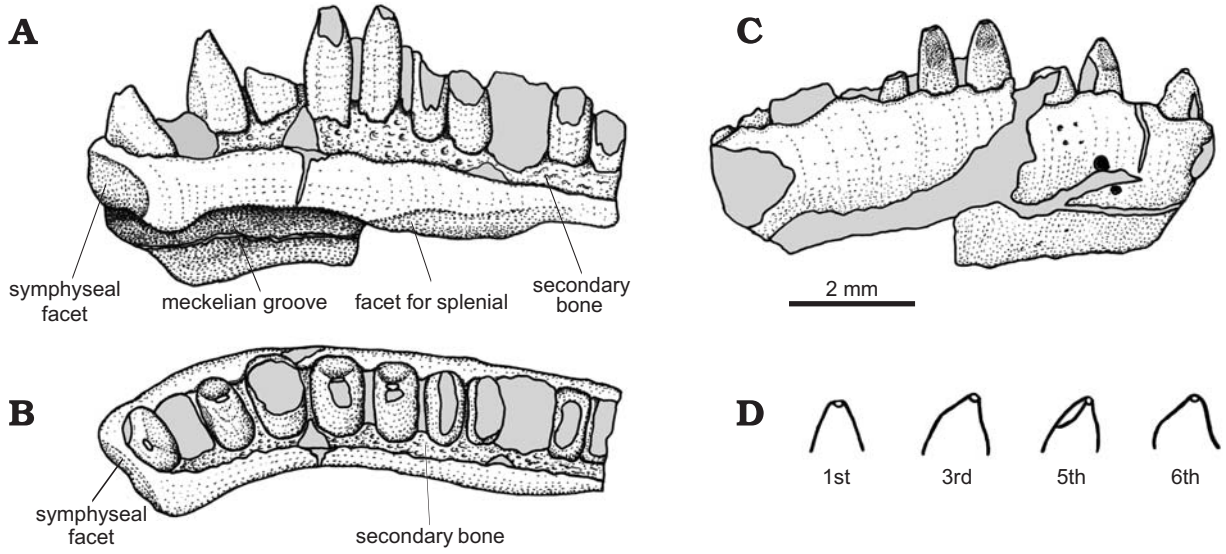


Fig. 5. Tetrapod *Kinelia broomi* Novikov 2002, Kutlukskaya Svita, uppermost Tatarian; PIN 4538/3 (holotype), partial right dentary. In medial (**A**), occlusal (**B**), and lateral (**C**) views. **D**. Schematic representation of the four well-preserved tooth crowns of the dentary teeth from posterior view. Lingual to the right, not to scale.

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groove, a facet for the attachment of the splenial and a transversely oval symphyseal facet are also visible on the medial side (Figs. 4A, 5A).

The teeth of *Kinelia* appeared to be individually ankylosed to the bone in the drawings of Bulanov (2002: fig. 3) but this is not the case. There is in fact a deep groove, with a higher labial wall, in which the teeth are sitting (Figs. 4, 5). Between the teeth and the lingual wall, and between the individual teeth, is a mass of porous bony substance, which is interpreted as secondary bone for tooth attachment (Fig. 5A, B). It is impossible to see if the teeth have roots or sockets within the dental groove, but the existence of the secondary bone, covering the tooth bases and attaching the teeth to the dental groove, implies that no roots were present and that the type of tooth attachment is "subpleurodont", a subtype of pleurodonty where tooth bases are extensively covered by bone of attachment (Presch 1974; Motani 1997). The illustrations of Bulanov (2002) imply there is a tooth pit/alveolus where the ninth tooth is missing, but the space within the dental groove here is actually filled with sediment that should be carefully removed to expose this area for study.

There are ten teeth on the dentary, and an indication of at least one more tooth, but several more could have been present. The first tooth is the smallest, and although its base is somewhat transversely broadened, it has a slightly conical shape with a concave posterior surface and a sharp tip (Fig. 5A–D). The size of the third tooth suggests that the teeth are successively taller until the sixth tooth, and possibly even further posteriorly, but this cannot be determined in the posteriormost teeth because the crowns have been damaged. In occlusal view, the teeth become slightly smaller in basal cross-section posteriorly. On each of the third, fifth and sixth teeth, where the crown is intact, the tip is transversely flattened and has moved into a position toward the lateral margin of the jaw (Fig. 5B). The teeth are also highly convex on their lingual side leading to the tip and concave on the labial side below the tip. This is most evident when the teeth are viewed from a position posterior to the tooth row (Fig. 5D).

