A new therocephalian (*Gorynychus masyutinae* gen. et sp. nov.) from the Permian Kotelnich locality, Kirov Region, 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

A new therocephalian taxon (*Gorynychus masyutinae* gen. et sp. nov.) is described based on a nearly complete skull and partial postcranium from the Permian Kotelnich locality of Russia. *Gorynychus* displays an unusual mixture of primitive ("pristerosaurian") and derived (eutherocephalian) characters. Primitive features of *Gorynychus* include extensive dentition on the palatal boss and transverse process of the pterygoid, paired vomers, and a prominent dentary angle; derived features include the absence of the postfrontal. *Gorynychus* can be distinguished from all other therocephalians by its autapomorphic dental morphology, with roughly denticulated incisors and postcanines. Phylogenetic analysis recovers *Gorynychus* as a non-lycosuchid, non-scylacosaurid therocephalian situated as sister-taxon to Eutherocephalia. The identification of *Gorynychus* as the largest predator from Kotelnich indicates that therocephalians acted as apex predators in middle-late Permian transition ecosystems in Russia, corroborating a pattern observed in South African faunas. However, other aspects of the Kotelnich fauna, and Permian Russian tetrapod faunas in general, differ markedly from those of South Africa and suggest that Karoo faunas are not necessarily representative of global patterns.

1 **A new therocephalian (*Gorynychus masyutinae* gen. et sp. nov.) from the Permian**

2 **Kotelnich locality, Kirov Region, Russia**

4 Christian F. Kammerer[1] and Vladimir V. Masyutin[2]

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

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

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

11 **Abstract.** A new therocephalian taxon (*Gorynychus masyutinae* gen. et sp. nov.) is described

12 based on a nearly complete skull and partial postcranium from the Permian Kotelnich locality of

13 Russia. *Gorynychus* displays an unusual mixture of primitive ("pristerosaurian") and derived

14 (eutherocephalian) characters. Primitive features of *Gorynychus* include extensive dentition on

15 the palatal boss and transverse process of the pterygoid, paired vomers, and a prominent

16 dentary angle; derived features include the absence of the postfrontal. *Gorynychus* can be

17 distinguished from all other therocephalians by its autapomorphic dental morphology, with

18 roughly denticulated incisors and postcanines. Phylogenetic analysis recovers *Gorynychus* as a

19 non-lycosuchid, non-scylacosaurid therocephalian situated as sister-taxon to Eutherocephalia.

20 The identification of *Gorynychus* as the largest predator from Kotelnich indicates that

21 therocephalians acted as apex predators in middle-late Permian transition ecosystems in

22 Russia, corroborating a pattern observed in South African faunas. However, other aspects of

23 the Kotelnich fauna, and Permian Russian tetrapod faunas in general, differ markedly from

24 those of South Africa and suggest that Karoo faunas are not necessarily representative of global

25 patterns.

27   **Keywords:** Synapsida, Therapsida, Therocephalia, Permian, Russia, phylogeny

29 **INTRODUCTION**

30 Therocephalians had perhaps the most unusual evolutionary trajectory of the major clades of

31 non-mammalian therapsids. Whereas other therapsid groups remained relatively static in terms

32 of niche occupation through time, therocephalians 'reinvented' themselves several times in their

33 history, each time following mass extinctions. The earliest known therocephalians

34 (Lycosuchidae and Scylacosauridae, historically united in the paraphyletic group

35 "Pristerosauria"), which are best represented in middle Permian sediments of the Karoo Basin of

36 South Africa, were large-bodied (skull length up to 40 cm) predators (Boonstra, 1969; van den

37 Heever, 1980, 1994). Following the extinction of dinocephalians (including the gigantic,

38 carnivorous anteosaurs) at the end of the Capitanian, therocephalians briefly served as the

39 apex predators of the Karoo during the middle–late Permian transition represented by the

40 *Pristerognathus* Assemblage Zone (AZ) (Kammerer, 2011; Abdala et al., 2014; Day et al.,

41 2015). However, by the end of the *Pristerognathus* AZ lycosuchids and scylacosaurids were

42 extinct, and the saber-toothed gorgonopsians had taken over as the dominant large-bodied

43 therapsid predators (Smith et al., 2012; Kammerer et al., 2015). The surviving late Permian

44 therocephalians all belong to the subclade Eutherocephalia, which were predominantly small-

45 bodied animals (skull length ≤10 cm), many of which were likely insectivores (Mendrez, 1975;

46 Kemp, 1986; Huttenlocker, 2009). A few eutherocephalians re-evolved large size and inferred

47 macropredatory habits by the end of the Permian (e.g., the whaitsiid *Theriognathus* and the

