

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

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

Christian F Kammerer ^{Corresp., 1}, Vladimir Masyutin ²

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.

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2 **Kotelnich locality of Russia**

3

4 Christian F. Kammerer¹ and Vladimir V. Masyutin²

5

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

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

8

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

10

11 **Abstract.** The early evolution of gorgonopsians is poorly understood. New material from the

12 Kotelnich locality in Russia expands our knowledge of middle/earliest late Permian

13 gorgonopsians from Laurasia. Two gorgonopsian taxa are recognized from Kotelnich:

14 *Viatkogorgon ivakhnenkoi* Tatarinov, 1999 and *Nochnitsa geminidens* gen. et sp. nov.

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16 tooth row, composed of pairs of teeth (a small anterior and larger posterior) separated by

17 diastemata. Both *Viatkogorgon* and *Nochnitsa* are relatively small gorgonopsians, comparable

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23 gorgonopsians). The high degree of endemism indicated in this analysis for gorgonopsians is

24 remarkable, especially given the extensive intercontinental dispersal inferred for coeval

25 therapsid groups.

26

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

28 **INTRODUCTION**

29 The therapsid subclade Gorgonopsia was an ~~abundant but~~ morphologically conservative group
30 of saber-toothed carnivores that included the apex predators of the late Permian (Sigogneau-
31 Russell, 1989; Kammerer, 2015, 2016). Despite their ~~omnipresence~~  in the late Permian
32 therapsid faunas of southern Africa (Smith et al., 2012), gorgonopsians are poorly represented
33 in the global fossil record. No gorgonopsian fossils have thus far been found in the middle-to-
34 late Permian deposits of western Europe, South America, or southeast Asia (Benton and
35 Walker, 1985; Sues and Munk, 1996; Bercovici et al., 2012; Dias-da-Silva, 2012; Boos et al.,
36 2015). Young (1979) described a supposed gorgonopsian taxon (*Wangwusaurus tayuensis*)
37 from the Jiyuan Formation of China, but the type material of this taxon consists of a chimaerical
38 assortment of temnospondyl and pareiasaur teeth (Liu et al., 2014). Although a serrated canine
39 from the Jiyuan Formation could represent an actual gorgonopsian (Liu et al., 2014), this
40 identification cannot be confirmed by this element alone (it could just as easily represent a
41 therocephalian, and indeed Liu et al. [2014] noted its similarity to teeth of the early
42 therocephalian *Lycosuchus*). As such, the presence of gorgonopsians in the Chinese record
43 remains dubious. Ray and Bandyopadhyay (2003) referred several skull fragments (premaxillary
44 and vomerine elements and isolated dentary symphyses) from the Kundaram Formation of India
45 to Gorgonopsia. These specimens are likely to represent true gorgonopsians: the steep, robust
46 morphology of these symphyses, with the incisor and canine tooth row elevated high above the
47 postcanine row, is typical of the group. However, although this morphology is typical for
48 gorgonopsians it is not exclusive to them; again, some therocephalian taxa exhibit a very similar
49 morphology (Durand, 1991). Of the extra-African regions yielding Permian tetrapod fossils, only
50 Russia has thus far produced definitive gorgonopsian remains.

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

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

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

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

80 *Leogorgon klimovenssis*, purportedly the first Russian rubidgeine gorgonopsian (Ivakhnenko,
81 2003; although see Kammerer [2016] for doubts on this identification).

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

88

89 **Nomenclatural acts**

90 The electronic version of this article in portable document format (PDF) will represent a
91 published work according to the International Commission on Zoological Nomenclature (ICZN),
92 and hence the new names contained in the electronic version are effectively published under
93 that Code from the electronic edition alone. This published work and the nomenclatural acts it
94 contains have been registered in ZooBank, the online registration system for the ICZN. The
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99 following digital repositories: PeerJ, PubMed Central, and CLOCKSS.

100

101 **Institutional abbreviations**

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

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

107

108 **GEOLOGICAL CONTEXT**

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

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

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

134 Benton et al. (2012) considered the Kotelnich faunal complex to be latest Guadalupian in
135 age, and equivalent to the *Pristerognathus* Assemblage Zone (AZ) of the South African Karoo
136 Basin. More recent research on the South African assemblage zones, however, indicates that
137 the boundary between the *Tapinocephalus* and *Pristerognathus* AZs is latest Guadalupian
138 (260.26 Ma) and the bulk of the *Pristerognathus* AZ may actually be early Lopingian (Day et al.,
139 2015). Kurkin (2011) suggested that the Kotelnich assemblage was better correlated with the
140 South African *Tropidostoma* AZ, based on the shared presence of toothed oudenodontid
141 dicynodonts (*Australobarbarus* in Russia and *Tropidostoma* in South Africa). However,
142 *Australobarbarus* fossils are found higher in section than most Kotelnich vertebrates (in the
143 Shestakovy Member) and are not necessarily indicative of the age of the Vanyushonki Member
144 fauna.

145 The specimen KPM 310 was collected by A. Khlyupin in 1994, in a red mudstone in the
146 middle part of the Vanyushonki Member along the north bank of the Vyatka River. It was
147 collected at the Sokol'ya Gora–Chizhi site, 43 meters upstream from the third ravine of the
148 Sokol'ya Gora lens. In situ, the skull of this specimen was oriented south-southeast. Following
149 collection, the specimen was mechanically prepared at the Vyatka Paleontological Museum by
150 O. Masyutina.

151

152 **SYSTEMATIC PALEONTOLOGY**

153 **Synapsida** Osborn, 1903

154 **Therapsida** Broom, 1905

155 **Gorgonopsia** Seeley, 1894

156

157 **Nochnitsa** gen. nov.

158

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

160 **Type species:** *Nochnitsa geminidens* sp. nov.

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

165 **Diagnosis:** As for type and only species.

166

167 ***Nochnitsa geminidens*** sp. nov.

168 (Figures 1–7)

169

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

353

354 ***Viatkogorgon*** Tatarinov, 1999a

355

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

357 **Diagnosis:** As for type and only species.