*Comments*.—Bulanov (2002) assigned *Kinelia* to Procolophonoidea, and more specifically to the Subfamily Spondylolestinae, based on the pronounced size-heterodonty of the anterior dentition. However, size-heterodonty of teeth is not something limited to procolophonoids and, for example, the parareptile *Macroleter poezicus* Tverdokhlebova and Ivakhnenko, 1984 from the Russian Permian has a dentition that is variable in size along the tooth row (Tsuji 2006). Furthermore, Spondylolestinae is not considered a valid clade anymore and *Spondylolestes* is possibly a nomen dubium (Spencer 2000; Spencer and Benton 2000; Modesto et al. 2001). Cisneros (2008a), on the other hand, considered *Kinelia* a procolophonid because it has transversely broadened teeth. Again, however, procolophonids are not the only contemporaneous group with transversely broadened teeth. Trilophosaurids (archosauromorph diapsids), the parareptile Belebey and many synapsids from the Permo-Triassic have transversely broadened dentition (Sues and Olsen 1993; Spencer and Benton 2000; Reisz et al. 2007). However, the dentition of *Kinelia* does, on a superficial level, resemble the dentition of derived procolophonids more than it resembles the dentition of any of other groups with transversely broadened dentition. The main difference, however, is the tooth attachment type. Recently, *Vitalia grata* Ivakhnenko, 1973 and *Coelodontognathus donensis* Otshev, 1967, Triassic reptiles from Russia with transversely broadened dentition, were excluded from Procolophonoidea by Spencer and Benton (2000) because they lack procolophonoid features. One of the differences between procolophonoids on the one hand and *Vitalia* and *Coelodontognathus* on the other is that the latter taxa both have very deep tooth roots (this can be clearly seen on PIN 4173/126, PIN 1043/628, and PIN 4173/127–128), a dental attachment type not found in any procolophonoid. These two taxa have now been tentatively reclassified as trilophosaurids (Arkhangelskii and Sennikov 2008) on the basis of tooth shape. Similarly, the subpleurodont dental attachment type of *Kinelia* is not known in procolophonoids.

Furthermore, the actual teeth of *Kinelia* are different from those of any procolophonoid. Owenettids have a conical dentition and many derived procolophonids have transversely broadened teeth, usually with two cusps on each tooth. *Contritosaurus* and *Phaanthosaurus* (which are regarded as synonyms by Spencer and Benton 2000), however, do have transversely broad tooth bases with only one cusp but there are many features on the dentition of *Kinelia* that differ from *Contritosaurus*, *Phaantosaurus*, and other procolophonoids. Most procolophonids, including *Phaanthosaurus* (PIN 1025/1), have a number of tall, conical caniniform teeth at the anterior end of the dentary, and even if there is a reduction in number, the remaining single caniniform tooth is massive in size (for example in *Hypsognathus*, Sues et al. 2000). In *Kinelia*, however, the first tooth is the smallest and shortest of all the preserved teeth. The following teeth are transversely expanded, and while the shape of the tooth bases is quite similar to those of the maxillary dentition of *Contritosaurus convector* (Fig. 3C), the crowns are unlike those of any procolophonid with their labially situated, flattened tips and the convex lingual and concave labial sides (Fig. 5B–D).

Of the badly broken dentary bone itself, the facet for the splenial is situated around the same region in *Kinelia* (Fig. 5A) as in procolophonids, but the oval symphyseal facet, situated just underneath the tooth-bearing ramus, is very different from the extensive renal-shaped facet of *Phaantosaurus* (PIN 1025/1), *Procolophon* (Carroll and Lindsay 1985) and *Leptopleuron* (BMNH R3931), that covers the whole anterior tip of the dentary. Thus, *Kinelia* displays many features that support its exclusion from, and none that would unequivocally support its inclusion in, Procolophonoidea. *Kinelia* is therefore considered Tetrapoda incertae sedis, although it clearly represents a valid taxon with unique autapomorphies. It could be a non-procolophonoid parareptile but this classification is uncertain because of the limited material.