48 akidnognathid *Moschorhinus*), but these taxa died out as a result of the end-Permian mass

49 extinction (*Moschorhinus* survived the main extinction pulse, but disappears from the record

50 shortly thereafter, making it an example of a 'dead clade walking'; Jablonski, 2002; Huttenlocker

51 & Botha-Brink, 2013; Huttenlocker, 2014). Remarkably, despite major losses in the end-Permian

52 mass extinction, therocephalians managed to reinvent themselves yet again, with a moderately

53 successful third act as small-bodied herbivores (the Bauriamorpha) in the Early–Middle Triassic

54 (Sigogneau-Russell & Sun, 1981; Abdala et al., 2014) before the clade was finally lost for good.

55   Basal therocephalians (lycosuchids and scylacosaurids) are the most common tetrapod

56   predators in middle and earliest late Permian deposits in South Africa, with hundreds of known

57   specimens (Smith et al., 2012) and 55 named species (although this number is clearly oversplit;

58   van den Heever, 1987). By contrast, very few basal therocephalian fossils have been found in

59   comparably-aged Laurasian rocks, despite extensive records of anomodonts, dinocephalians,

60   and pararreptiles from the middle Permian of China and Russia (Li 2001; Ivakhnenko 2003). No

61   therocephalians have ever been found in middle Permian Chinese rocks. Historically, only a

62   single species of therocephalian (*Porosteognathus efremovi*, a possible scylacosaurid from the

63   Isheevo locality, Apastovskii District, Tatarstan) was known from the middle Permian of Russia

64   (Vjuschkov 1955; Ivakhnenko 2011). Furthermore, *Porosteognathus* seems to be a minor

65   component of the Isheevo assemblage, which is dominated by dinocephalians and venyukovioid

66   anomodonts (many known from complete skulls and skeletons, whereas *Porosteognathus* is

67   known only from isolated skull bones).

68   The earliest Russian assemblage preserving a substantial number of therocephalians is

69   the Kotelnich locality in Kirov Region. Although known since the 1930s as a source of

70   spectacularly-complete pareiasaur skeletons (Hartmann-Weinberg, 1937), therocephalians were

71   not described from Kotelnich until the 1990s (Tatarinov, 1995a, 1995b, 1997, 1999). Now,

72   however, they are the most species-rich tetrapod clade known from the site, with eight named

73   species (*Chlynovia serridentatus*, *Karenites ornamentatus*, *Kotelcephalon viatkensis*, *Muchia*

74   *microdenta*, *Perplexisaurus foveatus*, *Scalopodon tenuisfrons*, *Scalopodontes kotelnichi*, and

75   *Viatkosuchus sumini*), although these may be somewhat oversplit (Ivakhnenko, 2011). The age

76   of the Kotelnich assemblage is somewhat uncertain, with both middle and late Permian ages

77   having been proposed (Tatarinov 2000; Benton et al. 2012). Currently, an early late Permian

78   age is considered most likely, equivalent with the South African *Tropidostoma* AZ based on

79   anomodont comparisons (Kurkin 2011). Benton et al. (2012) suggested equivalency between

80   the Kotelnich assemblage and the *Pristerognathus* AZ. However, the described therocephalian

81   fauna of Kotelnich is composed entirely of eutherocephalians (all of which other than

82   *Viatkosuchus* are very small, i.e. <10 cm skull length), not the large scylacosaurids or

83   lycosuchids characteristic of the *Pristerognathus* AZ in South Africa.

84   Here we describe a new taxon representing the first large, basal (i.e., non-

85   eutherocephalian) therocephalian from the Kotelnich locality. This species is represented by two

86   specimens and is the largest known predatory therapsid from Kotelnich, indicating

87   therocephalian occupation of apex predator niches in the Northern as well as Southern

88   Hemisphere during the transition between middle and late Permian tetrapod faunas.

89

90   **Nomenclatural acts**

91   The electronic version of this article in portable document format (PDF) will represent a

92   published work according to the International Commission on Zoological Nomenclature (ICZN),

93   and hence the new names contained in the electronic version are effectively published under

94   that Code from the electronic edition alone. This published work and the nomenclatural acts it

95   contains have been registered in ZooBank, the online registration system for the ICZN. The

96   ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information

97   viewed through any standard web browser by appending the LSID to the prefix

98   http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:CA4D73A1-8FA7-

99   40DD-A464-621AC01421B6. The online version of this work is archived and available from the

100   following digital repositories: PeerJ, PubMed Central, and CLOCKSS.

101

102   **Institutional abbreviation**

103   **KPM**, Vyatka Paleontological Museum, Kirov, Russia.

