

Gorgonopsian therapsids (*Nochnitsa* gen. nov. and *Viatkogorgon*) from the Permian Kotelnich locality of Russia (#25869)

1

First submission

Editor guidance

Please submit by **7 Apr 2018** for the benefit of the authors (and your \$200 publishing discount).



Structure and Criteria

Please read the 'Structure and Criteria' page for general guidance.



Custom checks

Make sure you include the custom checks shown below, in your review.



Raw data check

Review the raw data. Download from the [materials page](#).



Image check

Check that figures and images have not been inappropriately manipulated.

Privacy reminder: If uploading an annotated PDF, remove identifiable information to remain anonymous.

Files

Download and review all files from the [materials page](#).

10 Figure file(s)

1 Raw data file(s)

! Custom checks

New species checks



Have you checked our [new species policies](#)?



Do you agree that it is a new species?



Is it correctly described e.g. meets ICZN standard?



Structure your review

The review form is divided into 5 sections.

Please consider these when composing your review:

1. BASIC REPORTING

2. EXPERIMENTAL DESIGN

3. VALIDITY OF THE FINDINGS

4. General comments

5. Confidential notes to the editor

 You can also annotate this PDF and upload it as part of your review

When ready [submit online](#).

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your [guidance page](#).

BASIC REPORTING

-  Clear, unambiguous, professional English language used throughout.
-  Intro & background to show context. Literature well referenced & relevant.
-  Structure conforms to [PeerJ standards](#), discipline norm, or improved for clarity.
-  Figures are relevant, high quality, well labelled & described.
-  Raw data supplied (see [PeerJ policy](#)).

EXPERIMENTAL DESIGN

-  Original primary research within [Scope of the journal](#).
-  Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
-  Rigorous investigation performed to a high technical & ethical standard.
-  Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

-  Impact and novelty not assessed. Negative/inconclusive results accepted. *Meaningful* replication encouraged where rationale & benefit to literature is clearly stated.
-  Data is robust, statistically sound, & controlled.
-  Conclusions are well stated, linked to original research question & limited to supporting results.
-  Speculation is welcome, but should be identified as such.

Standout reviewing tips

3



The best reviewers use these techniques

Tip

Support criticisms with evidence from the text or from other sources

Example

Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.

Give specific suggestions on how to improve the manuscript

Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).

Comment on language and grammar issues

The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult.

Organize by importance of the issues, and number your points

1. Your most important issue
2. The next most important item
3. ...
4. The least important points

Please provide constructive criticism, and avoid personal opinions

I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC

Comment on strengths (as well as weaknesses) of the manuscript

I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.

Gorgonopsian therapsids (*Nochnitsa* gen. nov. and *Viatkogorgon*) from the Permian Kotelnich locality of Russia

Christian F Kammerer^{Corresp., 1}, Vladimir Masyutin²

¹ North Carolina Museum of Natural Sciences, Raleigh, North Carolina, United States of America

² Vyatka Paleontological Museum, Kirov, Russia

Corresponding Author: Christian F Kammerer
Email address: jonkeria@gmail.com

The early evolution of gorgonopsians is poorly understood. New material from the Kotelnich locality in Russia expands our knowledge of middle/earliest late Permian gorgonopsians from Laurasia. Two gorgonopsian taxa are recognized from Kotelnich: *Viatkogorgon ivakhnenkoi* Tatarinov, 1999 and *Nochnitsa geminidens* gen. et sp. nov. *Nochnitsa* can be distinguished from all known gorgonopsians by its unique upper postcanine tooth row, composed of pairs of teeth (a small anterior and larger posterior) separated by diastemata. Both *Viatkogorgon* and *Nochnitsa* are relatively small gorgonopsians, comparable in size to the South African middle Permian taxon *Eriphostoma*. Inclusion of *Viatkogorgon* and *Nochnitsa* in a phylogenetic analysis of gorgonopsians recovers them in basal positions, with *Nochnitsa* representing the earliest-diverging gorgonopsian genus. All other gorgonopsians fall into two major subclades: Inostrancevioidea (containing the Russian taxa *Inostrancevia*, *Pravoslavlevia*, *Sauroctonus*, and *Suchogorgon*) and Gorgonopioidea (containing all African gorgonopsians). The high degree of endemism indicated in this analysis for gorgonopsians is remarkable, especially given the extensive intercontinental dispersal inferred for coeval therapsid groups.

**Gorgonopsian therapsids (*Nochnitsa* gen. nov. and *Viatkogorgon*) from the Permian
Kotelnich locality of Russia**

Christian F. Kammerer¹ and Vladimir V. Masyutin²

¹North Carolina Museum of Natural Sciences, 11 W. Jones Street, Raleigh, North Carolina, USA

²Vyatka Paleontological Museum, Spasskaya ulitsa 22, Kirov, Russia 610000

Correspondence to: C. F. Kammerer (christian.kammerer@naturalsciences.org)

Abstract. The early evolution of gorgonopsians is poorly understood. New material from the Kotelnich locality in Russia expands our knowledge of middle/earliest late Permian gorgonopsians from Laurasia. Two gorgonopsian taxa are recognized from Kotelnich: *Viatkogorgon ivakhnenkoi* Tatarinov, 1999 and *Nochnitsa geminidens* gen. et sp. nov. *Nochnitsa* can be distinguished from all known gorgonopsians by its unique upper postcanine tooth row, composed of pairs of teeth (a small anterior and larger posterior) separated by diastemata. Both *Viatkogorgon* and *Nochnitsa* are relatively small gorgonopsians, comparable in size to the South African middle Permian taxon *Eriphostoma*. Inclusion of *Viatkogorgon* and *Nochnitsa* in a phylogenetic analysis of gorgonopsians recovers them in basal positions, with *Nochnitsa* representing the earliest-diverging gorgonopsian genus. All other gorgonopsians fall into two major subclades: Inostrancevioidea (containing the Russian taxa *Inostrancevia*, *Pravoslavlevia*, *Sauroctonus*, and *Suchogorgon*) and Gorgonopioidea (containing all African gorgonopsians). The high degree of endemism indicated in this analysis for gorgonopsians is remarkable, especially given the extensive intercontinental dispersal inferred for coeval therapsid groups.

27 **Keywords:** Synapsida, Therapsida, Gorgonopsia, Permian, Russia, phylogeny, biogeography

INTRODUCTION

The therapsid subclade Gorgonopsia was an abundant but morphologically conservative group of saber-toothed carnivores that included the apex predators of the late Permian (Sigogneau-Russell, 1989; Kammerer, 2015, 2016). Despite their omnipresence in the late Permian therapsid faunas of southern Africa (Smith et al., 2012), gorgonopsians are poorly represented in the global fossil record. No gorgonopsian fossils have thus far been found in the middle-to-late Permian deposits of western Europe, South America, or southeast Asia (Benton and Walker, 1985; Sues and Munk, 1996; Bercovici et al., 2012; Dias-da-Silva, 2012; Boos et al., 2015). Young (1979) described a supposed gorgonopsian taxon (*Wangwusaurus tayuensis*) from the Jiyuan Formation of China, but the type material of this taxon consists of a chimaerical assortment of temnospondyl and pareiasaur teeth (Liu et al., 2014). Although a serrated canine from the Jiyuan Formation could represent an actual gorgonopsian (Liu et al., 2014), this identification cannot be confirmed by this element alone (it could just as easily represent a therocephalian, and indeed Liu et al. [2014] noted its similarity to teeth of the early therocephalian *Lycosuchus*). As such, the presence of gorgonopsians in the Chinese record remains dubious. Ray and Bandyopadhyay (2003) referred several skull fragments (premaxillary and vomerine elements and isolated dentary symphyses) from the Kundaram Formation of India to Gorgonopsia. These specimens are likely to represent true gorgonopsians: the steep, robust morphology of these symphyses, with the incisor and canine tooth row elevated high above the postcanine row, is typical of the group. However, although this morphology is typical for gorgonopsians it is not exclusive to them; again, some therocephalian taxa exhibit a very similar morphology (Durand, 1991). Of the extra-African regions yielding Permian tetrapod fossils, only Russia has thus far produced definitive gorgonopsian remains.

The history of gorgonopsian discoveries in Russia dates back to the 1890s, beginning with the massive excavations of V. P. Amalitzky at the Sokolki locality along the North Dvina River (Ochev and Surkov, 2000). Amalitzky collected extensive remains of late Permian

gorgonopsians, which were initially, briefly described as a new species in a posthumous publication (Amalitzky, 1922). This first Russian gorgonopsian, *Inostrancevia alexandri*, remains the best-known taxon from the Northern Hemisphere, and has become one of the most famous Permian animals because of its gigantic  (among gorgonopsians, rivaled only by *Rubidgea atrox* from southern Africa). The genus name of this animal was spelled “*Inostranzevia*” in its initial description (Amalitzky, 1922), but the spelling *Inostrancevia* has since come into universal usage and must be maintained (under Art. 33.3.1 of The Code). Pravoslavlev (1927) subsequently produced a monographic account of the North Dvina gorgonopsians, recognizing two additional species of *Inostrancevia* (*I. proclivis* and *I. parva*) and the new genus *Amalitzkia* (containing two species, *A. wladimiri* and *A. annae*).

Hartmann-Weinberg (1938) described another new species of Russian gorgonopsian, albeit placing it in the South African genus *Arctognathus*: *A. progressus* from the Tetyushkii District of Tatarstan. Whereas South African gorgonopsian discoveries continued at an alarming pace during this time, this was mostly a fallow period for Russian gorgonopsian research, with few new specimens being collected. Vjuschkov (1953) revised the North Dvina gorgonopsians, recognizing a new genus (*Pravoslavlevia*) for the small species *Inostrancevia parva* (which Efremov [1940] had previously considered to represent a juvenile of one of the larger *Inostrancevia* species). Bystrov (1955) revised *A. progressus*, placing it in a new genus, *Sauroctonus*. Tatarinov (1974) revised all theriodonts from the Soviet Union in a comprehensive monograph on the group, and named a new species of *Inostrancevia* (*I. uralensis*) based on an isolated braincase from the Blumental-3 locality of the Orenburg Region.

Additional Russian gorgonopsian taxa were not recognized until the turn of the century, with the description of the small gorgonopsians *Viatkogorgon ivakhnenkoi* from the Kotelnich locality of the Kirov Region (Tatarinov, 1999a) and *Suchogorgon golubevi* from the Ust'e Strel'ny locality of the Vologda Region (Tatarinov, 2000a). Most recently, another isolated braincase (from the Klimovo-1 locality of the Vologda Region) was made the holotype of

Leogorgon klimovenssis, purportedly the first Russian rubidgeine gorgonopsian (Ivakhnenko, 2003; although see Kammerer [2016] for doubts on this identification).

Since the description of *Viatkogorgon*, no other gorgonopsians have been described from the Kotelnich locality, despite an explosion in the therocephalian diversity reported from this area (Tatarinov, 1999b, 2000b; Ivakhnenko, 2011). Here, we provide evidence for a second taxon of Kotelnich gorgonopsian based on a complete skull and partial skeleton in the collections of the Vyatka Paleontological Museum, redacted be the cranium of *Viatkogorgon* for comparison, and place these taxa in a phylogenetic context.

Nomenclatural acts

The electronic version of this article in portable document format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>. The LSID for this publication is: urn:lsid:zoobank.org:pub:397E7247-DB64-4B99-B24E-5A2E2DA87B48. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central, and CLOCKSS.

Institutional abbreviations

BP, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; **GPIT**, Paläontologische Sammlung, Eberhard-Karls-Universität Tübingen, Germany; **KPM**, Vyatka Paleontological Museum, Kirov, Russia; **PIN**, Paleontological Institute of the Russian

Academy of Sciences, Moscow, Russia; **SAM**, Iziko: The South African Museum, Cape Town, South Africa; **UMZC**, University Museum of Zoology, Cambridge, UK.

GEOLOGICAL CONTEXT

The Kotelnich locality consists of a series of Permian red bed exposures along the banks of the Vyatka River in the Kotel'nichskii District of Kirov Region. This locality is one of the most productive Permian tetrapod sites in Russia, and is especially well known for its pareiasaur remains (Efremov & Vjuschkov, 1955). Although the paleontological importance of the Kotelnich beds has long been recognized (Hartmann-Weinberg, 1937), the geology and stratigraphy of this locality was poorly understood until work by Coffa (1997a, 1997b, 1998, 1999) as part of his (still unpublished) PhD research. He recognized four primary lithological members making up the Kotelnich red beds: (in descending order) the Sokol'ya-Gora Member (brown fine-grained fluvial sandstone), Shestakovy Member (brown-gray mudstone), Boroviki Member (orange fine-grained aeolian sandstone), and Vanyushonki Member (red-brown calcareous clay and mudstone). The Vanyushonki Member is the oldest of these units and the source of most of the fossil tetrapods from Kotelnich. Skeletal remains are abundant in this member and often consist of complete, articulated skeletons.

The Vanyushonki Member is dominated by mudstones (silty clays and clay , silts with small quantities of fine-grained sand) that are predominantly pale or moderate brown in color. This horizon also contains an inclusion of gray and bluish-gray mudstone and two conspicuous horizons of dark red mudstone at the base of the exposure. The mudstones of the Vanyushonki Member were probably deposited from suspension in standing water bodies on floodplains or in shallow ephemeral lakes . This member has yielded the most diverse vertebrate assemblage at Kotelnich. In addition to the extremely abundant pareiasaurs (*Deltavjatia rossica*), the Vanyushonki Member has also produced 'nycteroleter' parareptiles (*Emeroleter laevis*) and various therapsid taxa (including the basal anomodont *Suminia getmanovi* , the gorgonopsian

Viatkogorgon ivakhnenkoi, and the therocephalians *Chlynovia serridentata*, *Karenites ornamentatus*, *Perplexisaurus foveatus*, *Scalopodon tenuisfrons*, *Scalopodontes kotelnichi*, and *Viatkosuchus sumini*) (Masyutin and Masyutina, 2016).