358

359 ***Viatkogorgon ivakhnenkoi*** Tatarinov, 1999a

360 (Figures 4–5)

361

362 **Holotype:** PIN 2212/61, a complete skeleton from the Kotelnich locality, Kotel'nichskii

363 District, Kirov Region, Russia.

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

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

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

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

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

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

416 ventrally. The posterior border of the maxilla is smoothly sloping in *Nochnitsa*, with progressively
417 shorter contributions to the snout from the prefrontal, lacrimal, and jugal (Fig. 5B). In
418 *Viatkogorgon*, the lacrimal has an anterior process breaking up the posterior border of the
419 maxilla posteriorly and extending to the same extent as the anterior tip of the prefrontal (Fig.
420 5A). As mentioned above, the lacrimal extends further dorsally along the rim of the orbit in
421 *Viatkogorgon* than *Nochnitsa*. As in *Nochnitsa*, there is no exit on the lateral surface of the
422 lacrimal for the lacrimal foramen, which is restricted to the orbital wall.

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

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

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

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

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

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

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

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

469

470 **PHYLOGENETIC ANALYSIS**

471 *Nochnitsa geminidens* and *Viatkogorgon ivakhnenkoi* were included in an expanded version of
472 the only existing published phylogenetic analysis of gorgonopsians, that of Kammerer (2016,
473 2017). The analysis of Kammerer (2016) was focused on rubidgeine gorgonopsians in
474 particular; in order better understand the relationships of the Kotelnich gorgonopsians, taxon
475 sampling was expanded to include the Russian taxa *Inostrancevia*, *Pravoslavlevia*,
476 *Sauroctonus*, and *Suchogorgon*.

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

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

493 2017:fig. 10). In rubidgeines, this invagination is particularly prominent, because the
494 premaxillary palatal plate is anteroposteriorly expanded relative to the condition in
495 biarmosuchians and early gorgonopsians like *Eriphostoma*.

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

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

521

522 **Character 9:** Vomerine-ptyergoid contact. Previously (as character 7 of Kammerer [2016]), this
523 character had two states, (0) present and (1) absent. The absence of a contact between the
524 vomer and pterygoid is one of the classic gorgonopsian synapomorphies (Hopson & Barghusen,
525 1986). However, as discussed in further detail below, Russian gorgonopsians with well-
526 prepared palates (*Inostrancevia*, *Sauroctonus*, and *Suchogorgon*) show that they still retained a
527 narrow but clearly present contact between the vomer and pterygoid (Fig. 8). The minimal
528 contact between these bones in these taxa still clearly distinguishes them from non-
529 gorgonopsian therapsids, so this character has been reformatted as ordered multistate: (0)
530 present, broad, (1) present, narrow, and (2) absent.

531

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

544

545 **Character 17:** Parabasisphenoid blade position: (0) restricted to posterior edge of basicranial
546 girder; (1) extending throughout length of basicranial girder. New character. In most
547 gorgonopsians, the parabasisphenoid rostrum bears a tall, narrow, blade-like ventral crest. In
548 rubidgeines this 'blade' is absent, and the ventral surface of the parabasisphenoid exhibits a
549 reversal to the biarmosuchian condition, in which a narrow median channel separates the two
550 edges of the parabasisphenoid. The presence/absence of this feature is covered in character
551 15, but does not address an important difference in morphology between the Russian
552 gorgonopsians *Inostrancevia*, *Sauroctonus*, and *Suchogorgon* (the parabasisphenoid rostrum is
553 not well preserved in *Pravoslavlevia*) and non-rubidgeine African gorgonopsians. In the Russian
554 taxa, the 'blade' is nearly semi-circular in lateral view and restricted to the posterior portion of
555 the parabasisphenoid, near the back of the basicranial girder (as is also the case in
556 therocephalians), whereas in the African taxa the 'blade' is semi-oval and more elongate,
557 extending for almost the entire length of the basicranial girder (Fig. 9).

558

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

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

574

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

592

593 **Character 50:** Lateral surface of reflected lamina. Previously (as character 45 of Kammerer
594 [2016]), this character had two states: (0) lobate sculpturing and (1) well-developed
595 dorsoventrally-oriented bar, with weakly-developed crossbar. The cruciate laminar sculpturing of
596 state (1) is characteristic of gorgonopsians. Uniquely among gorgonopsians, the reflected

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

601

602 This expanded version of the Kammerer (2016) data matrix (available as Supplementary Data)
603 is made up of 22 operational taxonomic units (all species-level taxa except for *Inostrancevia*,
604 which was coded at the genus-level due to uncertain alpha taxonomy) and 52 characters. All
605 characters are discrete-state, and of these six are ordered multistate characters (characters 11,
606 14, 26, 28, 31, 50). The phylogenetic analysis was run in PAUP* (Swofford, 2002) v4.0 (build
607 159) using branch-and-bound searching. Bootstrap analysis was done using “fast” stepwise-
608 addition on 1000 replicates.

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

620

621 **DISCUSSION**

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

628 Remarkably, the remaining Russian gorgonopsian genera (*Inostrancevia*,
629 *Pravoslavlevia*, *Sauroctonus*, and *Suchogorgon*) were found to form a monophyletic group
630 outside of the clade containing all African gorgonopsians. The monophyly of this group is
631 currently weakly-supported, but their position outside of the ‘African clade’ is supported by
632 several notable characters. The canonical synapomorphy of Gorgonopsia is a midline contact
633 between the palatines, excluding the vomer from contact with the pterygoid; previous
634 researchers considered this morphology to be present in all gorgonopsians (Hopson and
635 Barghusen, 1986; Sidor, 2000). However, our examination of the well-preserved holotype skull
636 of *Sauroctonus progressus* (PIN 156/6) revealed that, contra previous descriptions (Tatarinov,
637 1974; Sigogneau-Russell, 1989; Gebauer, 2014), there is actually a narrow vomerine-ptyergoid
638 contact (Fig. 8A, C). Although this contact is substantially narrower than in any other therapsid
639 clade, it clearly prevents midline contact of the palatines. Further examination of the best-
640 preserved Russian gorgonopsian palatal material indicates that this contact is also retained in
641 *Suchogorgon* (Fig. 8B, D) and *Inostrancevia* (the palate is too poorly-preserved in the only
642 known skull of *Pravoslavlevia* to determine).