104

105   **GEOLOGICAL CONTEXT**

106 The Kotelnich locality is a rich, primarily tetrapod-bearing fossil assemblage in the Kirov region

107 of European Russia. The first fossils from this locality were collected by A. P. Hartmann-

108 Weinberg in the 1930s and consisted mainly of pareiasaurs, but more recent (1990s–present)

109 excavations have revealed a substantially more diverse fauna. Several fossiliferous layers are

110 present at the locality: the lowest red beds represent a more aquatic system which famously

111 preserves numerous complete, fully articulated skeletons of the mid-sized pareiasaur *Deltavjatia*

112 *rossica*. This level (the Vanyushonki Member of Coffa [1997]) has also produced the majority of

113 synapsid finds, including spectacular examples such as the complete, articulated specimen of

114 the small gorgonopsian *Viatkogorgon ivakhnenkoi* (Tatarinov, 1999) and the block of 15

115 skeletons of the arboreal anomodont *Suminia getmanovi* (Fröbisch and Reisz, 2011). Above this

116 level the most common fossils are skulls and disarticulated skeletal material of the

117 oudenodontid dicynodont *Australobarbarus*. In addition to these "red beds", lenses of later

118 deposition, producing mainly plant and fish remains but also highly fragmentary tetrapods

119 (primarily isolated teeth) are present at the top of the section (Benton et al., 2012).

120   The specimens of the new therocephalian described herein were all found in the lower

121 red beds (Vanyushonki Member) of the Kotelnich locality. The holotype was discovered in 2008

122 by I. Shumov, 10.15 meters below the marker bed and 413 meters upstream from the village of

123 Nizhnaya Vodskaya. These specimens were mechanically prepared by O. Masyutina and are

124 housed in the collections of the Vyatka Paleontological Museum in Kirov.

125

126 **SYSTEMATIC PALEONTOLOGY**

127 **Synapsida** Osborn, 1903

128 **Therapsida** Broom, 1905

129 **Therocephalia** Broom, 1903

130

131 *Gorynychus* gen. nov.

132

133   **LSID:** urn:lsid:zoobank.org:act:CD10EB7C-57C0-45BA-8467-75309411E0DD

134   **Type species:** *Gorynychus masyutinae* sp. nov.

135   **Etymology:** Named for the legendary Russian dragon Zmey Gorynych (Змей

136 Горыныч), in reference to the fearsome appearance of this taxon and its status as the largest

137 known predator in the Kotelnich assemblage. Also a play on the English word 'gory' (meaning

138 bloody) and the Ancient Greek ὄνὔχος (Latinized 'onychus', meaning claw), in reference to this

139 taxon's inferred behavior being 'red in tooth and claw.'

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

141

142 *Gorynychus masyutinae* sp. nov.

143 (Figs. 1–10)

144

145   **LSID:** urn:lsid:zoobank.org:act:105CB020-2584-4AD1-BF98-2B555EE69644

146   **Holotype:** KPM 346–349 (Figs. 1–8), a single individual (skull and cervical vertebrae in

147 articulation, pectoral and rib elements disarticulated but directly associated with skull) broken

148 into four pieces: KPM 346, a nearly complete skull (with damaged intertemporal region, occiput,

149 and left temporal arcade) and lower jaws with the anterior 4 1/2 cervicals in articulation; KPM

150 347, postcranial elements including remaining half of fifth cervical (precise break, originally

151 articulated with anterior portion) and worn sixth and seventh cervicals, ribs, partial clavicle, and

152 left scapulocoracoid impression; KPM 348, isolated but associated incisor with intact crown; and

153 KPM 349, isolated but associated incisor with damaged crown.

154   **Paratype:** KPM 291 (Figs. 9, 10), a block of fragmentary, disarticulated elements

155 including the anterior portion of a partial right dentary, an isolated incisor, a jugal, at least four

156 vertebrae, several ribs, a fibula, and various indeterminate bone fragments.

157   **Etymology:** Named in honor of Olga Masyutina for her skillful preparation of the

158   holotype of this taxon, as well as numerous other important specimens from the Kotelnich

159   locality.

160   **Diagnosis:** Therocephalian distinguished from all other members of the group by its

161   autapomorphic dental morphology: all marginal teeth serrated, with serrations forming distinct

162   denticles that are especially prominent on the incisors and postcanines. Postcanines 'spade'-

163   shaped and reduced in number (three in the maxilla) relative to most therocephalians. Further

164   distinguished from the other known Russian basal therocephalian *Porosteognathus efremovi* by

165   a shorter tooth row on the pterygoid transverse process situated on a more discrete, raised boss

166   and an anterolaterally-curved and expanded pterygoid palatal boss with fewer (8–9) teeth

167   (transversely broad with ~14 teeth in *Porosteognathus*).