Benton et al. (2012) considered the Kotelnich faunal complex to be latest Guadalupian in age, and equivalent to the *Pristerognathus* Assemblage Zone (AZ) of the South African Karoo Basin. More recent research on the South African assemblage zones, however, indicates that the boundary between the *Tapinocephalus* and *Pristerognathus* AZs is latest Guadalupian (260.26 Ma) and the bulk of the *Pristerognathus* AZ may actually be early Lopingian (Day et al., 2015). Kurkin (2011) suggested that the Kotelnich assemblage was better correlated with the South African *Tropidostoma* AZ, based on the shared presence of toothed ouidenodontid dicynodonts (*Australobarbarus* in Russia and *Tropidostoma* in South Africa). However, *Australobarbarus* fossils are found higher in section than most Kotelnich vertebrates (in the Shestakov Member) and are not necessarily indicative of the age of the Vanyushonki Member fauna.

The specimen KPM 94.0 was collected by A. Khlyupin in 1994, in a red mudstone in the middle part of the Vanyushonki Member along the north bank of the Vyatka River. It was collected at the Sokol'ya Gora–Chizhi site, 43 meters upstream from the third ravine of the Sokol'ya Gora lens. In situ, the skull of this specimen was oriented south-southwest. Following collection, the specimen was mechanically prepared at the Vyatka Paleontological Museum by O. Masyutina.

SYSTEMATIC PALEONTOLOGY

Synapsida Osborn, 1903

Therapsida Broom, 1905

Gorgonopsia Seeley, 1894

Nochnitsa gen. nov.

LSID: urn:lsid:zoobank.org:act:8FF18791-BAAD-45AC-946A-722A3BF83139

Type species: *Nochnitsa geminidens* sp. nov.

Etymology: Named after a nocturnal spirit in Slavic legend (also the namesake for *Myotis* bats in modern Russian), often portrayed as a horrific female apparition that attacks sleeping humans. Name intended as a regionally-appropriate counterpart to the usual gorgonopsian generic stem ‘gorgon’, referring to monstrous hags from Greek myth. Feminine.

Diagnosis: As for type and only species.

Nochnitsa geminidens sp. nov.

(Figures 1–7)

LSID: urn:lsid:zoobank.org:act:DA63D0AC-4592-4E4A-AB19-6E253B0FE5EE

Holotype: KPM 310, a nearly complete skull and lower jaws with articulated vertebrae, ribs, and partial right forelimb from the Kotelnich locality, Kotel’nichskii District, Kirov Region, Russia.

Etymology: From the Latin *geminus* (‘twin’) and *dens* (‘tooth’), referring to the autapomorphic ‘twinned’ sets of postcanines in this species. A noun in apposition.

Diagnosis: Distinguished from all other known gorgonopsians by the autapomorphic ‘twinned’ of its upper postcanines, with the postcanine tooth row consisting of pairs of teeth separated by short diastemata. Further distinguished from the co-occurring gorgonopsian *Viatkogorgon ivakhnenkoi* by the higher upper postcanine tooth count (six, versus four in *Viatkogorgon*), upper incisor tooth row nearly in-line with postcanine tooth row (instead of elevated above it), absence of a maxillary flange around the canines, straight (rather than recurved) postcanine crowns, weak mandibular symphysis without a steep, distinct ‘chin’,

proportionally longer snout, smaller orbit, broader intertemporal region, and shorter temporal fenestra, dorsoventrally narrower subtemporal arch, absence of a squamosal flange at the posteroventral corner of the temporal fenestra, dorsoventrally narrower dentary ramus, and relatively posterior position of the reflected lamina (mostly beneath the temporal fenestra rather than the orbit). Distinguished from the South African middle Permian gorgonopsian *Eriphostoma microdon* by the absence of a labial emargination on the maxilla, longer snout, narrower postorbital bar, and higher upper postcanine tooth count (three in *Eriphostoma*).

Description: The type and only known specimen of *Nochnitsa geminidens* (KPM 310) consists of an almost-complete skull, anterior axial column, and right forelimb (Figs. 1, 2). The skull is relatively small for a gorgonopsian (82 mm dorsal length). The right side of the skull is obscured by the radius, ulna, and autopodial elements (Fig. 2), but the left side is fully exposed (Fig. 1). The skull is generally well preserved (Figs. 3, 4B, 5B), although some sutural details are obscure and the snout has suffered some surface cracking (Fig. 3). Additionally, the left side of the skull is largely undistorted, although the right side has suffered from some lateral compression (Figs. 6, 7). A large crack extends from the anterior edge of the left orbit across the interorbital region to the right temporal fenestra and has been filled with plaster (Fig. 7), additional small cracks have been filled with silicone rubber (Figs. 3, 7).

The premaxilla is damaged anteriorly, with the internarial bar broken off, and the palatal surface is completely obscured by the occluded mandible (Fig. 5B). The left premaxilla is largely worn off, although the roots of the incisors remain in place (Fig. 2). The right facial portion of the premaxilla has some surficial cracking but is otherwise intact. The premaxilla has a very short contribution to the side of the snout (6 mm out of a 46 mm long snout), being mostly overlapped by the maxilla laterally (Fig. 5B). The premaxillary-maxillary suture is immediately ventral to the septomaxilla, and terminates between I2 and I3 at the alveolar margin of the snout. Five upper incisors are present, as in most gorgonopsians. The incisors are mesiodistally narrow and needle-like anteriorly but become progressively apicobasally shorter and mesiodistally broader

posteriorly. The upper incisors are weakly recurved and finely serrated on their distal margins (no mesial serrations are evident, although as the mesial margin of these teeth is slightly angled inwards they may be obscured).

The septomaxilla has a broad plate making up the floor of the external naris ventrally, a constricted middle section separating the external naris from the large maxillo-septomaxillary foramen, and a narrow, attenuate posterior process extending between the maxilla and nasal (Fig. 5B).

The maxilla in *Nochnitsa* is relatively long and low (Fig. 5B) compared to other gorgonopsians, even similarly long-snouted forms such as *Cyonosaurus* (Olson, 1937; Sigogneau-Russell, 1989). The lateral surface of the maxilla bears distinct dermal sculpturing in the form of radiating ridges extending outwards from the region around the canine root (Fig. 3). The lateral surface of the maxilla is also densely foraminated, particularly above the tooth row. The posterior process of the maxilla is a narrow, attenuate structure underlying the jugal, which terminates below the midpoint of the orbit. The alveolar margin of the maxilla is weakly convex, with a marked embayment anteriorly at the diastema between the incisors and canine. The canine is relatively small and narrow (18 mm apicobasal length, 6 mm width at base) for a gorgonopsian. The canine is clearly serrated posteriorly, but there is no evidence of anterior serrations (although as for the incisors, because of the angulation of the canines and some matrix covering, the absence of anterior serrations should not be taken as certain). Both functional canines are in the anterior alveoli in this specimen, with replacement canines erupting in the posterior alveoli at the time of death (Fig. 5B, 6B). The right replacement canine was more fully erupted—although it is badly damaged, its tip would have reached near mid-height of the right canine (Fig. 6B). The left replacement canine is present only as a newly-erupted tip, shorter than any of the postcanines (Fig. 5B). Six right and five left upper postcanines are present. The morphology of the right upper postcanine tooth row is unique among therapsids, consisting of three pairs of postcanines separated by short (~2 mm) diastemata (Fig. 6).

Furthermore, in each of these pairs the anterior tooth is smaller than its posterior counterpart (lengths of PC1: 5 mm vs. PC2: 7 mm; PC3: 5 mm vs. PC4: 8 mm; PC5: 5 mm, PC6 damaged so length uncertain, but anteroposteriorly broader than PC5). Other than their size, all postcanines are morphologically identical, being elongate, weakly posteriorly-canted but not recurved, and bearing fine posterior serrations (and in these teeth, the anterior face is well-exposed enough to confidently state that anterior serrations are absent). On the left side, the anterior three postcanines do not form similarly distinct pairs, but PC1 may be missing as part of the replacement history of the dentition. If this is the case, then the first preserved left postcanine represents PC2. This tooth is shorter than any other upper postcanine and appears to be newly-erupted—if the pairs erupt in tandem a shorter PC1 may not yet have erupted. Under this interpretation, PC3 and 4 can be interpreted as a pair: although their bases are not in direct contact as in the other pairs, PC3 (4 mm length) is shorter than PC4 (6 mm length), comparable to the right postcanines. PC5 and 6 on the left side are paired in exactly the same way as all the right side pairs (PC5: 3.5 mm vs. PC6: 6 mm length).

The nasal is an elongate bone making up the dorsal roof of the snout (Fig. 7A). It bears low anteroposterior ridges but is overall weakly ornamented compared to the maxilla. Its posterior suture with the frontal is situated anterior to the orbits.

The prefrontal is a dorsoventrally low but anteroposteriorly extensive bone at the anterodorsal margin of the orbit (Figs. 5B, 7A). It has a sharp margin at the edge of the orbit but not an expanded or rugose circumorbital rim. Below the prefrontal, the lacrimal is a small, rhomboidal bone. Both of these elements bear irregular, ridged dermal sculpturing. The lacrimal foramen does not exit laterally on the lacrimal, it is restricted to the internal orbital surface.

The jugal has a broad facial portion below the lacrimal (Fig. 5B), but this facial portion is relatively small compared to other gorgonopsians (see, e.g., *Viatkogorgon*; Fig. 5A). Posterior to this the jugal is a narrow, rod-like bone forming the zygoma. It is overlapped by the postorbital under the postorbital bar. It makes a small contribution to the posterior base of the lateral

surface of the postorbital bar and medial face of the bar but does not have an extensive dorsal process participating in the bar as in therocephalians (Durand, 1991; van den Heever, 1994). The jugal is distinctly bowed in the zygoma, so that there is a ventral concavity below the postorbital bar. Posteriorly, the jugal makes up part of the subtemporal bar but is mostly overlain by the zygomatic ramus of the squamosal.

The squamosal has a small contribution to the medial margin of the temporal fenestra dorsally, but is mostly confined to the occiput and zygomatic arch (Fig. 5B). The sutures of the occiput are largely indeterminable in this specimen, but given the proportions of the occiput it is likely that the squamosals made up much of the lateral edge of the occiput as in other gorgonopsians (Fig. 7A). The occipital and zygomatic portions of the squamosal are separated by a sharp ridge with a flange-like ventral edge, anterior to which is a triangular depression, the squamosal sulcus. Restriction of the sulcus to the zygomatic portion of the squamosal is an unusual feature, usually this sulcus extends uninterrupted from the occiput around to the zygoma or is entirely restricted to the occiput (as in rubidgein rubidgeines; Kammerer, 2016). The only other taxon with this morphology is *Viatkogorgon* (Fig. 5A). The zygomatic ramus of the squamosal terminates in a pointed anterior process dividing the jugal in lateral view; it does not reach the level of the postorbital bar.

The frontal is a hexagonal bone of the interorbital region (Figs 5B, 7A). It has a broad contribution to the orbit compared to many gorgonopsians (in most rubidgeines it is excluded entirely; Kammerer, 2016). Posteriorly, it terminates in a narrow, sliver-like process extending between the postfrontal and a complementary anterior process of the parietal (Fig. 7A).

The postfrontal is relatively large in *Nochnitsa* (Fig. 7A), which is typical for basal therapsids but independently modified in most therapsid clades (lost in eutheriocephalians, cynodonts, and some anomodonts, and reduced in size in some later gorgonopsians [e.g., *Arctognathus*]; Hopson and Barghusen, 1986; Kammerer, 2015). The postfrontal makes up the

posterodorsal corner of the orbit and extends posteriorly between the frontal and postorbital until the level of the anterior border of the pineal foramen.

The postorbital is composed of a laminar dorsal ramus making up the medial border of the temporal fenestra and a rod-like ventral ramus making up almost the entirety of the postorbital bar (Fig. 5B). A weak fossa serving as an attachment site for jaw musculature is present on the ventrolateral edge of the dorsal ramus and continues onto the posterior edge of the postorbital bar. The postorbital bar is weakly curved anteriorly and terminates in only a slight anteroposterior expansion ventrally, unlike the massively expanded ventral postorbital tips of most gorgonopsians (Sigogneau, 1970; Laurin, 1998; Kammerer et al., 2015; Kammerer, 2016).

The preparietal is a roughly rhomboidal median element situated between the frontals and parietals (Fig. 7A). It is flush with the skull roof and unornamented. It is separated from the pineal foramen by a short mid-parietal suture; it does not abut the foramen directly as in the majority of anomodonts and biarmosuchians (King, 1988; Sidor and Rubidge, 2006).

The parietal is the primary skull roofing bone of the intertemporal region (Fig. 7A). It has attenuate anterior and posterior processes; the latter mirrors the postorbital in following the edge of the temporal fenestra. The anterior portion of the parietal midline is split by the small (3 mm diameter), subcircular pineal foramen. It is surrounded by a distinct, collar-like rim but is not elevated on a 'chimney'-like boss as in many basal therapsids.