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

648 rostrum has been secondarily lost. In *Inostrancevia*, *Sauroctonus*, and *Suchogorgon*, by
649 contrast (this region is not well-preserved in *Pravoslavlevia*), the parabasisphenoid blade is a
650 tab-like structure restricted to the posterior part of the basicranial girder (Fig. 9C, D). This is
651 more similar to the condition in therocephalians than to African gorgonopsians (van den Heever,
652 1994), and may represent the ancestral morphology within Theriodontia.

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

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

679 At present, all described inostrancevioids are Russian, and all known gorgonopioids are
680 African. The purported Russian rubidgeine gorgonopioid *Leogorgon klimovensis* is not
681 recognizable as a rubidgeine, and may not even be gorgonopsian (Kammerer 2016). Gebauer
682 (2014) considered the Tanzanian gorgonopsian previously known as *Scymnognathus*
683 *parringtoni* to be referable to the genus *Sauroctonus*. However, personal examination of the
684 type and only specimen of *S. parringtoni* (GPIT/RE/7113) indicates that it has the typical
685 parabasisphenoid and palatine morphologies of other African gorgonopsians, and that cranial
686 similarities between it and *Sauroctonus* (which consist primarily of proportional characters that
687 are variable among gorgonopsians) are superficial. **Endemism in gorgonopsians was previously**
688 **unsuspected, and is surprising considering the many Russo-African sister-taxon relationships in**
689 **other therapsid groups, particularly dicynodonts and burnetiamorphs (Sidor and Smith, 2007;**
690 **Kammerer et al., 2011). However, tetrapod biogeography in the Permian remains poorly known,**
691 **and the inferred dispersal abilities of various therapsid taxa are often discordant with the**
692 **observed record (Sidor et al., 2013; Kammerer et al., 2016). Additional research, particularly**
693 **from regions outside of the well-sampled Karoo Basin of South Africa, is required to understand**
694 **the factors underlying tetrapod distribution during this time.**

695

696 CONCLUSIONS

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

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

713

714 **ACKNOWLEDGEMENTS**

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

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932 FIGURE CAPTIONS

933

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

938

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

943 [planned for page width]

944

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

947

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

952

953 **Figure 5.** Interpretive drawings of Kotelnich gorgonopsians compared in lateral view. **A.** PIN
954 2212/6, holotype of *Viatkogorgon ivakhnenkoi*, in right lateral view. **B.** KPM 310, holotype of
955 *Nochnitsa geminidens*, in left lateral view (mirrored for comparative purposes). **Abbreviations:**
956 **an**, angular; **ar**, articular; **C**, upper canine; **c**, lower canine; **d**, dentary; **fr**, frontal; **I**, upper
957 incisor; **i**, lower postcanine; **j**, jugal; **la**, lacrimal; **mf**, maxillary flange; **mx**, maxilla; **na**, nasal; **pa**,

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

962 [planned for page width]

963

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

967 [planned for page width]

968

969 **Figure 7.** Holotype skull of *Nochnitsa geminidens* (KPM 310) in dorsal view; **A**, interpretive
970 drawing, and **B**, photograph. Gray indicates matrix, hatching indicates plaster. Scale bar equals
971 1 cm. [planned for page width]

972

973 **Figure 8.** Photographs and interpretive drawings of inostranceviid palates, illustrating the
974 presence of a narrow contact between the vomer and pterygoid. **A**, **C**. PIN 156/5, holotype of
975 *Sauroctonus progressus*. **B**, **D**. PIN 4548/1, referred specimen of *Suchogorgon golubevi*.

976 **Abbreviations:** **ec**, ectopterygoid; **mx**, maxilla; **PCa**, postcanine alveolus; **pl**, palatine; **ppl**,
977 palatal boss of palatine; **ppt**, palatal boss of pterygoid; **pt**, pterygoid; **tpt**, transverse process of
978 pterygoid; **v**, vomer. Scale bars equal 1 cm. [planned for page width]

979

980 **Figure 9.** Photographs of the basicranial girder in inostranceviid and gorgonopid
981 gorgonopsians, illustrating the difference in morphology of the parabasisphenoid blade between
982 these families: elongate and sloping in Gorgonopidae, short and tab-like in Inostranceviidae. **A**.
983 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.

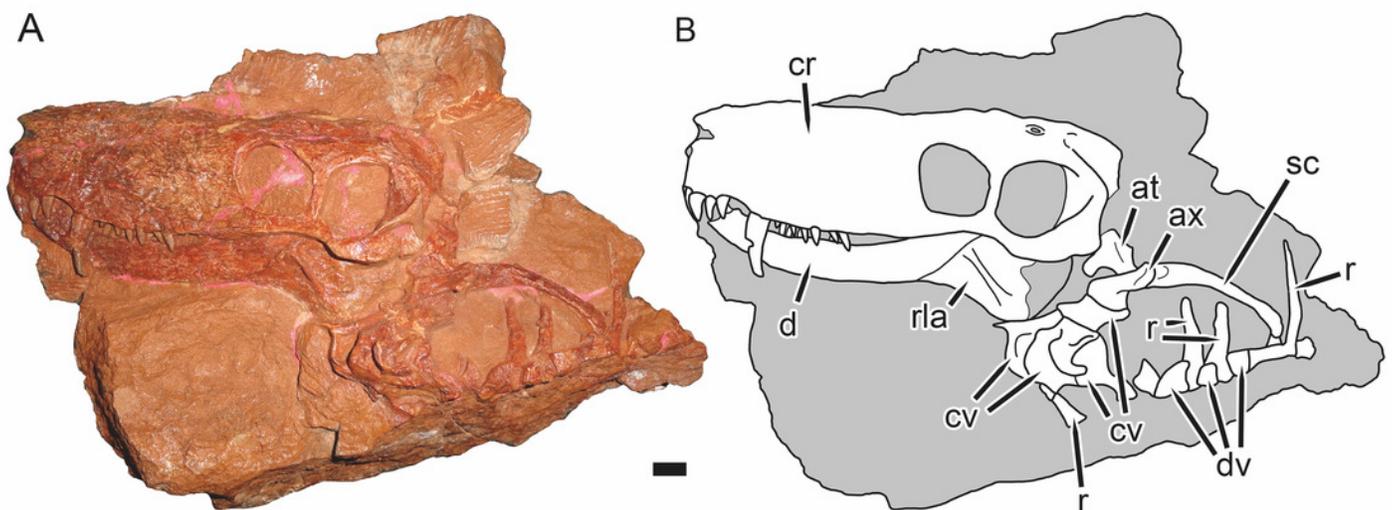


Figure 2

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.