*Stratigraphic and geographic range*.—Vyatkian (uppermost Tatarian) of European Russia.

## Excluded taxa

### *Microphon exiguus* Ivakhnenko, 1983

Figs. 6, 7.

*Microphon exiguus*, from the Upper Permian (Tatarian) of Russia, was long considered the earliest record of Procolophonidae (Ivakhnenko 1983; Spencer and Benton 2000; Modesto et al. 2001). Bulanov (2002), however, excluded *Microphon* from Procolophonoidea after reidentifying it as a seymouriamorph, and confirmed this in an extensive review of seymouriamorphs that includes many illustrations of paratypes referable to the species *M. exiguus* and the genus *Microphon*, previously assigned to the genera *Raphanodon* or *Raphaniscus* (Bulanov 2003). However, the holotype of *M. exiguus,* PIN 3585/31, was the only specimen illustrated by Ivakhnenko (1983) and Bulanov (2002), and both papers featured only line drawings that differ from each other considerably. Furthermore, the seymouriamorph review of Bulanov (2003) also only has a reconstructive drawing of the holotype specimen, again somewhat different from previous drawings, leaving it unclear what the holotype actually looks like and whether it is comparable to the seymouriamorph specimens included in the genus. Photographs, accompanied by line drawings, are provided here to clarify the affinities of this specimen (Figs. 6, 7).

The holotype specimen, PIN 3538/31, is an isolated maxilla, and the anterior end of the specimen was at some point broken off and subsequently glued back in the wrong position, with the marginal teeth pointing medially (Figs. 6, 7A, C). This erroneous orientation of the anterior part of the maxilla causes the anterior extension of the tooth shelf, which should be pointing horizontally on the medial side, to be visible in lateral view and was illustrated by Ivakhnenko (1983: fig. 1), where it appears similar to the "maxillary depression" of procolophonids. Bulanov (2002) pointed out this mistake and illustrated the anterior part of the maxilla in a more true orientation, but even his depiction (Bulanov 2002: fig. 1) is not entirely correct when compared to how the maxilla would look with the anterior end in its true orientation (Fig. 7B).

Ivakhnenko's (1983) illustration also depicts the maxilla as having a large foramen behind the "maxillary depression", another feature found in procolophonoids (and several other parareptiles), but this foramen is absent in the illustrations of Bulanov (2002, 2003). The specimen, in fact, has a hole in this location but this has an unnatural shape and does not continue into the bone (Fig. 7A). This "foramen" was caused by damage during preparation (Valery Bulanov, personal communication 2006), a fact supported by the damage around the "foramen", and was left out of the illustrations of Bulanov (2002, 2003) for this reason. In other respects, the drawings of Bulanov (2002, 2003) are fairly accurate and illustrate the clearly pleurodont dentition, the numerous foramina on the medial

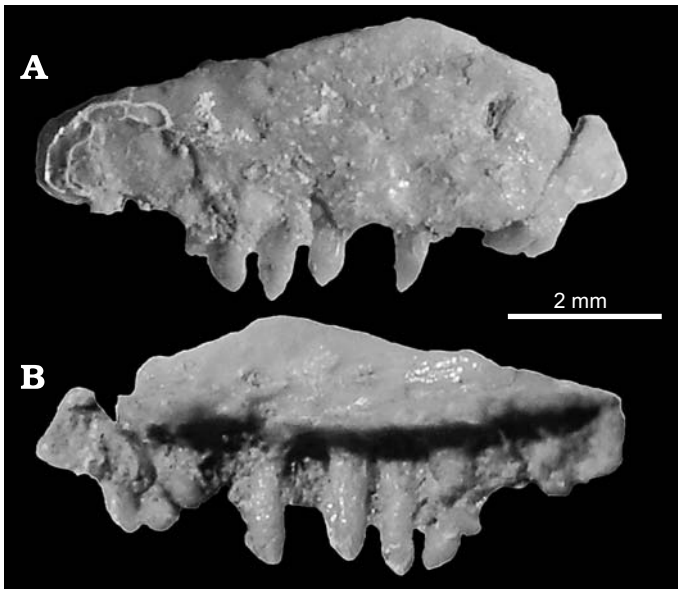


Fig. 6. Seymouriamorph *Microphon exiguus* Ivakhnenko, 1983, Severodvinian Gorizont, Tatarian; PIN 3585/31 (holotype), right maxilla, in lateral (**A**) and medial (**B**) views.