As mentioned above, the bones of the occiput are not readily differentiable in this specimen. There is a long, well-developed nuchal crest (Fig. 7A) that runs uninterrupted from the top of the occipital plate to the foramen magnum along the midlines of what are probably the postparietal and supraoccipital (from comparison with other gorgonopsians).

The dentary of *Nochnitsa* is very unusual for a gorgonopsian, much more closely resembling that of a typical therocephalian. Notably, it lacks a steep, robust symphysis with a distinct mentum, instead having a long, gradually sloping anterior face (Fig. 5A). The dentary ramus posterior to the symphysis is relatively low and narrow, and the coronoid region is only

weakly sloped upward, with a convex posterior edge. In most gorgonopsians (including *Viatkogorgon*; Fig. 5A) the dentary coronoid process is strongly dorsally directed with a distinctly concave posterior face. The roots of four incisors (the standard number for gorgonopsians) can be seen on the damaged right side of the dentary symphysis. They are similar in morphology to their upper counterparts, except apicobasally shorter (crown height 4 mm in i1, vs. 6 mm in I1). The lower canines are mostly obscured by the upper jaw but their bases are visible—these teeth are similar in size to the upper canine and situated anterior to them. The lower postcanines are very similar in individual morphology to the uppers but are not paired; instead, they form a continuous row of close-packed, posteriorly-canted teeth (Fig. 6). Six lower postcanines are exposed on each side, but in different parts of the tooth row (the posteriormost left lower postcanines are exposed in the diastema between PC4 and 5, whereas the posteriormost right lower postcanines are exposed in the diastema between PC2 and 3). This suggests that the actual lower postcanine count exceeds six, especially considering that the close spacing of these teeth necessitates more of them for the lower tooth row to approximate the length of the upper.

The only exposed postdentary element is the reflected lamina of the angular, which is best preserved on the left side (Fig. 5B). The entire reflected lamina is intact; it is angled posteroventrally. This lamina is remarkably elongate and narrow (10 mm maximum length), and tapers somewhat ventrally. A single robust ridge runs along the long axis of the reflected lamina. This ridge is common to all gorgonopsians, but usually there is a second, horizontal ridge making a cruciate pattern (Sigogneau-Russell, 1989), which is absent in *Nochnitsa*. Although the articular is not exposed in this specimen, the proximity of the reflected lamina to the ventral part of the squamosal that borders the quadrate necessitates that this taxon would have the reflected lamina very close to the jaw articulation, which is the primitive condition for therapsids, but unlike most gorgonopsians in which the reflected lamina is separated from the articular by a length of non-laminar angular (Kammerer, 2016).

Part of the postcranium is preserved in articulation with the skull, including the cervicals, some dorsals with associated ribs, and right forelimb (Figs. 1, 2). The cervical series is curled around the left of the rear of the skull and still partially embedded in matrix (Fig. 1B). The axial spine is broadly rounded and similar in morphology to that of other gorgonopsians (Sigogneau-Russell, 1989; Gebauer, 2014). The dorsals are preserved as fragments of centrum and transverse processes interspersed with ribs. The ribs are simple, elongate elements. Above these ribs on the left side of the specimen, the top of the right scapula is exposed. It is elongate, narrow, and weakly curved, comparable to that of other small gorgonopsians (e.g., *Cyonosaurus*) but unlike the anteroposteriorly expanded scapular spines of *Inostrancevia* (Sigogneau-Russell, 1989). The right humerus, radius, ulna, and most of the manual elements are preserved in partial articulation (Fig. 2B). The humerus is relatively gracile, with a short, weakly-developed deltopectoral crest. The radius and ulna show distinct distal curvature, and the distal tip of the radius forms a discrete edge differentiated from the shaft. No olecranon process is visible on the ulna, but it is possible that this is the result of damage (the proximal tip of this element is not complete and has partially been replaced by sandstone).

Viatkogorgon Tatarinov, 1999a

Type species: *Viatkogorgon ivakhnenkoi* Tatarinov, 1999a.

Diagnosis: As for type and only species.

Viatkogorgon ivakhnenkoi Tatarinov, 1999a

(Figures 4–5)

Holotype: PIN 2212/61, a complete skeleton from the Kotelnich locality, Kotel'nichskii District, Kirov Region, Russia.

Diagnosis: Distinguished from all other known gorgonopsians by the extremely large squamosal sulcus, extending onto a squamosal flange impinging on the ventral edge of the temporal fenestra. Also characterized by unusually large orbit with proportionally large sclerotic ring. Distinguished from all gorgonopsians other than *Nochnitsa* by the narrow ventral terminus of the postorbital bar. Further distinguished from *Nochnitsa* by the suite of features noted above.

Description: The type specimen of *Viatkogorgon ivakhnenkoi* is one of the most complete gorgonopsian specimens in the world, with nearly the entire postcranium preserved intact, including elements very rarely preserved in therapsid specimens such as the gastralia. Regrettably, the skull is poor by comparison—although the right side is reasonably well-preserved, the left side and palate are badly broken up and other than the snout tip and left postorbital the skull roof is entirely reconstructed in plaster. Furthermore, the skull as a whole has suffered from lateral compression, making it narrower in dorsal view than it would have been in life. Detailed description of the postcranium of *Viatkogorgon* will greatly improve our understanding of gorgonopsian skeletal anatomy; unfortunately it was not available for study during the course of the current research (as it was part of a traveling exhibition) and must be dealt with in a future contribution (a preliminary description was provided by Tatarinov [2004]). The following description will focus on comparisons with *Nochnitsa*, necessarily centering on the overlapping preserved portions of the skull (primarily the lateral surface and mandible).

Like that of *Nochnitsa*, the premaxilla of *Viatkogorgon* has limited exposure on the facial surface of the snout (Fig. 5A). Although damaged even on the right side, its suture with the maxilla is visible, and is in a similar position to that of *Nochnitsa* (below the base of the septomaxillary footplate). The internarial bar is preserved, and is curved slightly posteriorly in lateral view, so that the anterolateral margin of the snout in *Viatkogorgon* is blunt rather than pointed. The dorsal tip of the premaxilla extends to the anterodorsal edge of the external naris. Few upper incisors are preserved intact, but the typical gorgonopsian count of five appear to be present based on the partial roots and alveoli. They are weakly recurved and spatulate with

clear distal serrations. It is uncertain whether they decrease in size posteriorly, as in *Nochnitsa*, because the only incisors with intact crowns are both interpreted as the I5 of their respective sides.

The septomaxilla has a narrower constricted portion and smaller maxillo-septomaxillary foramen than *Nochnitsa* and a shorter posterior facial process (Fig. 5A). Although the facial process separates the nasal and maxilla, as in most therapsids (Hopson and Barghusen, 1986), the absolute tip of the septomaxilla actually extends between anterodorsal portions of the maxilla. The maxilla is proportionally taller and shorter than that of *Nochnitsa*. Whereas the dorsal margin of the maxilla is broadly rounded in *Nochnitsa* (Fig. 5B), in *Viatkogorgon* there is a broad posterodorsal process that extends between the nasal and lacrimal. The posterior process of the maxilla is shorter in *Viatkogorgon* than *Nochnitsa*, not reaching the midpoint of the orbit. The lateral surface of the maxilla is damaged on both sides of the skull, but at least some radiating surface ridges were clearly present, as in *Nochnitsa* (Fig. 4). The precanine 'step' between the incisors and canine is notably steeper in *Viatkogorgon* than *Nochnitsa*, and the canine-bearing portion of the maxilla in general is strongly convex, giving the appearance of a flange in lateral view. The canine is relatively small for a gorgonopsian, similar to *Nochnitsa*. It is serrated posteriorly. The postcanine tooth row is short, consisting of only four close-packed postcanines. These postcanines are recurved, unlike *Nochnitsa*. The maxilla is weakly emarginated above the postcanine tooth row, to a greater extent than *Nochnitsa* but not to the degree of *Eriphostoma* (Kammerer et al., 2015) or rubidgeines (Kammerer, 2016).

The nasal is somewhat broader anteriorly (at the level of the posterior edge of the external naris) in *Viatkogorgon* than *Nochnitsa*, although this has been exaggerated in lateral view by lateral compression in the skull (Fig. 5A). The prefrontal of *Viatkogorgon* is proportionally shorter than that of *Nochnitsa* and contributes less to the anterodorsal margin of the orbit (which instead has a greater contribution from the lacrimal). The prefrontal has irregular, ragged edges with weak interdigitation with the maxilla anteriorly and lacrimal

ventrally. The posterior border of the maxilla is smoothly sloping in *Nochnitsa*, with progressively shorter contributions to the snout from the prefrontal, lacrimal, and jugal (Fig. 5B). In *Viatkogorgon*, the lacrimal has an anterior process breaking up the posterior border of the maxilla posteriorly and extending to the same extent as the anterior tip of the prefrontal (Fig. 5A). As mentioned above, the lacrimal extends further dorsally along the rim of the orbit in *Viatkogorgon* than *Nochnitsa*. As in *Nochnitsa*, there is no exit on the lateral surface of the lacrimal for the lacrimal foramen, which is restricted to the orbital wall.

A well-preserved, nearly undistorted sclerotic ring is preserved within the right orbit of *Viatkogorgon*, consisting of 15 ossicles (Fig. 5A). This ring is remarkably large even within the proportionally very large orbit (outer diameter 2.3 cm, inner diameter 1.5 cm, orbit diameter 2.8 cm), falling well within the lower reaches of what is considered scotopic in therapsids (Angielczyk and Schmitz, 2014) and suggesting nocturnal habits for *Viatkogorgon*. Fragments of the left sclerotic ring are also preserved in the left orbit.

The jugal of *Viatkogorgon* has a more extensive facial contribution than that of *Nochnitsa* (Fig. 5A). Its proportions in the zygoma, including the short contribution to the posterior base of the postorbital bar, are very similar to those of *Nochnitsa*. However, it is substantially taller in the subtemporal bar (which is taller in general than that of *Nochnitsa*) and more obscured by the more anteriorly-extending squamosal (which extends almost to the level of the postorbital bar.) In lateral view, the ventral portion of the jugal contribution to the subtemporal bar is barely exposed, unlike the condition in *Nochnitsa*, where it is longer than the dorsal portion (Fig. 5B).

Little of the frontal is preserved in *Viatkogorgon*; only the portion contributing to the orbital wall is intact (Fig. 5A). Within the orbit, the anterior border of the frontal is bifurcated by a posterior process of the prefrontal. The postfrontal is represented solely by a thin strip of bone at the posterodorsal edge of the orbit; it is otherwise reconstructed in plaster.

The dorsal ramus of the postorbital, like the rest of the intertemporal skull roof, is missing in this specimen (Fig. 5A). The ventral ramus is a thin rod making up the postorbital bar (similar

to that of *Nochnitsa*, but somewhat anteroposteriorly broader). The postorbital bar is a straight rod in lateral view, lacking the anteroventral curvature of *Nochnitsa*. It also has a weak posterior fossa, presumably for attachment of the jaw muscles.

The zygomatic portion of the squamosal shows the same distinctly bounded squamosal sulcus with posteroventral flange as in *Nochnitsa*, but is much larger and more expansive, and extends onto an anterodorsal flange at the ventral edge of the temporal fenestra (Fig. 5A). It is also taller anterior to the sulcus and extends further forward on the subtemporal bar. Below the squamosal sulcus the lateral edge of the quadrate is exposed, having disarticulated slightly from the slot it fits into. The quadrate is preserved in articulation with the articular.

Unlike *Nochnitsa*, *Viatkogorgon* has the typical gorgonopsian jaw morphology, with a tall mandibular symphysis bearing a distinct mentum (Fig. 5A). The lower dentition is poorly preserved: a single intact incisor and postcanine are exposed on the left side, and the base of the canine is visible on the right, anterior to the upper. The morphology of the lower teeth is very similar to the uppers: the one preserved incisor is recurved and spatulate, the lower postcanine is also weakly recurved, and both have at least posterior serrations. The dentary of *Viatkogorgon* is generally taller in the ramus than that of *Nochnitsa* and has a more sharply sloping coronoid process, with the weakly concave posterior edge typical of gorgonopsians. Unfortunately the postdentary bones of *Viatkogorgon* are badly damaged, such that the morphology of the reflected lamina is almost completely unknown. A narrow strip of this lamina is preserved immediately posterior to the posteroventral edge of the dentary, but it shows no morphology of note. What is evident is that the reflected lamina was situated well anterior to the jaw articulation, like all gorgonopsians other than *Nochnitsa*. The surangular is exposed as a narrow strip of bone at the top of the jaw posterior to the coronoid process of the dentary. It extends to the articular posteroventrally but the contact between these bones is indistinct. The articular is typical of gorgonopsians, with a ventrally-protruding retroarticular process. Damage

to this process makes it uncertain whether it had a hook-like anterior tip as in later gorgonopsians.

PHYLOGENETIC ANALYSIS

Nochnitsa geminidens and *Viatkogorgon ivakhnenkoi* were included in an expanded version of the only existing published phylogenetic analysis of gorgonopsians, that of Kammerer (2016, 2017). The analysis of Kammerer (2016) was focused on rubidgeine gorgonopsians in particular; in order better understand the relationships of the Kotelnich gorgonopsians, taxon sampling was expanded to include the Russian taxa *Inostravvia*, *Pravoslavlevia*, *Sauroctonus*, and *Suchogorgon*.