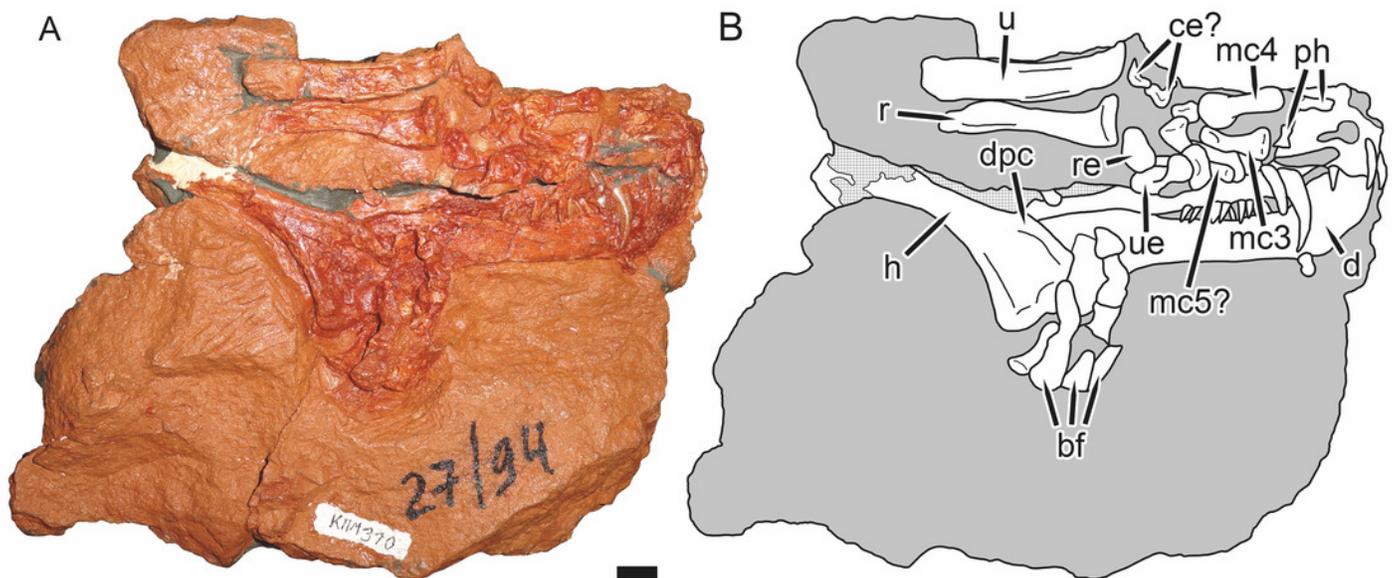


Figure 3

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

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

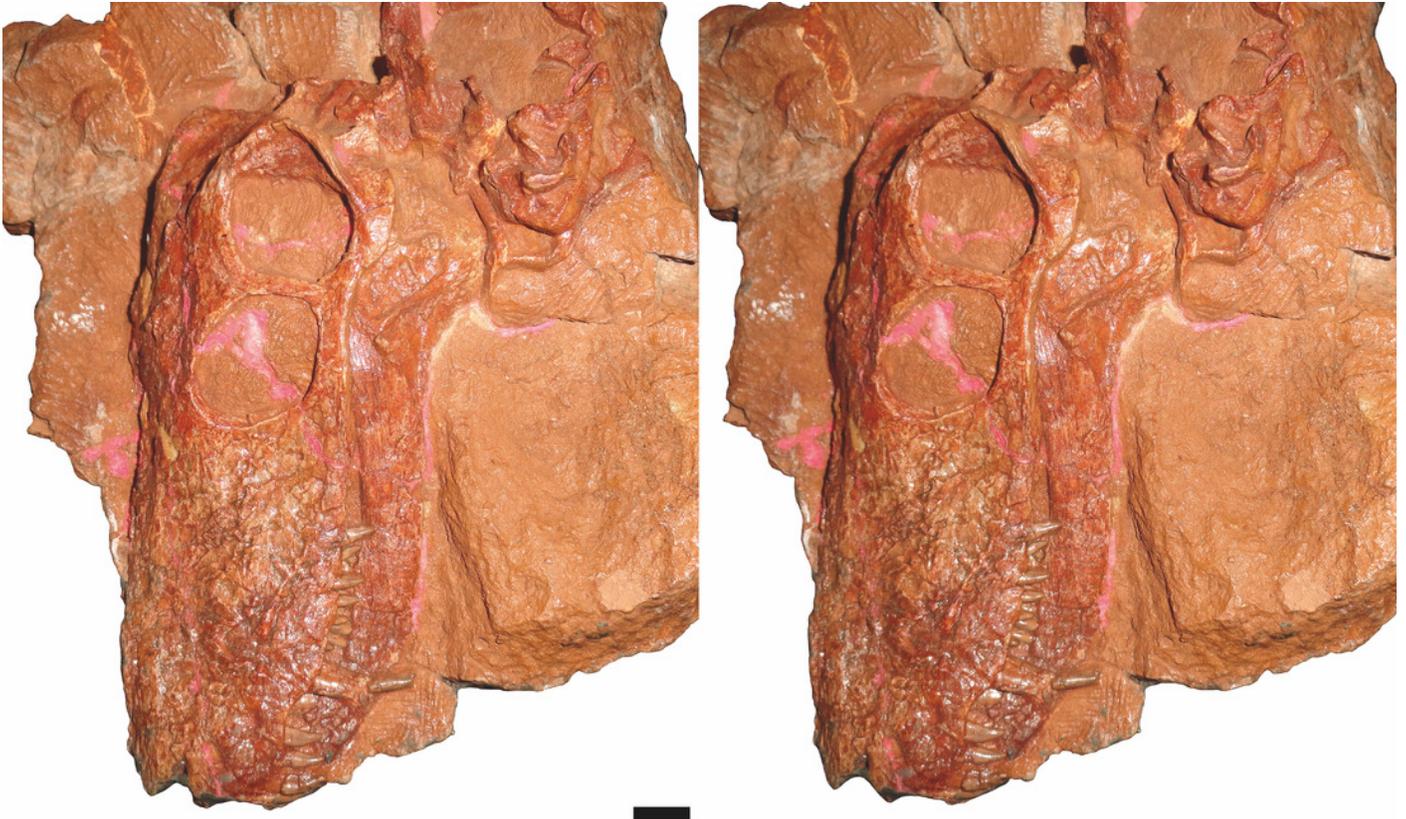