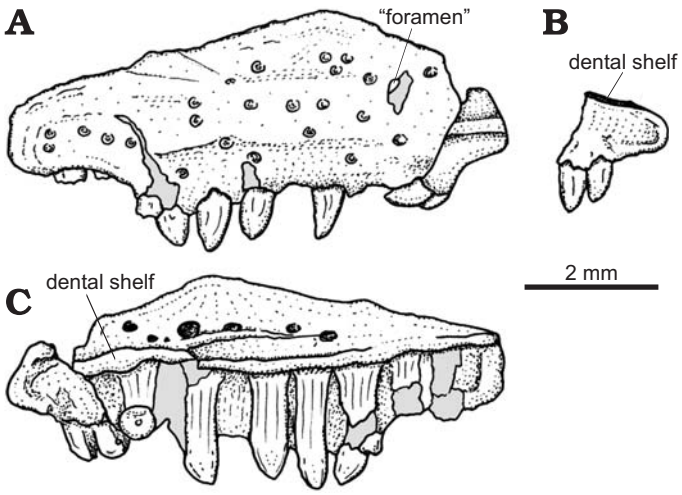


Fig. 7. Seymouriamorph *Microphon exiguus* Ivakhnenko, 1983, Severodvinian Gorizont, Tatarian; PIN 3585/31 (holotype), right maxilla, in lateral view (**A**), lateral view of the anterior end (**B**; attached to the maxilla incorrectly in A), and medial view (**C**).

side and the pitted surface of the lateral side that can be seen on the specimen (Fig. 7). These are all compatible with the identification of *Microphon* as a seymouriamorph (Bulanov 2002, 2003), and additional material, consisting of well-preserved cranial remains, confirms this (Bulanov 2003).

### Genus *Nyctiphruretus* Efremov, 1938

### *Nyctiphruretus acudens* Efremov, 1938

### *Nyctiphruretus optabilis* Bulanov, 2002

This genus of parareptile found in Mezen' River basin of Russia, Upper Middle Permian (Guadalupian) (Ivakhnenko 1990), has been considered a member of the order Procolophonomorpha, family Nyctiphruretidae, and understood to

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be the most basal of the Russian "procolophons" (Ivakhnenko 1979, 1987, 1997; Tverdockhlebova and Ivakhnenko 1994; Bulanov 2002). The recent phylogenetic analyses of Lee (1995), Tsuji (2006), and Müller and Tsuji (2007), however, do not support the view of *Nyctiphruretus* as a basal "procolophon" and instead recognise *Nyctiphruretus* as a non-procolophonoid parareptile, possibly more closely related to pareiasaurs than procolophonoids (Tsuji 2006). However, Tsuji (2006) points out that the published reconstructions of *Nyctiphruretus* (Efremov 1940; Chudinov 1957; Ivakhnenko 1979; Lee 1995, 1997) differ from each other markedly, and an in-depth study of this taxon is needed to resolve its real phylogenetic position. There are currently over one hundred specimens of *Nyctiphruretus acudens*, including cranial and postcranial remains, housed at PIN, whereas *Nyctiphruretus optabilis* is known from only one fragmentary dentary (Bulanov 2002). A detailed ontogenetic study of *Nyctiphruretus* is forthcoming by Valery Bulanov, and a study of the cranial osteology and phylogenetic position of *Nyctiphruretus* is being prepared by the author. Preliminary results of the osteological and phylogenetic study, however, indicate that while *Nyctiphruretus* appears to share several more characters with procolophonoids than has been recognized in previous studies and might be a close relative of procolophonoids, it does not fall within the superfamily Procolophonoidea.