In addition to expanding the taxon sample, the character matrix has been emended by adding new characters and making alterations to several previous characters. These changes are detailed below:

Character 2: Posterior margin of palatal premaxilla. Previously (Kammerer, 2016), the states for this character were formulated as (0) gently rounded and (1) with deep invaginations. The biarmosuchian outgroups (*Biarmosuchus* and *Hipposaurus*) and the middle Permian gorgonopsian *Eriphostoma* were the only taxa coded as (0) for this character; all other gorgonopsians were coded as (1), or (?) if the anterior palate was not preserved or exposed. This character was originally intended to encompass an important difference in palatal morphology between gorgonopsians and non-gorgonopsian therapsids. In non-gorgonopsian basal therapsids, such as biarmosuchians, the anterior margin of the internal choana is gently rounded, with an even, gradual curvature between the premaxillary palatal plate (the portion bearing and immediately posterior to the incisor alveoli) and the vomerine process of the premaxilla (see, e.g., Sidor, 2003:fig. 3). In gorgonopsians, the anterior portion of the internal choana generally extends further forwards in the form of a narrow channel, producing a distinct invagination between the palatal premaxillary plate and vomerine process (see, e.g., Kammerer,

2017:fig. 10). In rubidgeines, this invagination is particularly prominent, because the premaxillary palatal plate is anteroposteriorly expanded relative to the condition in biarmosuchians and early gorgonopsians like *Eriphostoma*.

Kammerer (2016) coded *Eriphostoma microdon* as (0) for this character based on a CT-reconstruction of the palate in the holotype (Kammerer, 2014), although the premaxillary morphology in that specimen is not exactly concordant with that of biarmosuchians. In the Russian gorgonopsians in which this region is exposed (*Inostrancevia*, *Sauroctonus*, and *Suchogorgon*), the premaxillary morphology is very similar to that of *Eriphostoma*. However, the material of *Suchogorgon* is much better preserved than that of *Eriphostoma* and reveals that, although it is not as distinctive as in rubidgeines, an invagination is present at the anterior edge of the internal choana in that taxon (Ivakhnenko, 2005). One of the ‘exploded’ skulls of *Suchogorgon* (PIN 4548/138)  particularly informative on this point, as the premaxillary-vomerine complex of this specimen has been isolated and completely prepared. This specimen shows the invagination to be morphologically distinct from (but probably representing the ancestral state of) that of rubidgeines. Rather than being an elongate channel between expanded lobes of the palatal premaxillary plate and vomerine process, the invagination in *Suchogorgon* is simply the result of the vomerine process sloping dorsally, leaving a dorsoventral opening between its anterolateral edge and the more ventrally-situated palatal premaxillary plate. In poorly preserved specimens, such as the holotype of *Eriphostoma microdon*, this gap is difficult to see, but re-examination of the CT-scan files for that specimen  indicate that it was indeed present. Accordingly, character state (1) has been changed from “with deep invaginations” to simply “invaginated”, with *Eriphostoma* now coded (1). The distinction between the morphology in *Eriphostoma*/*Suchogorgon* and that of rubidgeines appears to be of phylogenetic importance and is worthy of further study. At present it is difficult to encapsulate this distinction in character form, however, because it seems to have undergone gradual transformation in gorgonopsian evolution—in *Gorgonops*, for instance, the invagination

is intermediate in morphology between that of *Suchogorgon* and that of rubidgeines (see Kammerer, 2015:fig. 12C).

Character 9: Vomerine-ptyergoid contact. Previously (as character 7 of Kammerer [2016]), this character had two states, (0) present and (1) absent. The absence of a contact between the vomer and pterygoid is one of the classic gorgonopsian synapomorphies (Hopson & Barghusen, 1986). However, as discussed in further detail below, Russian gorgonopsians with well-prepared palates (*Inostrancevia*, *Sauroctonus*, and *Suchogorgon*) show that they still retained a narrow but clearly present contact between the vomer and pterygoid (Fig. 8). The minimal contact between these bones in these taxa still clearly distinguishes them from non-gorgonopsian therapsids, so this character has been reformatted as ordered multistate: (0) present, broad, (1) present, narrow, and (2) absent.

Character 10: Palatine foramina: (0) small or absent; (1) large, well-developed near maxillary border. In the Russian gorgonopsians *Inostrancevia*, *Sauroctonus*, and *Suchogorgon*, there is a series of large, well-developed foramina on the palatine, near the border with the maxilla (this region is not well-preserved in *Pravoslavlevia*). These foramina appear to be absent in most African gorgonopsian taxa (this portion of the palatine is not exposed in *Nochnitsa* or *Viatkogorgon*). The palatine surface is poorly-preserved (or more usually, poorly-prepared) in many African gorgonopsian specimens, so this absence may be partially artifactual. However, some African gorgonopsian specimens with excellently-prepared palates (e.g., UMZC T891, *Ruhuhucerberus haughtoni*, and SAM-PK-K11458, *Arctognathus curvimola*) clearly lack large palatine foramina. Comparable foramina are present and well-developed in *Sycosaurus nowaki*, however, based on the specimen Kemp (1969) described as *Leontocephalus intactus* (UMZC T878).

Character 17: Parabasisphenoid blade position: (0) restricted to posterior edge of basicranial girder; (1) extending throughout length of basicranial girder. New character. In most gorgonopsians, the parabasisphenoid rostrum bears a tall, narrow, blade-like ventral crest. In rubidgeines this ‘blade’ is absent, and the ventral surface of the parabasisphenoid exhibits a reversal to the biarmosuchian condition, in which a narrow median channel separates the two edges of the parabasisphenoid. The presence/absence of this feature is covered in character 15, but does not address an important difference in morphology between the Russian gorgonopsians *Inostrancevia*, *Sauroctonus*, and *Suchogorgon* (the parabasisphenoid rostrum is not well preserved in *Pravoslavlevia*) and non-rubidgeine African gorgonopsians. In the Russian taxa, the ‘blade’ is nearly semi-circular in lateral view and restricted to the posterior portion of the parabasisphenoid, near the back of the basicranial girder (as is also the case in therocephalians), whereas in the African taxa the ‘blade’ is semi-oval and more elongate, extending for almost the entire length of the basicranial girder (Fig. 9).

Character 28: Postorbital bar. Previously (as character 24 of Kammerer [2016]), this was treated as an order multistate character with three states: (0) unexpanded, (1) expanded (>10% of basal skull length), and (2) greatly expanded (>20% of basal skull length). The primary distinction in this formulation was between non-rubidgeine and rubidgeine gorgonopsians, with the latter having anteroposteriorly expanded (and greatly expanded in the case of rubidgeins) postorbital bars. However, this formulation did not address a difference between gorgonopsians and outgroups like Biarmosuchia. In almost all known gorgonopsians, the ventral tip of the postorbital bar is expanded where it contacts the jugal, even if it is narrow for the rest of its length. The only known exceptions are *Nochnitsa* and *Viatkogorgon*, in which the postorbital bar is nearly the same width throughout its length (as in biarmosuchians). To reflect this, the states for this character have been changed to (0) unexpanded (including biarmosuchians, *Nochnitsa*, and *Viatkogorgon*), (1) expanded ventrally (non-rubidgeine gorgonopsians), (2) expanded

throughout length (>10% of skull length) (non-rubidgein rubidgeines), and (3) greatly expanded throughout length (>20% of skull length) (rubidgeins). The character is retained as ordered, as it reflects increasing levels of expansion of this bone.

Character 29: Facial portion of jugal. Previously (as character 25 of Kammerer [2016]), this character had two states: (0) confluent with suborbital zygomatic portion and (1) depressed relative to zygomatic portion. State 1 was intended to describe the condition in some rubidgeines, where there is a sharp break in height between the zygomatic and facial portions of the jugal, with the latter depressed relative to the former. *Pravoslavlevia* and *Inostrancevia* also exhibit a depressed facial portion of the jugal, but in a fundamentally different way than in rubidgeines. In rubidgeines, the facial portion of the jugal is depressed relative to the zygoma, but not adjacent facial bones (i.e., the jugal is not strongly depressed relative to the maxilla and lacrimal, the surfaces of these bones are roughly confluent). In *Pravoslavlevia* and *Inostrancevia*, there is a broad, deep preorbital fossa composed of the depressed facial surfaces of the lacrimal and jugal. These bones are depressed relative to the adjacent prefrontal and maxilla as well as the zygomatic portion of the jugal. Here, these different styles of facial jugal depression are treated as separate, unordered character states, with the new states for this character being (0) lateral surface confluent with other facial bones and suborbital zygomatic portion of jugal, (1) depressed relative to zygomatic portion but not other facial bones, and (2) bears broad fossa extending onto lacrimal surface, facial portion of jugal depressed relative to both zygomatic portion and other (non-lacrimal) facial bones.

Character 50: Lateral surface of reflected lamina. Previously (as character 45 of Kammerer [2016]), this character had two states: (0) lobate sculpturing and (1) well-developed dorsoventrally-oriented bar, with weakly-developed crossbar. The cruciate laminar sculpturing of state (1) is characteristic of gorgonopsians. Uniquely among gorgonopsians, the reflected

lamina of *Nochnitsa* bears only the main, dorsoventrally-oriented bar, no crossbar is present. As such this character has been changed to ordered multistate to reflect the intermediate condition in *Nochnitsa*: (0) lobate sculpturing, (1) well-developed dorsoventrally-oriented bar only, and (2) well-developed dorsoventrally-oriented bar, with weakly-developed crossbar.

This expanded version of the Kammerer (2016) data matrix (available as Supplementary Data) is made up of 22 operational taxonomic units (all species-level taxa except for *Inostrancevia*, which was coded at the genus-level due to uncertain alpha taxonomy) and 52 characters. All characters are discrete-state, and of these six are ordered multistate characters (characters 11, 14, 26, 28, 31, 50). The phylogenetic analysis was run in PAUP* (Swofford, 2002) v4.0 (build 159) using branch-and-bound searching. Bootstrap analysis was done using “fast” stepwise-addition on 1000 replicates.

The phylogenetic analysis recovered 6 most parsimonious trees (MPTs) of length 101 (Fig. 10). These trees differ only in the relative positions of *Arctognathus curvimola*, *Lycaenops ornatus*, and the clade made up of (*Arctops willistoni*+*Smilesaurus ferox*). These taxa are always recovered just outside of Rubidgeinae but vary in precise position, with *Arctognathus* recovered as the sister-taxon of Rubidgeinae in some MPTs and the (*Arctops*+*Smilesaurus*) in others (*Lycaenops* is recovered either as sister to (*Arctops*+*Smilesaurus*) or outside a clade containing those taxa and Rubidgeinae). *Nochnitsa* is recovered as the earliest-diverging gorgonopsian taxon, followed by *Viatkogorgon* then a large clade containing the remaining gorgonopsian OTUs. This clade is broken into two major subclades, one containing only Russian gorgonopsians (*Suchogorgon*, *Sauroctonus*, *Pravoslavlevia*, and *Inostrancevia*) and the other containing all the African gorgonopsians included in the analysis.

DISCUSSION

The position of *Nochnitsa* as the basalmost known gorgonopsian is supported by a number of plesiomorphic characters, such as the low symphysis, low, sloping, therocephalian-like posterior dentary, reflected lamina close to jaw articulation, no “cross-bar” in reflected lamina surface, and elongate tooth row (not restricted as in *Viatkogorgon*). *Viatkogorgon* is found to occupy a position one node up from *Nochnitsa*, but also outside the main burst of gorgonopsian diversification (based on the lack of ventral expansion of the postorbital bar).

Remarkably, the remaining Russian gorgonopsian genera (*Inostrancevia*, *Pravoslavlevia*, *Sauroctonus*, and *Suchogorgon*) were found to form a monophyletic group outside of the clade containing all African gorgonopsians. The monophyly of this group is currently weakly-supported, but their position outside of the ‘African clade’ is supported by several notable characters. The canonical synapomorphy of Gorgonopsia is a midline contact between the palatines, excluding the vomer from contact with the pterygoid; previous researchers considered this morphology to be present in all gorgonopsians (Hopson and Barghusen, 1986; Sidor, 2000). However, our examination of the well-preserved holotype skull of *Sauroctonus progressus* (PIN 156/6) revealed that, contra previous descriptions (Tatarinov, 1974; Sigogneau-Russell, 1989; Gebauer, 2014), there is actually a narrow vomerine-ptyergoid contact (Fig. 8A, C). Although this contact is substantially narrower than in any other therapsid clade, it clearly prevents midline contact of the palatines. Further examination of the best-preserved Russian gorgonopsian palatal material indicates that this contact is also retained in *Suchogorgon* (Fig. 8B, D) and *Inostrancevia* (the palate is too poorly-preserved in the only known skull of *Pravoslavlevia* to determine).

African gorgonopsians typically have a conservative morphology of the parabasisphenoid rostrum: this structure bears a blade-like ridge extending the length of the basicranial girder, from the anterior edge of the basal tubera to the posterior edge of the transverse processes of the pterygoids (Fig. 9A, B). This blade is tallest in its posterior half but slopes gradually forwards, the only exception being in rubidgeines in which the blade-like

rostrum has been secondarily lost. In *Inostrancevia*, *Sauroctonus*, and *Suchogorgon*, by contrast (this region is not well-preserved in *Pravoslavlevia*), the parabasisphenoid blade is a tab-like structure restricted to the posterior part of the basicranial girder (Fig. 9C, D). This is more similar to the condition in therocephalians than to African gorgonopsians (van den Heever, 1994), and may represent the ancestral morphology within Theriodontia.