Figure 4

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.

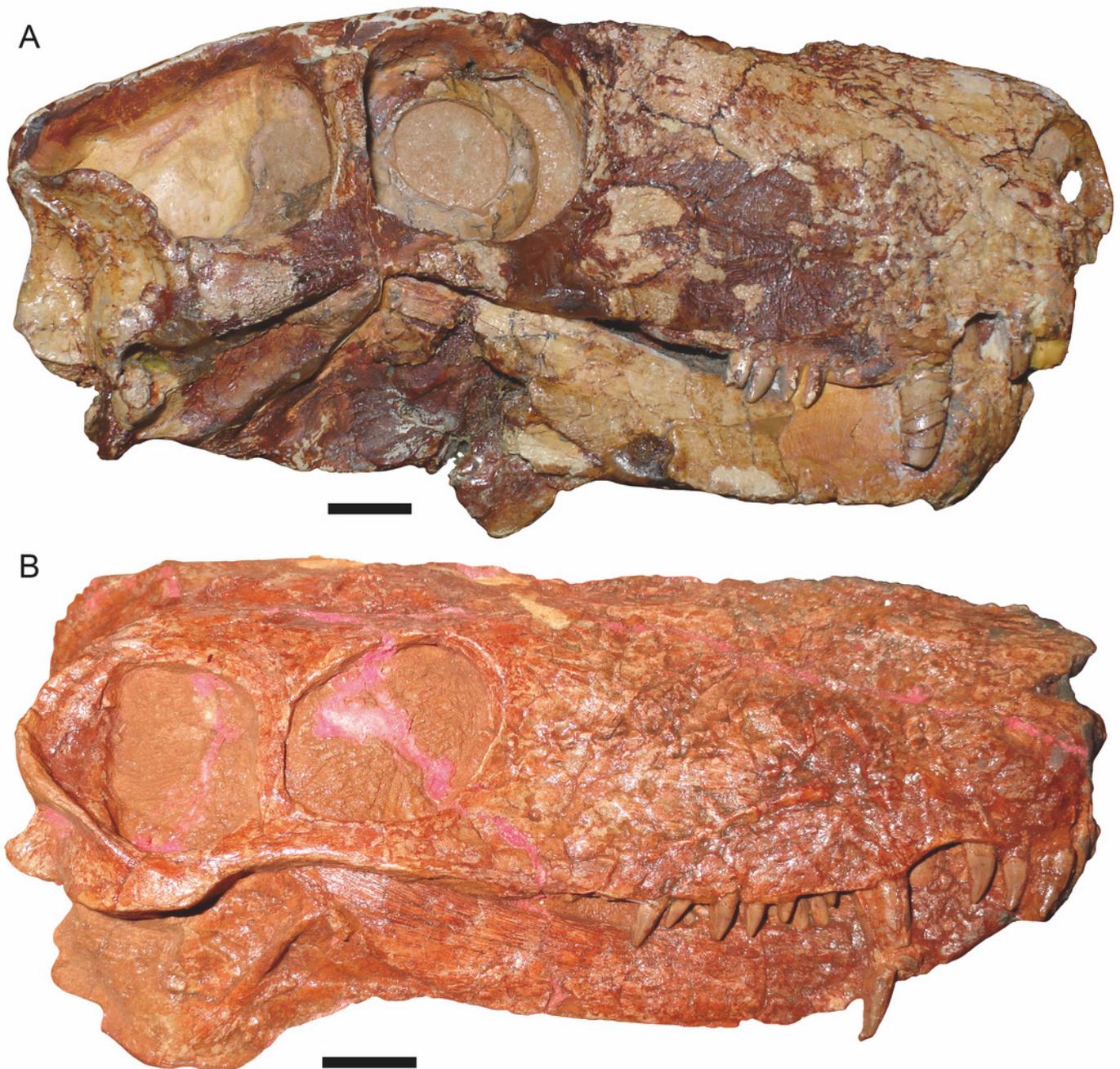


Figure 5

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.