168

169   **DESCRIPTION**

170   The holotype is generally well preserved (Fig. 1), with good bone quality showing surface

171   ornamentation and sutural boundaries on most of the snout and palate (Figs. 2–6). However,

172   the skull is somewhat crushed, the left temporal arch is broken off, and the intertemporal region

173   is badly eroded. The anterior five cervicals are reasonably well preserved (although the atlas is

174   not exposed as prepared), but the subsequent members of the series are badly worn (Fig. 7).

175   Other postcranial elements are broken and worn, and the scapulocoracoid is preserved mainly

176   as an impression (Fig. 8). The paratype is a single block of disarticulated, fragmentary elements

177   (Fig. 9), although most of these elements show good bone preservation (Fig. 10). One of these

178   elements, an isolated incisor with intact crown, can confidently be referred to *Gorynychus*

179   *masyutinae* based on the presence of very large, curved denticles on its mediodistal edges. The

180   dentary fragment also has a tall, robust symphysis identical to that of the holotype; although it is

181   possible this could represent a gorgonopsian, the only gorgonopsians known from this locality

182   are much smaller and actually have weakly-developed dentary symphyses. Given the absence

183   of any other material that is not consistent with identification as *Gorynychus* and the lack of

184   overlapping elements, this set of fossils is interpreted to be the remains of a single *Gorynychus*

185   individual.

186

187   *Cranium*

188   The cranium of KPM 346 is 173 mm in standard basal length (from anteroventral edge of

189   premaxilla to posteroventral edge of occipital condyle) and 208 mm in total dorsal length (from

190   tip of snout to edge of temporal fenestra).

191   The palatal portion of the premaxilla is not exposed in the holotype because of occlusion

192   of the lower jaw. The only information available concerning the ventral surface of the premaxilla

193   comes from the edges of the incisor alveoli. Based on this, *Gorynychus* appears to have had an

194   upper incisor count of five. Although no incisors are preserved in place, two isolated teeth (KPM

195   348 and 349) preserved in association with the skull have root proportions identical to the empty

196   alveoli and are here interpreted as the upper incisors. Only one of these teeth (KPM 348)

197   preserves an intact crown (Fig. 2C). The crown of KPM 348 is elongate, triangular, and weakly

198   recurved with prominent mesiodistal serrations forming distinct denticles. The morphology of

199   these denticles is unique among therocephalians: they are extremely prominent, extend from

200   the tip of the crown right to the root, and each individual denticle is curved in the apical direction.

201   This only comparable morphology among therocephalians occurs in the postcanines of this

202   same specimen. The facial surface of the premaxilla is overlain by the maxilla posteriorly, near

203   the point between the alveoli for I4 and I5 (Figs. 2, 4, 5). The bone surface of the premaxilla is

204   rugose, with a series of well-developed foramina located 3–4 mm above the alveolar margin.

205   Anteriorly, three foramina are situated in a distinct channel that originates vertically beneath the

206   internarial bar then curves posterolaterally (Fig. 2B). The first and third foramina in this channel

207   are small (<1 mm diameter), but the second is large (1 mm diameter) and situated deep inside

208   the groove. Posterior to this channel, several additional foramina are present on the lateral face

209   of the premaxilla. The internarial bar is angled somewhat anteriorly, such that the snout comes

210   to a distinct 'point' in lateral view (Fig. 4). The ascending ramus of the premaxilla frames the

211   anterodorsal border of the external naris and terminates near the posterodorsal narial border.

212   The septomaxilla consists of a broad ventral plate making up the base of the external

213   naris, a constricted intranarial portion, and a facial process extending between the maxilla and

214   nasal (Figs. 2, 4, 5). The ventral plate is situated immediately dorsal to the premaxillary-

215   maxillary suture. Immediately ventral to this plate is a large, ovoid foramen (1.5 mm diameter)

216   that spans the premaxillary-maxillary suture. A weak groove extends anterior to this foramen for

217   the length of the ventral plate of the septomaxilla. The constricted intranarial portion of the

218   septomaxilla separates the main portion of the external naris from the maxillo-septomaxillary

219   foramen. It has a pointed, anteromedially-directed anterior process as is typical of

220   therocephalians, but not an expanded transverse lamina as in gorgonopsians. Posterodorsally,

221   the septomaxilla makes a broad, irregular contribution to the facial portion of the snout. This

222   facial process notably does not make up the entire posterior margin of the external naris—the

223   nasal occupies the posterodorsal narial corner (Fig. 2B).