To reflect the results of the current phylogenetic analysis, we here recognize two major subclades within Gorgonopsia: Inostrancevioidea von Huene, 1948, containing all Russian gorgonopsians other than *Nochnitsa* and *Viatkogorgon*, and Gorgonopioidea Lydekker, 1889, containing the African gorgonopsians (Fig. 10). Although there are numerous African gorgonopsian taxa that have yet to be included in a phylogenetic analysis (pending ongoing alpha taxonomic revision of the group), personal examination of those taxa indicates that they all have 'African'-style midline palatine contacts and elongate parabasisphenoid blades, suggesting that they also belong to this clade. However, we refrain from formally defining these subclades pending more robust support from subsequent analyses. The recovery of a monophyletic Inostrancevioidea containing the majority of Russian gorgonopsian taxa is novel to the current study. Previous authors recognized no close relationship between *Inostrancevia*, *Sauroctonus*, and *Suchogorgon* (although *Inostrancevia* and *Pravoslavlevia* have often been grouped together, and were initially placed in the same genus). Tatarinov (1974) classified the Russian gorgonopsians in different families, with *Inostrancevia* and *Pravoslavlevia* in Inostranceviidae (containing only these two genera) and *Sauroctonus* in the subfamily Cynariopinae of family Gorgonopidae (also containing the African genera *Aloposaurus*, *Aloposauroides*, *Cynarioides*, *Cynariops*, *Scylacognathus*, *Scylacops*, and *Sycocephalus*). Sigogneau-Russell (1989) classified *Inostrancevia* and *Pravoslavlevia* in the subfamily Inostranceviinae of family Gorgonopidae (one of only two gorgonopsian subfamilies she recognized, the other being Rubidgeinae), leaving *Sauroctonus* as an undifferentiated gorgonopid. Ivakhnenko (2003) classified *Inostrancevia* in a monogeneric Inostranceviidae,

placing *Pravoslavlevia*, *Sauroctonus*, and *Suchogorgon* in Gorgonopidae. Gebauer (2007) found *Inostrancevia* to be deeply nested within African gorgonopsians, forming the sister-taxon of Rubidgeinae. She recovered *Sauroctonus* as a basal gorgonopid, but also deeply-nested within a clade of otherwise-African taxa (as she considered *Aelurosaurus*, *Cyonosaurus*, and *Aelurosaurus* to be basal, non-gorgonopid gorgonopsians).

At present, all described inostrancevioids are Russian, and all known gorgonopoids are African. The purported Russian rubidgeine gorgonopoid *Leogorgon klimovensis* is not recognizable as a rubidgeine, and may not even be gorgonopsian (Kammerer 2016). Gebauer (2014) considered the Tanzanian gorgonopsian previously known as *Scymnognathus parringtoni* to be referable to the genus *Sauroctonus*. However, personal examination of the type and only specimen of *S. parringtoni* (GPIT/RE/7113) indicates that it has the typical parabasisphenoid and palatine morphologies of other African gorgonopsians, and that cranial similarities between it and *Sauroctonus* (which consist primarily of proportional characters that are variable among gorgonopsians) are superficial. Endemism in gorgonopsians was previously unsuspected, and is surprising considering the many Russo-African sister-taxon relationships in other therapsid groups, particularly dicynodonts and burnetiamorphs (Sidor and Smith, 2007; Kammerer et al., 2011). However, tetrapod biogeography in the Permian remains poorly known, and the inferred dispersal abilities of various therapsid taxa are often discordant with the observed record (Sidor et al., 2013; Kammerer et al., 2016). Additional research, particularly from regions outside of the well-sampled Karoo Basin of South Africa, is required to understand the factors underlying tetrapod distribution during this time.

CONCLUSIONS

Two distinct gorgonopsian taxa are now known from the Russian Kotelnich locality: *Viatkogorgon ivakhnenkoi* Tatarinov, 1999a and *Nochnitsa geminidens* gen. et sp. nov. Despite this addition to the fauna's gorgonopsian diversity, gorgonopsians remain notably less species-

rich at Kotelnich than therocephalians (Ivakhnenko, 2011). Low diversity and small size of the Kotelnich gorgonopsians suggests a predatory therapsid assemblage comparable to that of the *Pristerognathus* AZ in the Karoo (Kammerer et al., 2015), prior to the main burst of gorgonopsian diversification in South Africa. The phylogenetic position of *Nochnitsa* and *Viatkogorgon* is also intriguing in this regard, as they are recovered as the most basal gorgonopsians in our analysis. It is unlikely that this is actually indicative of an earlier age for the Kotelnich locality than middle Permian gorgonopsian-bearing strata in South Africa (e.g., the Abrahamskraal Formation, which yields *Eriphostoma* specimens), based on the other therapsid components of these faunas (notably the abundant eutheriocephalians and absence of dinocephalians at Kotelnich). However, even though the main Russian gorgonopsian subclade (Inostrancevioidea) probably had diverged by the time of the Kotelnich fauna, its absence at the locality does suggest it had not yet undergone substantial diversification in Russia, only later becoming the dominant therapsid predators in the region.

ACKNOWLEDGEMENTS

We are very grateful to director A. Toporov, curator T. Berestova, and the staff members of the Vyatka Paleontological Museum for permitting access to the holotype of *Nochnitsa* and for supporting research at Kotelnich. For access to comparative materials we thank Valeriy Golubev and the late Mikhail Ivakhnenko (PIN), Sifelani Jirah and Bernhard Zipfel (BP), Ingmar Werneburg (GPIT), Zaituna Erasmus and Roger Smith (SAM), and Matt Lowe (UMZC). CFK's research was supported by a grant (KA 3144/1-1) from the Deutsche Forschungsgemeinschaft.

REFERENCES

Amalitzky V. 1922. Diagnoses of the new forms of vertebrates and plants from the Upper Permian on North Dvina. *Bulletin de l'Académie des Sciences de Russie* (6)**16**:329–340.

Angielczyk KD, Schmitz L. 2014. Nocturnality in synapsids predates the origin of mammals by over 100 million years. *Proceedings of the Royal Society B* **281**:20141642. DOI 10.1098/rspb.2014.1642.

Benton MJ, Walker AD. 1985. Palaeoecology, taphonomy, and dating of Permo-Triassic reptiles from Elgin, north-east Scotland. *Palaeontology* **28**:207–234.

Benton MJ, Newell AJ, Khlyupin AY, Shumov IS, Price GD, Kurkin AA. 2012. Preservation of exceptional vertebrate assemblages in Middle Permian fluviolacustrine mudstones of Kotel'nich, Russia: stratigraphy, sedimentology, and taphonomy. *Palaeogeography, Palaeoclimatology, Palaeoecology* **319–320**:58–83.

Bercovici A, Bourquin S, Broutin J, Steyer J-S, Battail B, V éran M, Vacant R, Khenthavong B, Vongphamany S. 2012. Permian continental paleoenvironments in Southeastern Asia: New insights from the Luang Prabang Basin (Laos). *Journal of Asian Earth Sciences* **60**:197–211.

Boos ADS, Kammerer CF, Schultz CL, Paes Neto VD. 2015. A tapinocephalid dinocephalian (Synapsida, Therapsida) from the Rio do Rasto Formation (Paraná Basin, Brazil): Taxonomic, ontogenetic and biostratigraphic considerations. *Journal of South American Earth Sciences* **63**:375–384.

Broom R. 1905. On the use of the term Anomodontia. *Records of the Albany Museum* **1**:266–269.

Bystrov AP. 1955. [A gorgonopsian from the Upper Permian beds of the Volga]. *Voprosy Paleontologii* **1955**:7–18. [in Russian]

Coffa AA. 1997. Geology and stratigraphy of the Upper Permian Kotel'nich locality, Vyatka River, Russia. Unpublished PhD Thesis, Monash University.

Coffa AA. 1997. Stratigraphy and correlation of the continental red bed sequence at the Kotel'nich Upper Permian fossil tetrapod locality, Russia. *Geological Society of Australia Abstracts* **46**:15–17.

Coffa AA. 1998. Aeolian vs. fluvial origin for the Boroviki Member, Kotel'nich Upper Permian fossil tetrapod localities, Vyatka Basin, Russia. *Geological Society of Australia Abstracts* **52**:7.

Coffa AA. 1999. Sedimentology, stratigraphy and correlation of the continental red bed sequence at the Kotel'nich Late Permian fossil tetrapod localities, Russia. In: *Proceedings of International Symposium "Upper Permian Stratotypes of the Volga Region"*. Geos: Moscow, 77-86.

Day MO, Ramezani J, Bowring SA, Sadler PM, Erwin DH, Abdala F, Rubidge BS. 2015. When and how did the terrestrial mid-Permian mass extinction occur? Evidence from the tetrapod record of the Karoo Basin, South Africa. *Proceedings of the Royal Society B* **282**:20150834 DOI 10.1098/rspb.2015.0834.

Dias-da-Silva S. 2012. Middle-Late Permian tetrapods from the Rio do Rasto Formation, Southern Brazil: a biostratigraphic reassessment. *Lethaia* **45**:109–120.

- 777 **Durand JF. 1991.** A revised description of the skull of *Moschorhinus* (Therapsida,
778 Therocephalia). *Annals of the South African Museum* **99**:381–413.
- 779
- 780 **Efremov JA. 1940.** [On the composition of the Severodvinian Permian Fauna from the
781 excavation of V. P. Amalitzky]. *Comptes Rendus de l'Academie des Sciences de l'URSS*
782 **26**:893–896. [in Russian]
- 783
- 784 **Efremov JA, Vjushkov BP. 1955.** Catalogue of localities of the Permian and Triassic land
785 vertebrates on a territory of the USSR [in Russian]. *Trudy Paleontologicheskogo Instituta*
786 *Akademii Nauk SSSR* **46**:1–185.
- 787
- 788 **Gebauer EVI. 2014.** Re-assessment of the taxonomic position of the specimen GPIT/RE/7113
789 (*Sauroctonus parringtoni* comb. nov., Gorgonopsia). In: Kammerer CF, Angielczyk KD, Fröbisch
790 J, eds. *Early Evolutionary History of the Synapsida*. Dordrecht: Springer, 185–207, 337 pp. DOI
791 10.1007/978-94-007-6841-3_12.
- 792
- 793 **Hartmann-Weinberg AP. 1937.** Pareiasauriden als Leitfossilien. *Problemy Paleontologii*
794 **2/3**:649–712.
- 795
- 796 **Hartmann-Weinberg A. 1938.** Gorgonopsians as time indicators. *Problems of Paleontology*
797 **4**:47–123.
- 798
- 799 **Hopson JA, Barghusen HB. 1986.** An analysis of therapsid relationships. In: Hotton N III,
800 MacLean PD, Roth JJ, Roth EC, eds. *The Ecology and Biology of the Mammal-Like Reptiles*.
801 Washington, D.C.: Smithsonian Institution Press, 83–106, x + 326 pp.
- 802

Huene, F von. 1948. Short review of the lower tetrapods. In: Du Toit AL, ed. *Special Publication of the Royal Society of South Africa: Robert Broom Commemorative Volume*. Cape Town: Royal Society of South Africa, 65–106.

Ivakhnenko MF. 2003. Eotherapsids from the East European Placket (Late Permian). *Paleontological Journal* **37**:S339–S465.

Ivakhnenko MF. 2011. Permian and Triassic therocephals (Eutherapsida) of Eastern Europe. *Paleontological Journal* **49**:981–1144.

Kammerer CF. 2015. Cranial osteology of *Arctognathus curvimola*, a short-snouted gorgonopsian from the Late Permian of South Africa. *Papers in Palaeontology* **1**:41–58. DOI 10.1002/spp2.1002.

Kammerer CF. 2016. Systematics of the Rubidgeinae (Therapsida: Gorgonopsia). *PeerJ* **4**:e1608. DOI 10.7717/peerj.1608.

Kammerer CF, Angielczyk KD, Fröbisch J. 2011. A comprehensive taxonomic revision of Dicynodon (Therapsida, Anomodontia) and its implications for dicynodont phylogeny, biogeography, and biostratigraphy. *Society of Vertebrate Paleontology Memoir* **11**:1–158.

Kammerer CF, Bandyopadhyay S, Ray S. 2016. A new taxon of cistecephalid dicynodont from the upper Permian Kundaram Formation of India. *Papers in Palaeontology* **2**:569–584.

- Kammerer CF, Smith RMH, Day MO, Rubidge BS. 2015.** New information on the morphology and stratigraphic range of the mid-Permian gorgonopsian *Eriphostoma microdon* Broom, 1911. *Papers in Palaeontology* 1:201–221. DOI 10.1002/spp2.1012.
- King GM. 1988.** Anomodontia. *Handbuch der Paläoherpetologie* 17 C. Stuttgart: Gustav Fischer Verlag, 174 pp.
- Kurkin, AA. 2011.** Permian anomodonts: paleobiogeography and distribution of the group. *Paleontological Journal* 45: 432–444.
- Laurin M. 1998.** New data on the cranial anatomy of *Lycaenops* (Synapsida, Gorgonopsidae), and reflections on the possible presence of streptostyly in gorgonopsians. *Journal of Vertebrate Paleontology* 18:765–776. DOI 10.1080/02724634.1998.10011105.
- Liu J, Xu L, Jia S-H, Pu H-Y, Liu X-L. 2014.** The Jiyuan tetrapod fauna of the Upper Permian of China—2. stratigraphy, taxonomical review, and correlation. *Vertebrata Palasiatica* 52:328–339.
- Lydekker R. 1889.** Part III. Palæozoology: Vertebrata. in Nicholson, H. A., and R. Lydekker. *A Manual of Palæontology for the Use of Students. Vol. 2.* Edinburgh: William Blackwood and Sons.
- Masyutin V, Masyutina O. 2016.** The 100th anniversary of the Paleontological Society of Russia. Problems and prospects of paleontological research. *Paleontological society of the Russian Academy of Sciences (4-8 April 2016, St. Petersburg)*, 253-254, 352 pp.