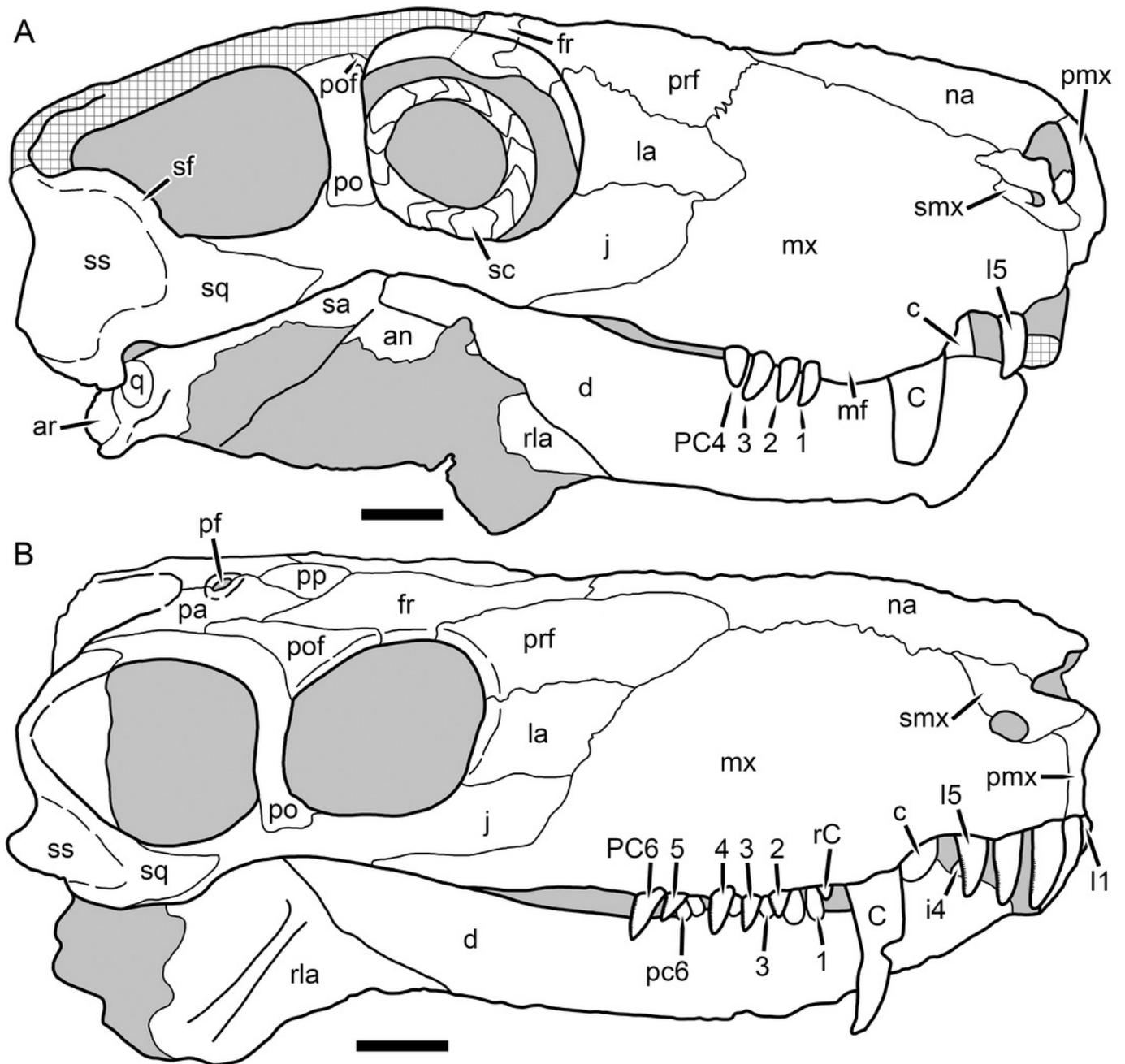


Figure 6

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.

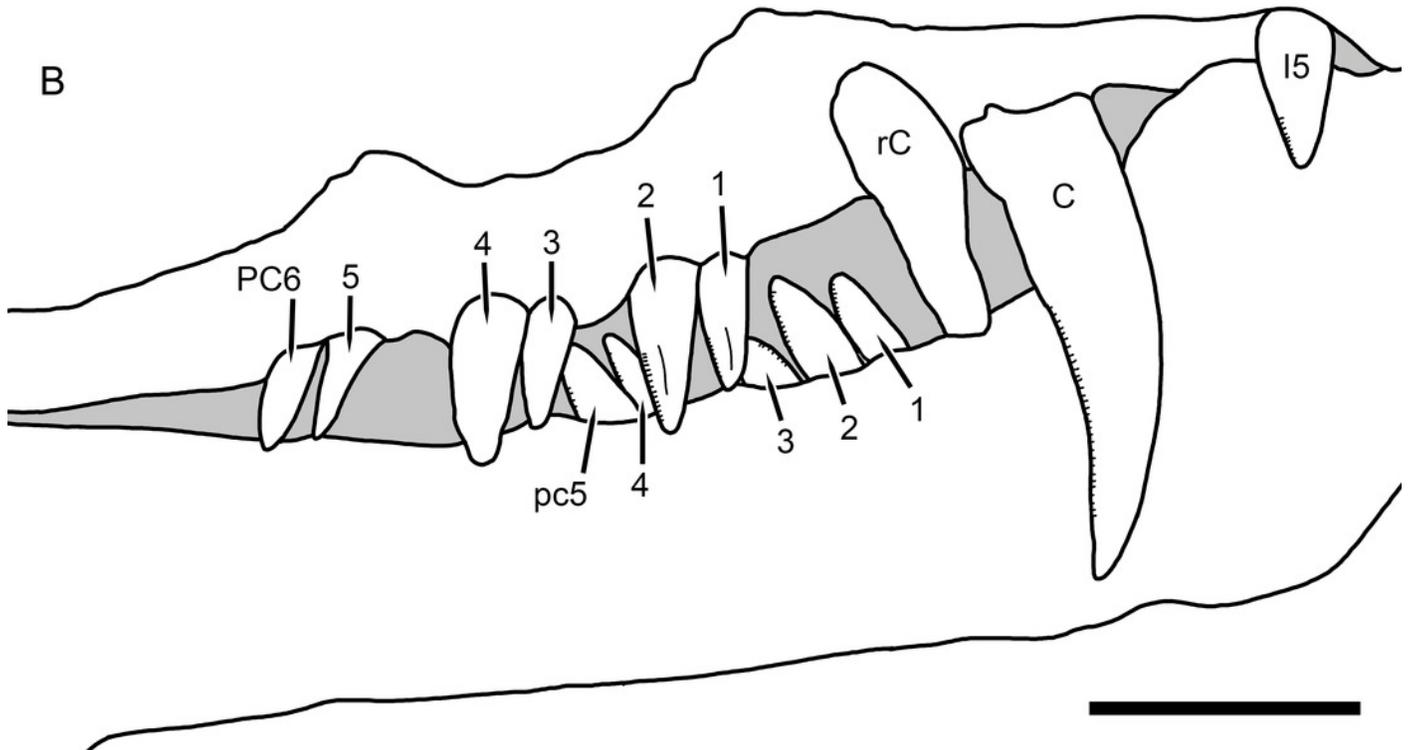


Figure 7

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.