# Discussion and conclusions

The Permian reptiles *Microphon exiguus* Ivakhnenko, 1983, *Kinelia broomi* Bulanov 2002, *Suchonosaurus minimus* Tverdokhlebova and Ivakhnenko, 1994, *Nyctiphruretus acudens* Efremov, 1938, and *N. optabilis* Bulanov, 2002 have each been previously considered as the earliest record of Procolophonidae,thus indicating a possible origin for this clade in the Guadalupian or Tatarian of Russia. This study concludes that of these taxa, *Microphon*, *Kinelia*, and *Nyctiphruretus* are not procolophonoid reptiles. *Microphon* is a seymouriamorph, as suggested by Bulanov (2002, 2003); *Kinelia* is a Tetrapoda incertae sedis; and *Nyctiphruretus* is a parareptile closely related to procolophonoids but does not fall within Procolophonoidea. However, study of the holotype and only specimen of *Suchonosaurus minimus* confirms that it can be included in Procolophonoidea as a member of Procolophonidae. It exhibits the procolophonid conditions of a circular external naris and a laterally visible maxillary depression, and although it has conical teeth with subcircular bases, the small number and the large size of these teeth supports its inclusion in Procolophonidae.

The more detailed phylogenetic position of *Suchonosaurus* is difficult to determine because of the fragmentary nature of the only known specimen, but this taxon shares many features with *Contritosaurus*/*Phaanthosaurus*, *Coletta* and *Pintosaurus.* These taxa have been recovered as the basal-most procolophonids in recent phylogenetic studies (Modesto and Damiani 2007; Cisneros 2008a, b; Säilä 2008). However, *Pintosaurus* is also known from only one fragmentary specimen (Piñeiro et al. 2004), and has been omitted from recent phylogenetic studies except for those of Piñeiro et al. (2004) and Cisneros (2008a). Furthermore, Modesto and Damiani (2007) postulate that *Pintosaurus* might not be a valid taxon because it appears to lack clear autapomorphies. Additionally, the species belonging to the Lower Triassic genera *Contritosaurus/Phaanthosaurus* from Russia need to be subjected to a rigorous restudy because the published descriptions of these taxa (Ivakhnenko 1974, 1979; Spencer and Benton 2000) appear to be somewhat misleading (PIN 1025/1, 3355/1, and 3357/2) and there are hundreds of undescribed/uncatalogued specimens comprising jaws and postcranial remains most likely attributable to the genera housed at PIN. Thus, poor preservation and lack of accurate information about the basal procolophonids means that the phylogenetic relationships between these taxa remain at a speculative level. Nevertheless, *Suchonosaurus* clearly belongs among the basal procolophonids.

The identification of *Suchonosaurus* as a procolophonid means that it is also the oldest known member of the family. The age of the basal procolophonid *Pintosaurus*, however, is currently uncertain because the South American sediments it was recovered from are identified either as Upper Permian or Lower Triassic (Piñeiro et al. 2004; Cisneros 2008a), and thus it could also be a Permian procolophonid. Furthermore, although many authors consider *Spondylolestes rubidgei* to be a nomen dubium (Spencer 2000; Spencer and Benton 2000; Modesto et al. 2001), Cisneros (2000a) illustrated *Spondylolestes* with a few new photographs that possibly indicate that is it could belong to the family Procolophonidae. Cisneros (2008a) also considers *Spondylolestes* to be of Late Permian age because its locality has mostly yielded Late Permian tetrapods (Kitching 1977). Many localities in the South African Karoo region, however, expose several different geological time zones and yield fossils of differing ages, and Broom (1937) originally listed *Spondylolestes* as an Early Triassic taxon based on the properties of the surrounding matrix. Thus, as there are no records of the actual terrestrial vertebrate biozone where *Spondylolestes* was recovered, the age of this taxon remains uncertain. At present, then, *Suchonosaurus* is the only unequivocal record of the clade Procolophonidae from the Permian. Furthermore, as numerous procolophonids, including *Contritosaurus/Phaantosaurus*, are found from Lower and Middle Triassic Russian sediments (Ivakhnenko 1979; Spencer and Benton 2000), this means that Russia is the only confirmed location with a record of Procolophonidae that crosses the Permian–Triassic boundary. South Africa and Madagascar have a similar record but the (Permian) taxa found there belong to Owenettidae (Modesto et al. 2001, 2002, 2003; Reisz and Scott 2002; Ketchum and Barrett 2004). Because *Kinelia, Microphon* and *Nyctiphruretus* were found to be non-procolophonoids, there is no record of Owenettidae in the Permian of Russia. This supports the current consensus that owenettids were confined to Gondwana.

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