- Ochev VG, Surkov MG. 2000.** The history of excavation of Permo-Triassic vertebrates from Eastern Europe. In: Benton MJ, Shishkin MA, Unwin DM, Kurochkin EN (eds.) *The Age of Dinosaurs in Russia and Mongolia*. Cambridge: Cambridge University Press, 1–16, 696 pp.
- Olson EC. 1937.** The cranial morphology of a new gorgonopsians. *Journal of Geology* **45**:511–527.
- Osborn HF. 1903.** On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. *Science* **17**:275–276.
- Pravoslavlev PA. 1927.** [Gorgonopsidae from the North Dvina expedition of V. P. Amalitzki]. *Severo-Dvinskie raskopki Prof. V. P. Amalitskogo* **3**:1–117. [in Russian]
- Ray S, Bandyopadhyay S. 2003.** Late Permian vertebrate community of the Pranhita-Godavari valley, India. *Journal of Asian Earth Sciences* **21**:643–654.
- Seeley HG. 1894.** Researches on the Structure, Organisation, and Classification of the Fossil Reptilia.—Part IX., Section 1. On the Therosuchia. *Philosophical Transactions of the Royal Society of London, Seires B, Biological Sciences* **185**:987–1018.
- Sidor CA, Rubidge BS. 2006.** *Herpetoskylax hopsoni*, a new biarmosuchian (Therapsida: Biarmosuchia) from the Beaufort Group of South Africa. In: Carrano MT, Gaudin TJ, Blob RW, Wible JR (eds.) *Amniote Paleobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles*. Chicago: University of Chicago Press, 76–113, 547 pp.

- Sidor CA, Smith RMH. 2007.** A second burnetiamorph therapsid from the Permian Teekloof Formation of South Africa and its associated fauna. *Journal of Vertebrate Paleontology* **27**:420–430.
- Sidor CA, Vilhena DA, Angielczyk KD, Huttenlocker AK, Nesbitt SJ, Peacock BR, Steyer JS, Smith RMH, Tsuji LA. 2013.** Provincialization of terrestrial faunas following the end-Permian mass extinction. *Proceedings of the National Academy of Sciences of the United States of America* **110**:8129–8133.
- Sigogneau D. 1970.** Révision systématique des gorgonopsiens sud-africains. *Cahiers de Paléontologie*. Paris: Centre National de la Recherche Scientifique. 417 pp.
- Sigogneau-Russell D. 1989.** Theriodontia I. *Handbuch der Paläoherpetologie* 17 B/I. Stuttgart: Gustav Fischer Verlag. 127 pp.
- Smith RMH, Rubidge BS, van der Walt M. 2012.** Therapsid biodiversity patterns and environments of the Karoo Basin, South Africa. In: Chinsamy A, ed. *Forerunners of Mammals: Radiation, Histology, Biology*. Bloomington and Indianapolis: Indiana University Press, 223–246, 330 pp.
- Sues H-D, Munk W. 1996.** A remarkable assemblage of terrestrial tetrapods from the Zechstein (Upper Permian: Tatarian) near Korbach (northwestern Hesse). *Paläontologische Zeitschrift* **70**:213–223.
- Swofford DL. 2002.** PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

- Tatarinov LP. 1974.** [Theriodonts of the USSR]. *Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR* **143**:1–226. [in Russian]
- Tatarinov LP. 1999a.** New theriodonts (Reptilia) from the Late Permian fauna of the Kotelnich Locality, Kirov Region. *Paleontological Journal* **33**:550–556.
- Tatarinov LP. 1999b.** The first scaloposaurid (Reptilia, Theriodontia) from Russia (Upper Permian, Kirov Region). *Paleontological Journal* **33**:278–288.
- Tatarinov LP. 2000a.** A new gorgonopid (Reptilia, Theriodontia) from the Upper Permian of the Vologda Region. *Paleontological Journal* **34**:75–83.
- Tatarinov LP. 2000b.** New material of scaloposaurians (Reptilia, Theriodontia) from the Upper Permian of the Kotelnich Locality, Kirov Region. *Paleontological Journal* **34**:S187–S202.
- Tatarinov LP. 2004.** A postcranial skeleton of the gorgonopian *Viatkogorgon ivachnenkoi* (Reptilia, Theriodontia) from the Upper Permian Kotelnich locality, Kirov Region. *Paleontological Journal* **38**: 437–447.
- van den Heever JA. 1994.** The cranial anatomy of the early Therocephalia (Amniota: Therapsida). *Universiteit van Stellenbosch Annale* **1**:1–59.
- Vjuschkov BP. 1953.** [On gorgonopsians from the Severodvinian Fauna]. *Doklady Akademiya Nauk SSSR* **91**:397–400. [in Russian]

930 **Young CC. 1979.** [A Late Permian fauna from Jiyuan, Henan]. *Vertebrata Palasiatica* **17**:99–
 931 113. [in Chinese]

FIGURE CAPTIONS

Figure 1. Holotype block of *Nochnitsa geminidens* (KPM 310) in **A**, left lateral view with **B**, interpretive drawing. **Abbreviations:** **at**, atlas; **ax**, axis; **cr**, cranium; **cv**, cervical vertebra; **d**, dentary; **dv**, dorsal vertebra; **rla**, reflected lamina of angular; **r**, rib; **sc**, scapula. Gray indicates matrix. Scale bar equals 1 cm. [planned for page width]

Figure 2. Holotype block of *Nochnitsa geminidens* (KPM 310) in **A**, right lateral view with **B**, interpretive drawing. **Abbreviations:** **bf**, unidentified bone fragments; **ce**, centrale; **d**, dentary; **dpc**, deltopectoral crest; **h**, humerus; **mc**, metacarpal; **ph**, phalanx; **r**, radius; **re**, radiale; **u**, ulna; **ue**, ulnare. Gray indicates matrix, hatching indicates plaster. Scale bar equals 1 cm. [planned for page width]

Figure 3. Stereopair of KPM 310, holotype of *Nochnitsa geminidens*, in left lateral view. Scale bar equals 1 cm. [planned for page width]

Figure 4. Kotelnich gorgonopsians compared in lateral view. **A.** PIN 2212/6, holotype of *Viatkogorgon ivakhnenkoi*, in right lateral view. **B.** KPM 310, holotype of *Nochnitsa geminidens*, in left lateral view (mirrored for comparative purposes and with non-cranial parts of block edited out). Scale bars equal 1 cm. [planned for page width]

Figure 5. Interpretive drawings of Kotelnich gorgonopsians compared in lateral view. **A.** PIN 2212/6, holotype of *Viatkogorgon ivakhnenkoi*, in right lateral view. **B.** KPM 310, holotype of *Nochnitsa geminidens*, in left lateral view (mirrored for comparative purposes). **Abbreviations:** **an**, angular; **ar**, articular; **C**, upper canine; **c**, lower canine; **d**, dentary; **fr**, frontal; **I**, upper incisor; **i**, lower postcanine; **j**, jugal; **la**, lacrimal; **mf**, maxillary flange; **mx**, maxilla; **na**, nasal; **pa**,

parietal; **PC**, upper postcanine; **pc**, lower postcanine; **pf**, pineal foramen; **pmx**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pp**, preparietal; **prf**, prefrontal; **rla**, reflected lamina of angular; **sa**, surangular; **sc**, sclerotic ring; **sf**, squamosal flange; **smx**, septomaxilla; **sq**, squamosal; **ss**, squamosal sulcus. Gray indicates matrix, hatching indicates plaster. Scale bars equal 1 cm. [planned for page width]

Figure 6. Right marginal dentition of *Nochnitsa geminidens*. **A**, close-up of holotype, KPM 310, with **B**, interpretive drawing. **Abbreviations:** **C**, upper canine; **I**, upper incisor; **PC**, upper postcanine; **pc**, lower postcanine; **rC**, replacement upper canine. Scale bar equals 1 cm. [planned for page width]

Figure 7. Holotype skull of *Nochnitsa geminidens* (KPM 310) in dorsal view; **A**, interpretive drawing, and **B**, photograph. Gray indicates matrix, hatching indicates plaster. Scale bar equals 1 cm. [planned for page width]

Figure 8. Photographs and interpretive drawings of inostranceviid palates, illustrating the presence of a narrow contact between the vomer and pterygoid. **A**, **C**. PIN 156/5, holotype of *Sauroctonus progressus*. **B**, **D**. PIN 4548/1, referred specimen of *Suchogorgon golubevi*. **Abbreviations:** **ec**, ectopterygoid; **mx**, maxilla; **PCa**, postcanine alveolus; **pl**, palatine; **ppl**, palatal boss of palatine; **ppt**, palatal boss of pterygoid; **pt**, pterygoid; **tpt**, transverse process of pterygoid; **v**, vomer. Scale bars equal 1 cm. [planned for page width]

Figure 9. Photographs of the basicranial girder in inostranceviid and gorgonopid gorgonopsians, illustrating the difference in morphology of the parabasisphenoid blade between these families: elongate and sloping in Gorgonopidae, short and tab-like in Inostranceviidae. **A**. BP/1/7275, referred specimen of *Eriphostoma microdon*. **B**. BP/1/4089, referred specimen of

984 *Gorgonops torvus*. **C.** Cast of PIN 2005/1587, holotype of *Inostrancevia alexandri*. **D.** PIN 156/6,
 985 holotype of *Sauroctonus progressus*. Parabasisphenoid blades highlighted in white to show
 986 outlines (dotted outline indicates broken surface). **A–C** in ventrolateral view, **D** in lateral view.
 987 [planned for page width]

988

989 **Figure 10.** Results of the phylogenetic analysis, showing the consensus of six most
 990 parsimonious trees. Values at nodes represent bootstrap support. [planned for page width]

Figure 1

Holotype block of *Nochnitsa geminidens* (KPM 310).

(A) Left lateral view with **(B)** interpretive drawing. **Abbreviations:** at, atlas; ax, axis; cr, cranium; cv, cervical vertebra; d, dentary; dv, dorsal vertebra; rla, reflected lamina of angular; r, rib; sc, scapula. Gray indicates matrix. Scale bar equals 1 cm.

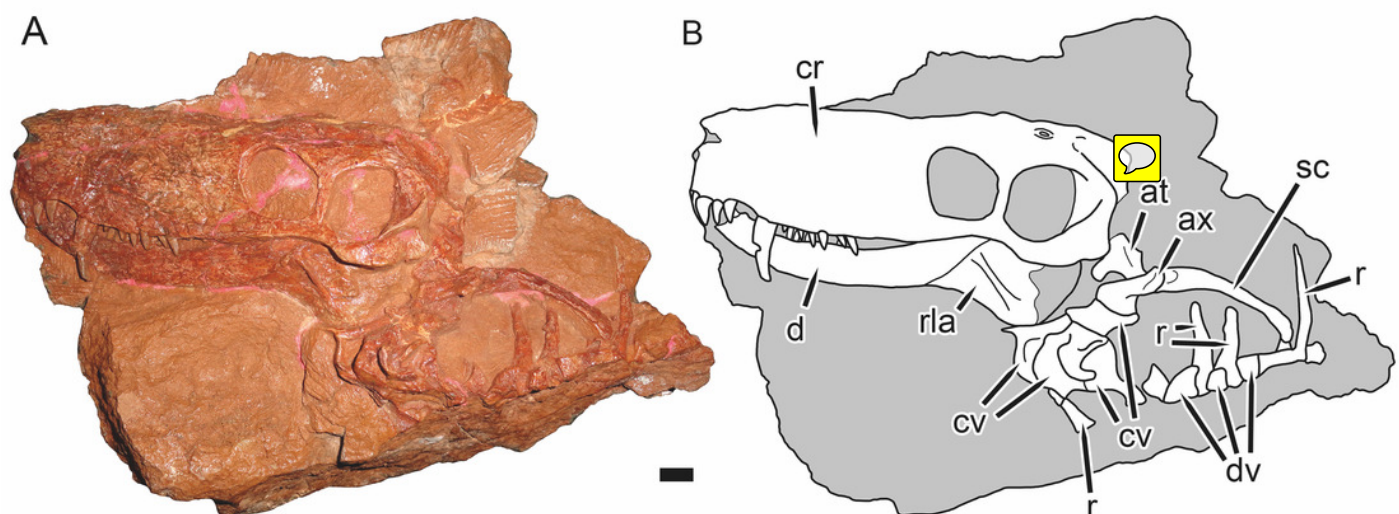


Figure 2

Holotype block of *Nochnitsa geminidens* (KPM 310).

(A) Right lateral view with **(B)** interpretive drawing. **Abbreviations:** bf, unidentified bone fragments; ce, centrale; d, dentary; dpc, deltopectoral crest; h, humerus; mc, metacarpal; ph, phalanx; r, radius; re, radiale; u, ulna; ue, ulnare. Gray indicates matrix, hatching indicates plaster. Scale bar equals 1 cm.