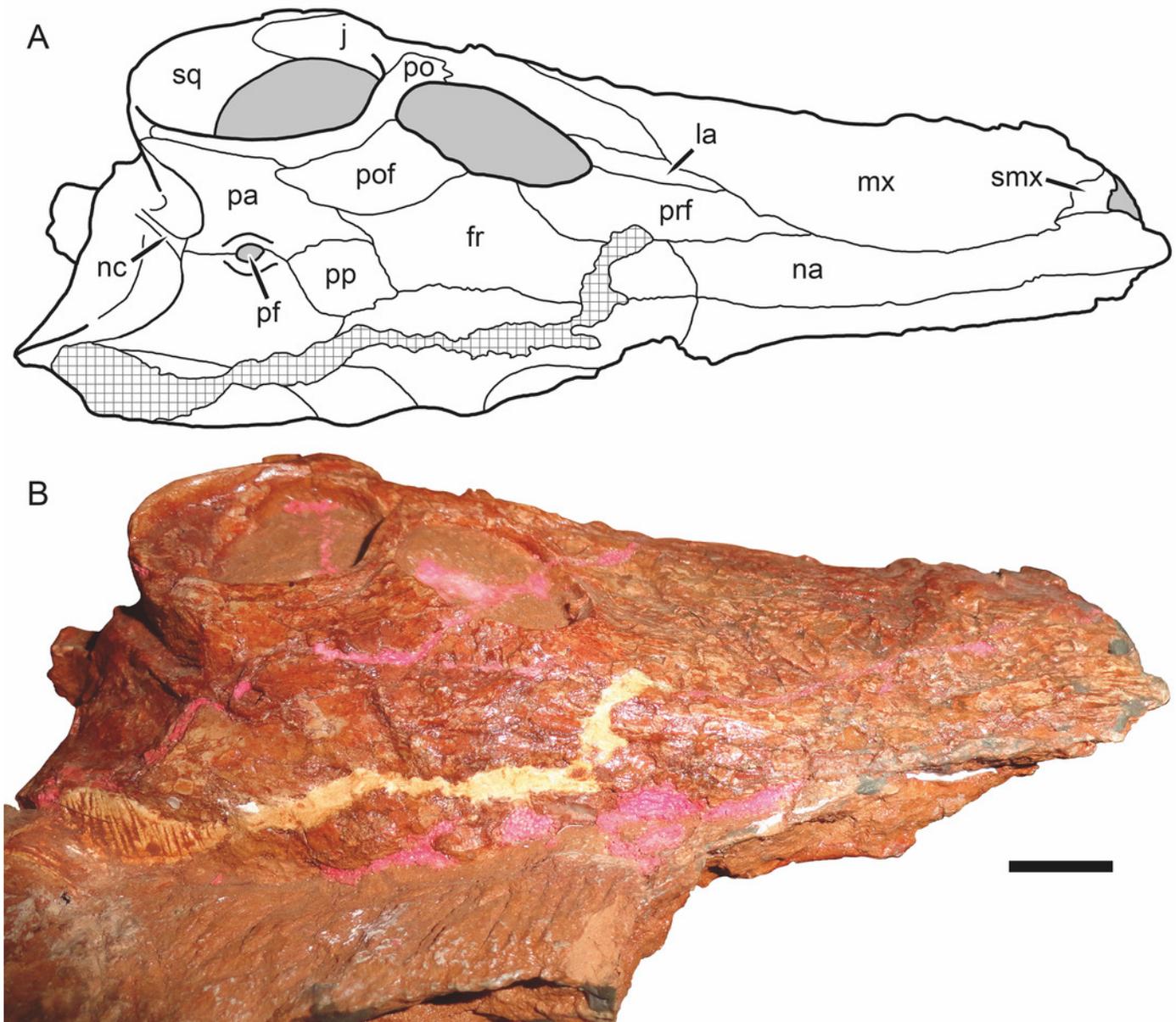


Figure 8

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.