224   The maxilla is a tall, gently curved bone making up the main lateral surface of the snout

225   (Figs. 4, 5). The facial surface of the maxilla is intensely sculptured with shallow, crater-like

226   structures and small foramina, similar to that of some other basal therocephalians (see, e.g.,

227   Abdala et al., 2008). A labial emargination is absent, unlike in *Lycosuchus*. The posterior

228   terminus of the maxilla is a process under the jugal that reaches the midpoint of the orbit. The

229   tip of this process is notably expanded and rugose, but the majority of this process is notable for

230   lacking the dermal sculpturing so prominent on the rest of the maxilla and bearing a weak lateral

231   groove. The maxilla houses four teeth: the enlarged, blade-like canine and three small

232   postcanines. The canine is recurved and has well-developed serrations fore and aft, as is usual

233   in basal therocephalians (van den Heever, 1994; Abdala et al., 2014). Only a single canine is

234   erupted on each side; unlike the usual condition in lycosuchids and a frequent condition in

235   scylacosaurids, there are not simultaneously-occupied anterior and posterior canine alveoli. The

236   tip of a replacement canine is erupting anterior to the right canine, however. The postcanine

237   morphology of *Gorynychus* is unique among therocephalians—these teeth are labiolingually

238   compressed and 'leaf' or 'spade-shaped', with proportionally large denticles (serrations) along

239   both mesial and distal edges. Although these denticles are not as large or exaggeratedly curved

240   as those on the incisors, they still show distinct curvature (unlike the finer, straight serrations on

241   the canine). As for the premaxilla, the palatal surface of the maxilla is for the most part not

242   visible in this specimen.

243   The nasal is a long, flat bone (Figs. 2–5). It also bears dermal sculpturing, albeit

244   developed to a lesser degree than in the facial portion of the maxilla. Dermal sculpturing to

245   some degree is present on all the bones of the snout, including (albeit very weakly) on the facial

246   portion of the jugal. The naso-frontal suture is gently bowed posteriorly and terminates near the

247   anterior margin of the orbit.

248   The prefrontal is a roughly trapezoidal bone making up part of the snout and the

249   anterodorsal margin of the orbit (Figs. 3–5). Its contribution to the orbital rim is unusually

250   pronounced and rugose. This is also true for the lacrimal, jugal, and frontal, such that that the

251   circumorbital rim is very prominent everywhere but on the postorbital bar. Anteriorly, the

252   prefrontal terminates in a short, blunt process extending between the maxilla and nasal. The

253   prefrontal makes up a large portion (roughly half) of the anterior face of the orbital wall, and

254   appears to exclude the frontal from contacting the lacrimal.

255   The lacrimal is a large facial bone, nearly equivalent in height to the prefrontal albeit not

256   as anteroposteriorly long (Figs. 4, 5). A similarly-sized lacrimal is also present in *Lycosuchus*,

257   and although this bone is less dorsoventrally expanded in scylacosaurids it is of similar

258   anteroposterior dimensions in that group as well (van den Heever, 1994). A large (1.5 mm

259   diameter) lacrimal foramen is present on its contribution to the anterior orbital wall; this foramen

260   does not exit onto the lateral surface. A second, smaller lacrimal foramen may be present

261   ventral to the first, but this is uncertain because of damage.

262   The jugal makes up the majority of the zygomatic arch (Fig. 4). Its facial portion is an

263   attenuate process terminating below the lacrimal, posterior to the anterior lacrimal margin. Its

264   facial portion is remarkably small for an early theriodont. In gorgonopsians, the jugal typically

265   terminates in a broad, plate-like contribution to the snout equalling (or exceeding) the lacrimal in

266   anterior extent (see, e.g., Kammerer, 2015; Kammerer et al., 2015). In *Lycosuchus* and other

267   early therocephalians, the facial portion of the jugal terminates well posterior to the anterior

268   edge of the lacrimal, but still forms a tall plate on the snout and occupies almost the entire

269   ventral margin of the orbit (van den Heever, 1994). The jugal is constricted beneath the

270   posterior margin of the orbit, before expanding to form a major part of the postorbital bar. In the

271   postorbital bar, an ascending process of the jugal extends dorsally between the postfrontal

272   anteriorly and a narrow lamina of the postorbital posteriorly. Posterior to the postorbital bar the

273   jugal makes a tall contribution to the subtemporal bar, narrowing posteriorly and curving

274   downwards. In the posterior half of the subtemporal bar, the jugal is bifurcated by an anterior

275   process of the squamosal. The ventral portion of the jugal extends nearly to the back of the

276   skull, and has a weakly bulbous terminus. In addition to being preserved in the holotype, an

277   isolated jugal is present on the paratype block (Fig. 9), identifiable by the characteristic

278   subtemporal curvature and well-developed process contributing to the postorbital bar.