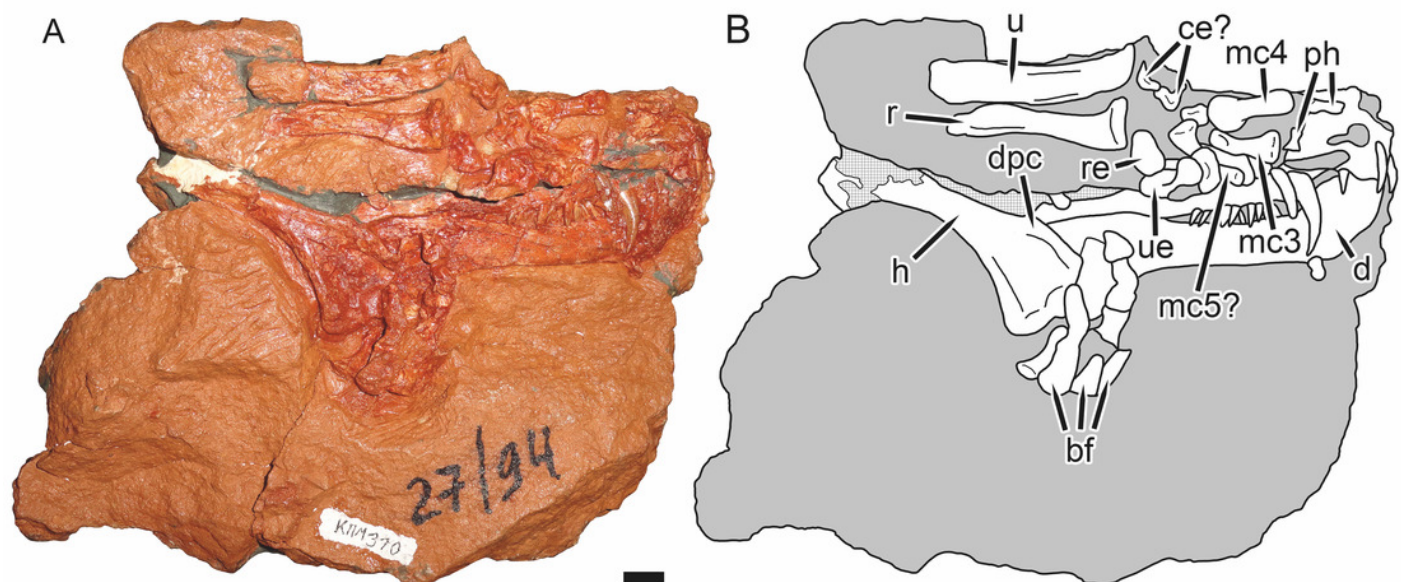


Figure 3

Stereopair of KPM 310, holotype of *Nochnitsa geminidens*.

Specimen in left lateral view. Scale bar equals 1 cm.



Figure 4

Kotelnich gorgonopsians compared in lateral view.

(A) PIN 2212/6, holotype of *Viatkogorgon ivakhnenkoi*, in right lateral view. **(B)** KPM 310, holotype of *Nochnitsa geminidens*, in left lateral view (mirrored for comparative purposes and with non-cranial parts of block edited out). Scale bars equal 1 cm.

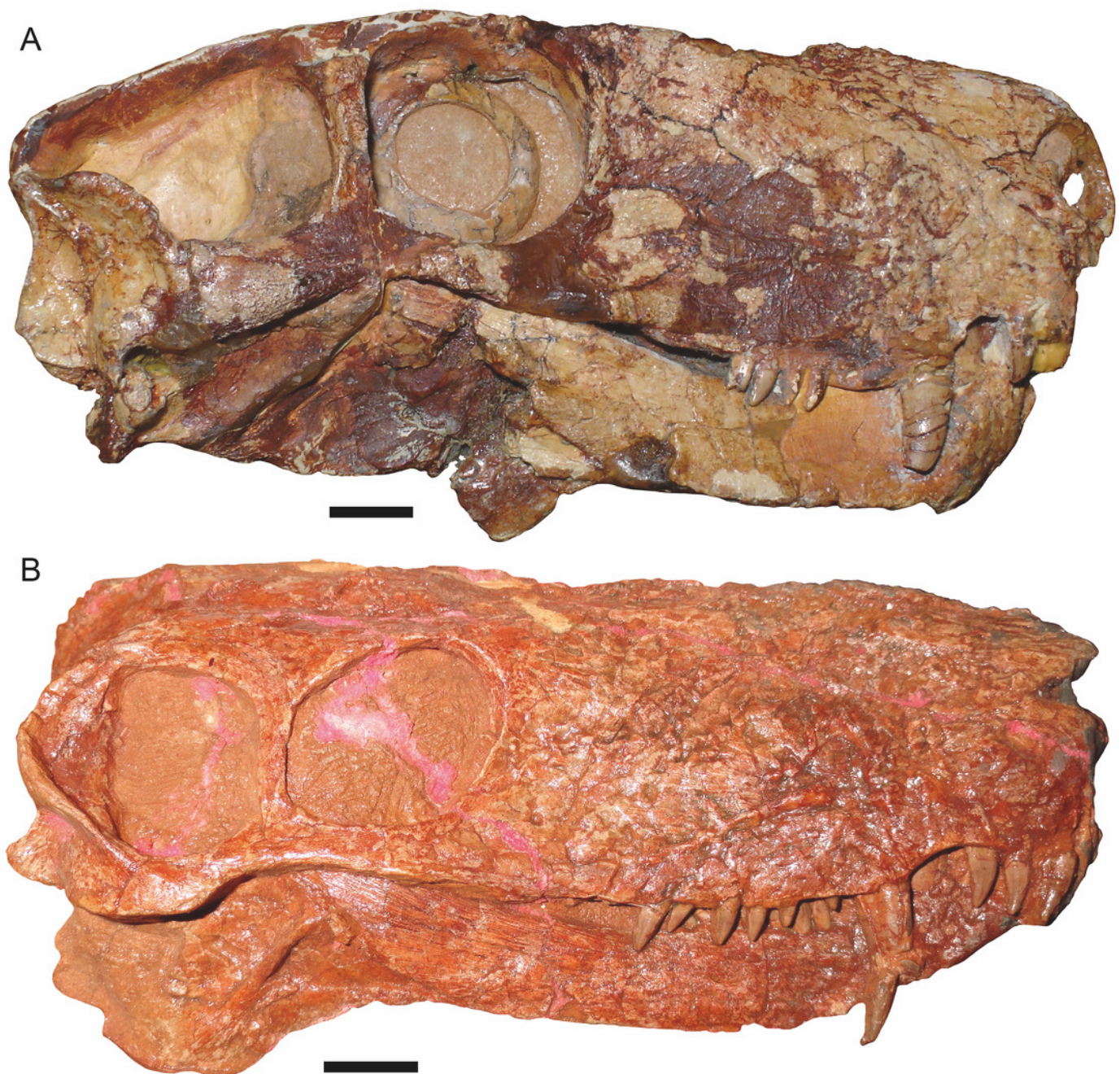


Figure 5

Interpretive drawings of Kotelnich gorgonopsians compared in lateral view.

(A) PIN 2212/6, holotype of *Viatkogorgon ivakhnenkoi*, in right lateral view. **(B)** KPM 310, holotype of *Nochnitsa geminidens*, in left lateral view (mirrored for comparative purposes).

Abbreviations: an, angular; ar, articular; C, upper canine; c, lower canine; d, dentary; fr, frontal; I, upper incisor; i, lower postcanine; j, jugal; la, lacrimal; mf, maxillary flange; mx, maxilla; na, nasal; pa, parietal; PC, upper postcanine; pc, lower postcanine; pf, pineal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; pp, preparietal; prf, prefrontal; rla, reflected lamina of angular; sa, surangular; sc, sclerotic ring; sf, squamosal flange; smx, septomaxilla; sq, squamosal; ss, squamosal sulcus. Gray indicates matrix, hatching indicates plaster. Scale bars equal 1 cm.

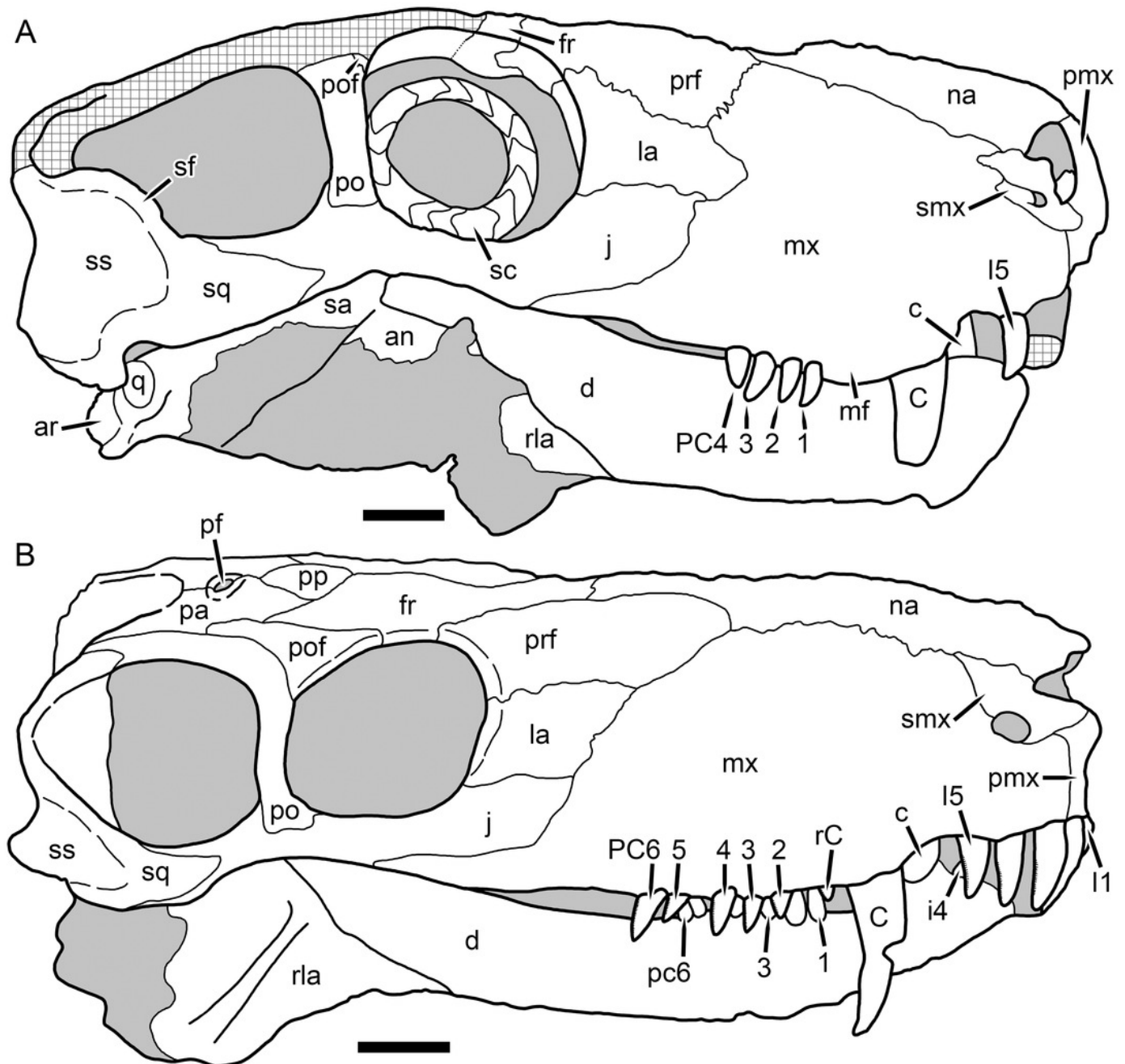


Figure 6

Right marginal dentition of *Nochnitsa geminidens*.

(A) Close-up of holotype, KPM 310, with **(B)** interpretive drawing. **Abbreviations:** C, upper canine; I, upper incisor; PC, upper postcanine; pc, lower postcanine; rC, replacement upper canine. Scale bar equals 1 cm.

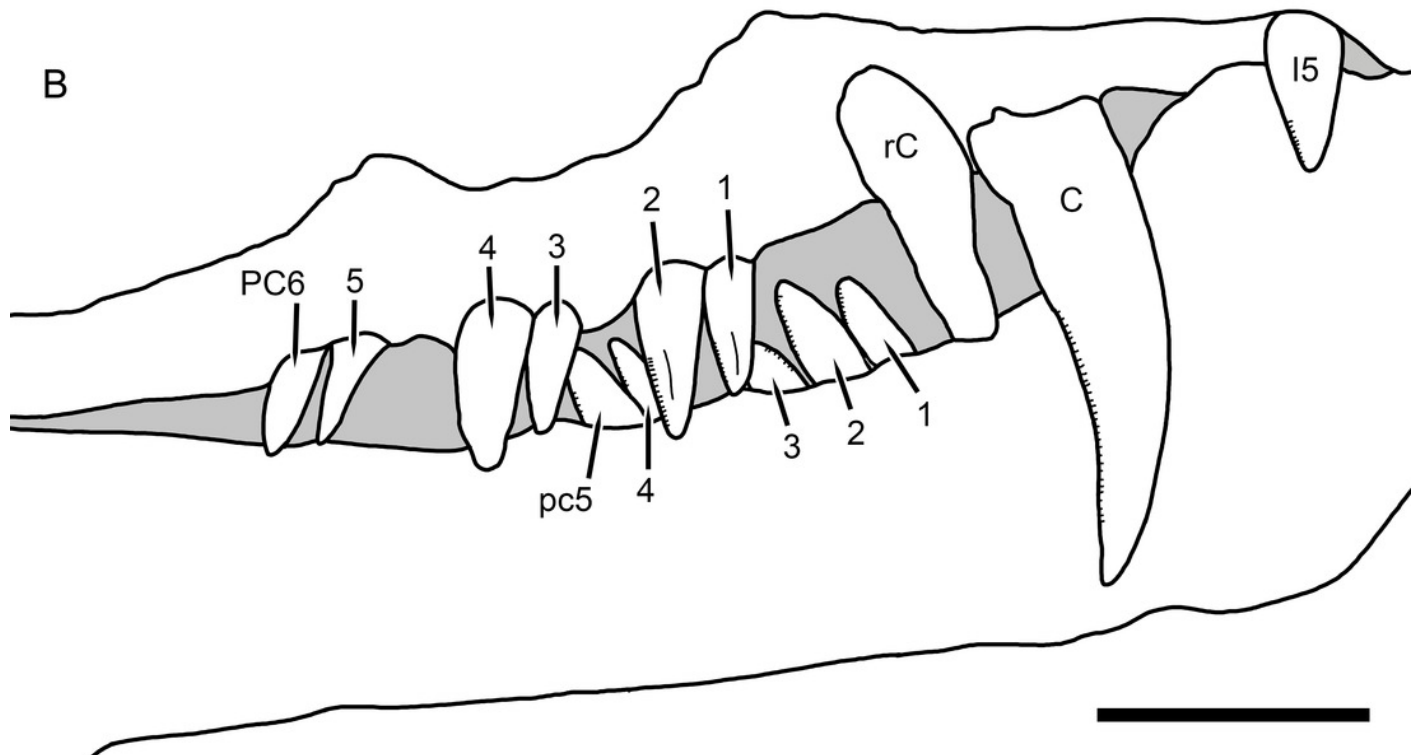


Figure 7

Holotype skull of *Nochnitsa geminidens* (KPM 310) in dorsal view.