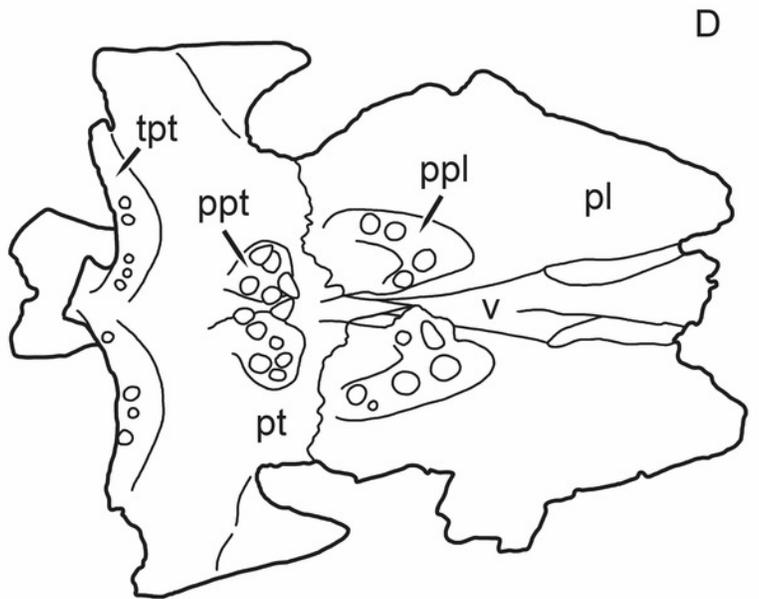
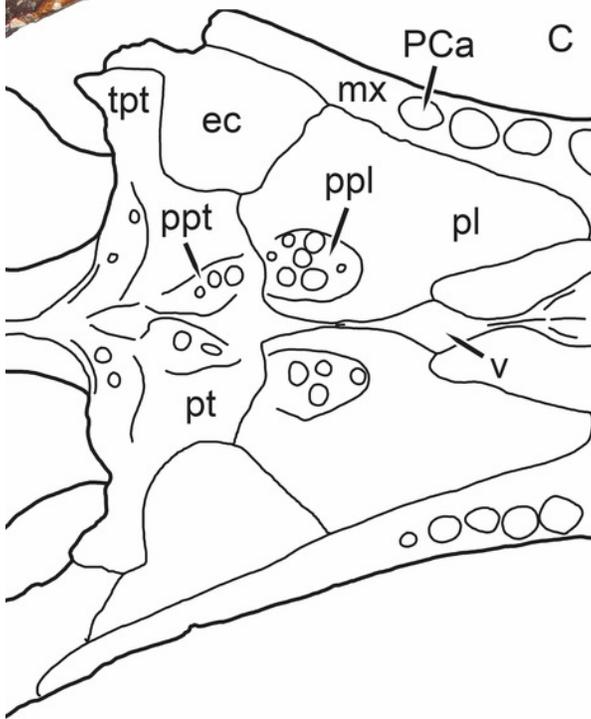
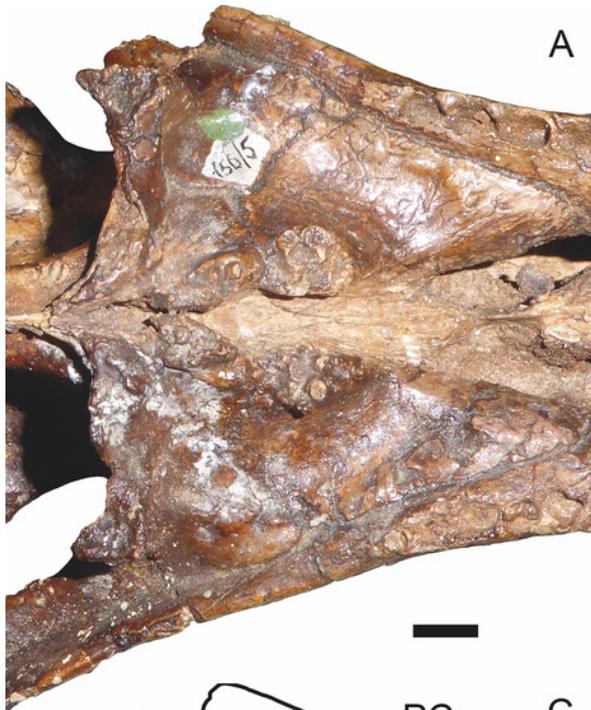


Figure 9

Photographs of the basicranial girder in inostrancevioid and gorgonopioid 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.

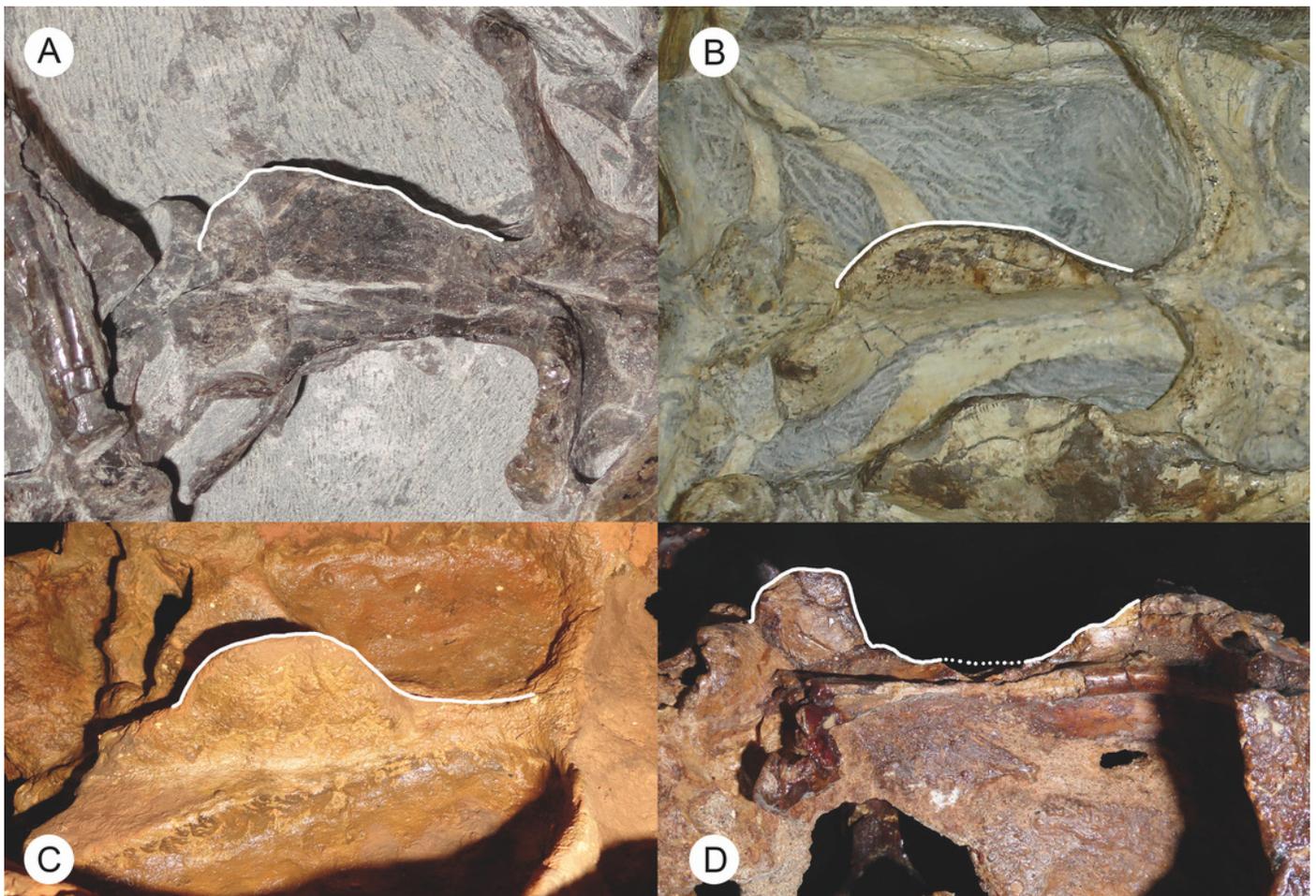


Figure 10

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

Values at nodes represent bootstrap support.