279   The squamosal is preserved mainly in its zygomatic ramus (Fig. 4), as the occiput and

280   intertemporal region are poorly preserved in this specimen (Fig. 1). It has a deep and fairly

281   restricted squamosal sulcus, giving it a 'forked' appearance in lateral view. Medially, it forms the

282   posterior portion of the lateral margin of the temporal fenestra (anteriorly, this margin is formed

283   by the jugal).

284   The frontal is a mostly-flat bone making up the interorbital skull roof (Fig. 3). The medial

285   portion of the frontal is damaged in this specimen, but its contribution to the orbit is well

286   preserved and shows that it was only weakly ornamented dorsally, until the very edge of the

287   orbit (in which it is expanded and rugose, like most of the circumorbital rim). The suture between

288   the frontal and postfrontal is poorly preserved and difficult to interpret, but it appears that the

289   frontal makes only a narrow contribution to the dorsal orbital wall (Fig. 4), as in *Lycosuchus* (van

290   den Heever, 1994).

291   A distinct postfrontal is absent in *Gorynychus*; this element may be fused with the

292   postorbital. The postorbital makes up a broad portion of the skull roof at the posterodorsal

293   margin of the orbit and continues as a posterior ramus making up the medial face of the

294   temporal fenestra (Figs. 3, 4). The latter ramus is badly damaged in this specimen, like most of

295   the posterior skull roof, and its posterior terminus and surface texture is indeterminable. The

296   intertemporal bar is narrow, as its typical of therocephalians. However, this region is too

297   damaged to determine its exact proportions or presence/absence of the pineal foramen or

298   sagittal crest. The occiput is even more badly damaged, being worn off entirely dorsal to the

299   occipital condyle (Fig. 5).

300   The vomer is not exposed anteriorly, but its posterior interchoanal portion is a tall,

301   narrow blade, like that of scylacosaurids and unlike the broad, vaulted morphology of

302   *Lycosuchus* (Fig. 6). The vomer is paired—a distinct mid-vomerine suture is visible in the

303   interchoanal portion. Posteriorly, the vomer forms a broad, triangular contribution to the palate,

304   extending between the palatines to contact the anterior margin of the pterygoids posteriorly. An

305   elongate palatal depression or fossa is present medially, originating near the anterior edge of

306   the plate-like palatal portion of the vomer and extending posteriorly until it reaches the

307   transverse processes of the pterygoids. Although the depth of this structure is likely

308   exaggerated by lateral compression in this specimen, its presence is natural.

309   The palatine is the largest bone of the palate (Fig. 6). It is a topologically complex

310   element composed of a laminar anterior process the forms much of the lateral margin of the

311   choana and a broad main portion with a prominent central ridge bounded by medial and lateral

312   depressions. This central ridge extends anterolaterally to posteromedially and is confluent

313   posteriorly with a ridge on the pterygoid, terminating with the palatal boss. A suborbital fenestra,

314   characteristic of therocephalians, is present at its posterolateral margin, bounded posteriorly by

315   the pterygoid. Presumably it is also bounded laterally by the ectopterygoid, but this element is

316   indistinct if present, probably due to poor preservation of the lateral margins of the palate.

317   As is typical of early therapsids, the pterygoid consists of three distinct processes:

318   palatal, transverse, and quadrate (Fig. 6). The palatal portion of the pterygoid has an

319   anteromedial-to-posteromedially-angled, strongly interdigitated suture with the palatine.

320   Anteriorly it forms a short portion of the prominent palatal ridges (central ridge of palatine)

321   before expanding into the dentigerous palatal bosses posteriorly. Dentigerous palatal bosses

322   are ancestral for therapsids; although they are present in scylacosaurids and even various

323   eutherocephalians (van den Heever, 1994; Huttenlocker & Smith, 2017), they are absent in

324   lycosuchids (*Lycosuchus* and *Simorhinella*) (Abdala et al., 2014). The palatal boss is 'teardrop'-

325   shaped, with a narrow posterior tip and broad, rounded anterior. It is curved anterolaterally. The

326   boss bears two tooth rows. On the left palatal boss (the more completely preserved of the two),

327   the posterior tooth row follows the curve of the boss and is made up of five teeth. The anterior

328   tooth row is transversely oriented and is made up of four teeth, for a total of nine (six are

329   present on the right boss, but as mentioned this boss is damaged and this is probably not the

330   complete complement of teeth). The transverse process of the pterygoid extends ventrolaterally:

331   it has a broad base medially, constricts in ventral view towards its midpoint, and then expands

332   into a rounded lateral tip where it braces the mandible. The anterior face of the transverse

333   process bears a broad, shallow depression. Unlike most therocephalians, but similar to

334   lycosuchids, the transverse process is dentigerous in *Gorynychus*. Unlike *Lycosuchus* and

335   *Simorhinella*, however, where the tooth row is relatively long (five teeth) and the teeth erupt

336   directly from the main ramus of the transverse process, in *Gorynychus* there are only 2–3 teeth

337   situated on discrete, ovoid bosses raised above the medial bases of the transverse processes.