(A) Interpretive drawing, and **(B)** photograph. Gray indicates matrix, hatching indicates plaster. Scale bar equals 1 cm.

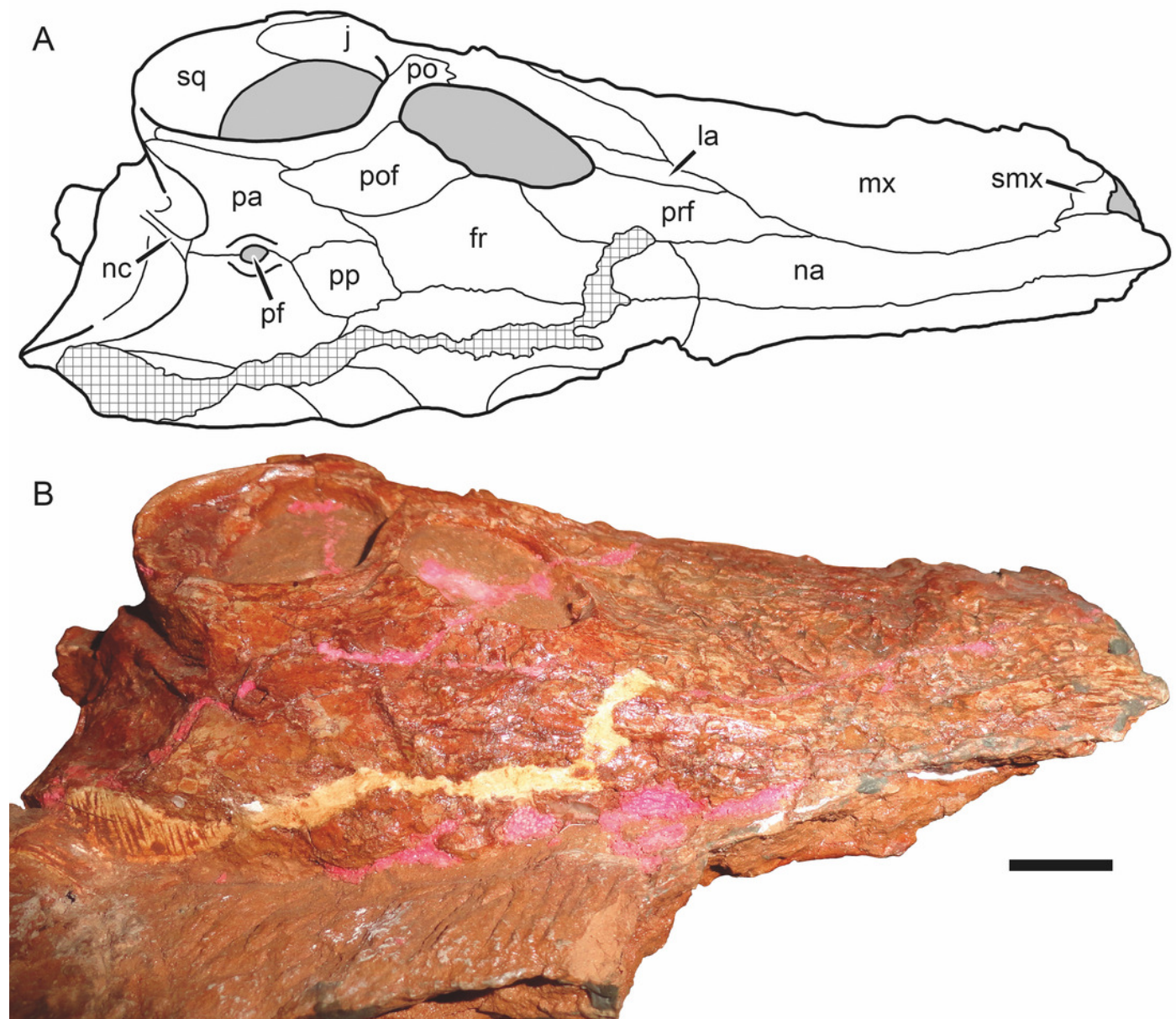


Figure 8

Photographs and interpretive drawings of inostrancevioid palates, illustrating the presence of a narrow contact between the vomer and pterygoid.

(A), (C) PIN 156/5, holotype of *Sauroctonus progressus*. **(B), (D)** PIN 4548/1, referred specimen of *Suchogorgon golubevi*. **Abbreviations:** ec, ectopterygoid; mx, maxilla; PCa, postcanine alveolus; pl, palatine; ppl, palatal boss of palatine; ppt, palatal boss of pterygoid; pt, pterygoid; tpt, transverse process of pterygoid; v, vomer. Scale bars equal 1 cm.

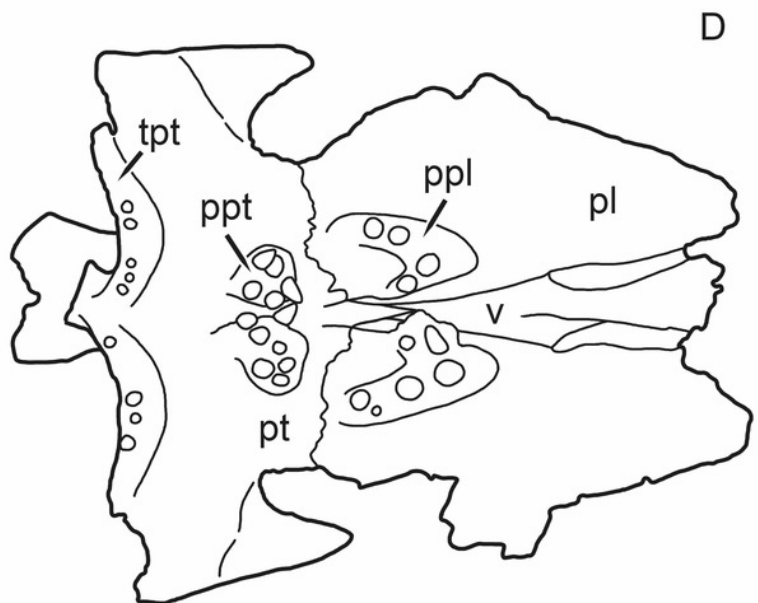
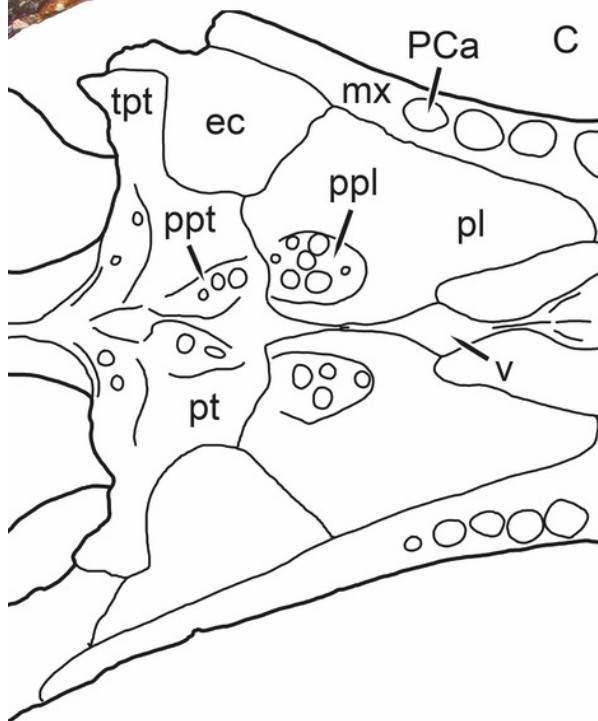


Figure 9

Photographs of the basicranial girder in inostrancevioid and gorgonopoid gorgonopsians.

Difference in morphology of the parabasisphenoid blade in gorgonopsians: elongate and sloping in Gorgonopoidea, short and tab-like in Inostrancevioidea. **(A)** BP/1/7275, referred specimen of *Eriphostoma microdon*. **(B)** BP/1/4089, referred specimen of *Gorgonops torvus*. **(C)** Cast of PIN 2005/1587, holotype of *Inostrancevia alexandri*. **(D)** PIN 156/6, holotype of *Sauroctonus progressus*. Parabasisphenoid blades highlighted in white to show outlines (dotted outline indicates broken surface). **A–C** in ventrolateral view, **D** in lateral view.

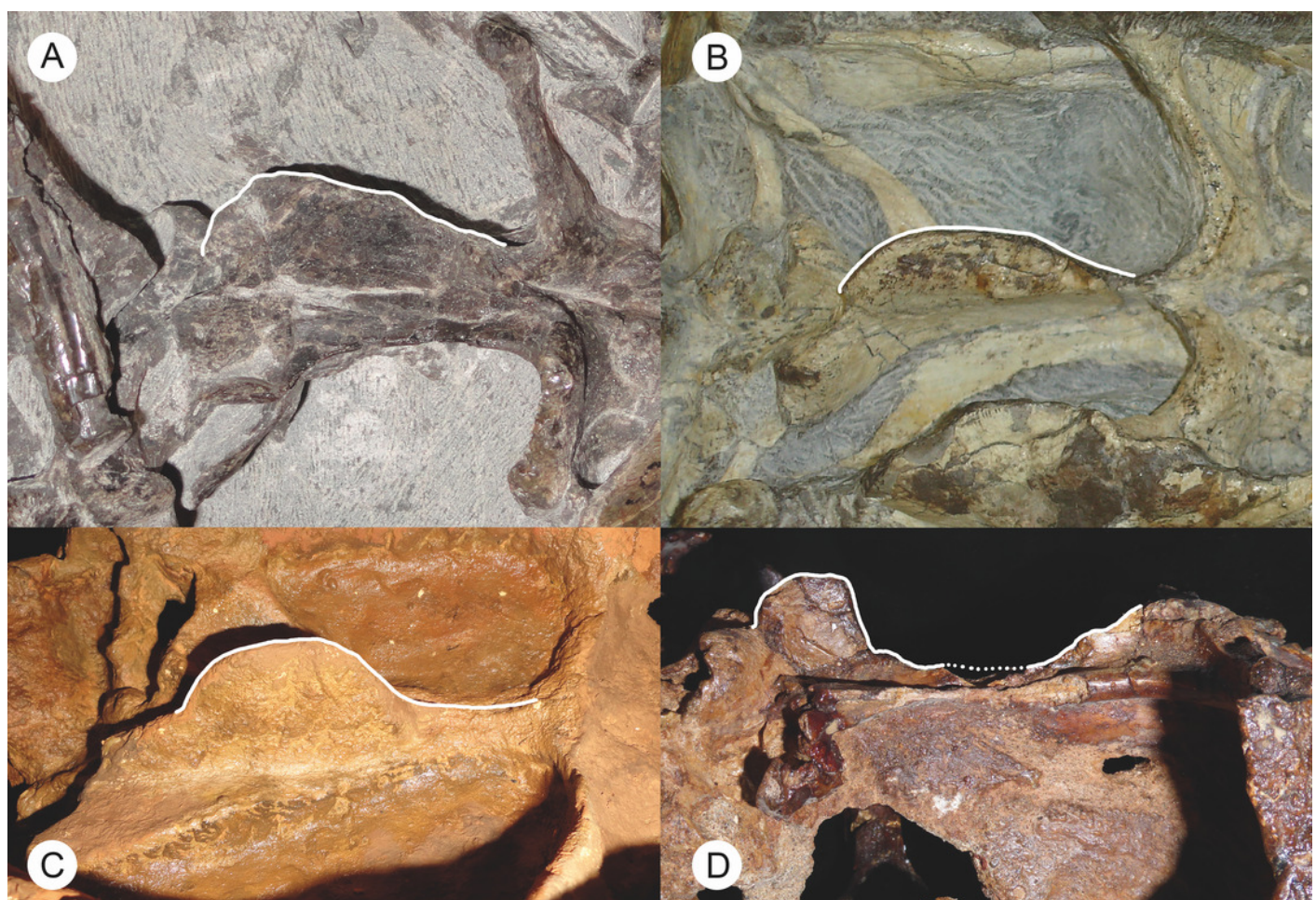


Figure 10

Results of the phylogenetic analysis, showing the consensus of six most parsimonious trees.

Values at nodes represent bootstrap support.