338   On the right transverse process there are only two teeth, a large lateral and small medial one;

339   on the left there are three teeth of equal size, similar to the small one of the right. No

340   interpterygoid vacuity is present; although there is a weak depression between the transverse

341   processes medially, it is entirely bounded by bone dorsally. The quadrate process of the

342   pterygoid is situated dorsal to the transverse process. It extends posterolaterally from a position

343   near the medial base of the transverse process towards the quadrate, weakly curving along its

344   length. The anterolateral margin of the quadrate process forms a tall, narrow ridge;

345   posteromedially it forms a broad, concave plate bounding the lateral edge of the parasphenoid

346   rostrum.

347   The parasphenoid-basisphenoid complex forms a narrow median rostrum originating

348   behind the transverse processes of the pterygoids and extending posteriorly to the basal tubera

349   (Fig. 6). Although tall and blade-like posteriorly, the anterior two-thirds of this rostrum are

350   divided by a narrow median groove. The posterior terminus of the rostrum is abrupt, with a

351   sharp drop to the base of the basal tubera (typical of early therocephalians) instead of a gradual

352   decrease in height. Dorsally, the parasphenoid forms a narrow median lamina above the

353   pterygoid, forming part of the mid-orbital plate (Fig. 5). Dorsal to this anteriorly is a tall, laminar

354   bone interpreted as the orbitosphenoid, which extends dorsally to contact the frontal-postfrontal

355   wall of the orbit. Dorsal to it posteriorly is the epipterygoid, which has an anteroposteriorly broad

356   footplate ventrally that sits atop the parabasisphenoid. The ascending process of the

357   epipterygoid narrows dorsally before expanding again at its contact with the ventral face of the

358   parietal. The basal tubera are broadly separated by a median depression (Fig. 6). They are

359   relatively slender and angled medially at their posterior end instead of forming distinct 'rings' (as

360   in dicynodonts). The left stapes is preserved in place, extending from the basal tuber to near the

361   quadrate. The stapes is dorsoventrally narrow but anteroposteriorly broad, although narrowing

362   along its length laterally (similar to *Lycosuchus*). No foramen or dorsal process is visible, but

363 these could be obscured by matrix. The basioccipital forms a plate posterior to the basal tubera

364 and terminates in the occipital condyle, which is similar to that of other early therocephalians.

365   The dentary is a massive, robust bone with a tall, well-developed symphysis more

366 similar to that of gorgonopsians than other early therocephalians (Figs. 2, 4, 5, 10A). The

367 anterior face of the symphysis is densely foraminated. The roots of at least three incisors are

368 exposed due to damage to the right dentary (Fig. 4), but it is probable that more were present,

369 given that these three do not occupy the entirety of the symphysial length. The crowns of the

370 lower incisors are not exposed. The lower canine is not exposed in the holotype but is well-

371 preserved in the disarticulated dentary fragment in the paratype (Figs. 9, 10A). The lower canine

372 is a tall, recurved tooth with well-developed fore and aft serrations. It is proportionally large,

373 taking up much of the alveolar margin of the symphysis. Based on this position, it would have

374 been situated anterior to the upper canine when in occlusion with the cranium. The lower

375 postcanines are mostly obscured in both known specimens of *Gorynychus*, only a single small

376 lower postcanine can be seen on the right mandibular ramus anterior to the upper PC1 in the

377 holotype. This postcanine is smaller than any of the upper postcanines (2 mm apicobasal

378 length, versus 4 mm in the uppers) but is otherwise identical in morphology, being 'spade'-

379 shaped with well-developed denticulation. The dentary is constricted behind the symphysis,

380 then expands posteriorly, with a well-developed angular process (Fig. 4). The dorsal and ventral

381 margins have raised edges, and a distinct lateral fossa is present between them, extending

382 anteriorly almost to the level of the symphysis. Although superficially similar to the masseteric

383 fossa of cynodonts, this fossa is likely non-homologous; there is no evidence that the superficial

384 masseter was present in therocephalians. The raised ventral margin of the dentary terminates

385 posteriorly in a broad, flattened rugose region serving as the attachment site for adductor

386 musculature. The coronoid process extends freely above the postdentary bones and has a

387 broad posterodorsal terminus, as in the other basal therocephalians (van den Heever, 1994).

388   Unlike *Lycosuchus*, however, in which the posterior edge of the coronoid process is broadly

389   rounded, in *Gorynychus* this edge is concave.

390   The postdentary bones are damaged on both sides of the skull: the surangular and

391   articular are more complete on the right side but the reflected lamina of the angular is broken off

392   ventrally; the surangular and posterior portion of the angular are broken off on the left side but

393   the reflected lamina is more complete (Figs. 4, 5). In general, the postdentary elements are very

394   similar to those of lycosuchids and scylacosaurids. The reflected lamina is large and occupies

395   the entire lateral surface of the angular (typical of early therapsids, but distinct from

396   gorgonopsians in which it is widely separated from the articular). The surface structure of the

397   reflected lamina is typical of early therocephalians: an anterodorsal depression becoming a

398   single broad ridge posteroventrally that then ramifies into ventral and posterior ridges. The

399   surangular is exposed laterally as a narrow, curved element atop the angular, contacting the

400   articular posteroventrally. A short angle is present at the posterior base of the coronoid process

401   of the dentary where it overlies the surangular, and the dentary is weakly raised laterally anterior

402   to this point, accommodating the internal anterior process of the surangular. The splenial is a

403   tall, 'ribbon'-like bone occupying the medial face of the anterior portion of the jaw ramus (Fig. 6).

404   It lacks any lateral exposure, being restricted to the internal surface of the jaw. It covers almost

405   all of the medial surface of the dentary anteriorly, but decreased in height posteriorly before

406   terminating at the level of the transverse process of the pterygoid. Dorsal to the splenial is a

407   narrow, laminar bone: the prearticular. This element broadens posteriorly and becomes more

408   raised and rod-like posterior to the dentary, terminating in an indistinct contact with the articular.

409   Dorsal to the prearticular at roughly the mid-length of the jaw ramus is a short, narrow, laminar

410   element interpreted as being the coronoid. The articular is poorly preserved on both sides in this

411   specimen, but a bulbous, cup-like terminus articulating with the (equally poorly preserved)

412   quadrate can be discerned in medial view on the left side (Figs. 4, 6). Although mostly worn off,

413   the base of a large retroarticular process is present.

414

415   *Postcranium*

416   Little of the postcranium is preserved in the holotype of *Gorynychus masyutinae*. The majority of

417   the cervical series is preserved in articulation with the skull and some ribs and pectoral

418   elements are preserved posterior to this (Fig. 1). The atlas-axis complex is somewhat damaged

419   and obscured by the skull and surrounding matrix and C5-7 are broken and badly worn, but C3

420   and 4 are well-preserved and exposed on both sides (Fig. 7). The cervical vertebrae are

421   amphicoelous (except, presumably, the atlas) and are separated ventrally by small, wedge-

422   shaped intercentra. The transverse processes are short and blunt. At least one cervical rib is

423   preserved on the right side of the specimen in association with but disarticulated from vertebra

424   C3. This rib has a broadly falcate head and mediolaterally narrow main body. Well-developed,

425   stout prezygapophyses (12 mm anteroposterior length) extending anterior to the centra are

426   present in C3 and 4, contacting the associated postzygaphophyses of the anterior vertebrae

427   ventrally (and slightly laterally, as the prezygapophysis bulges out somewhat at its anterodorsal

428   edge). No anapophyses are present. The neural spines of C3 (17 mm tall) and 4 are constricted

429   immediately above their point of origin but expand dorsally into broad, rounded tips (15 mm

430   wide in C3). The axial neural spine is definitely anteroposteriorly broader than that of the

431   subsequent vertebrae (Fig. 7), but its exact dimensions (including height relative to subsequent

432   neural spines) are uncertain due to crushing. An isolated vertebra interpreted as the axis in the

433   paratype KPM 291 preserves a tall, broad neural spine (Fig. 9), suggesting that the axial spine

434   was substantially taller and broader than subsequent neural spines, as is typical for theriodonts

435   (Jenkins, 1971). The other vertebrae preserved in KPM 291 have relatively lower, longer centra

436   and shorter neural spines (Fig. 10B) than those of C3 and 4 in the holotype. They likely

437   represent dorsals or even anterior caudals, although most are too poorly preserved to identify

438   with any confidence.

439   The non-vertebral postcranial elements in the holotype are mostly damaged (Fig. 8) The

440   remains of at least eight ribs are present, but little of their morphology is exposed other than

441   simple, curved shafts. A robust, curved elongate bone exposed in worn cross-section probably

442   represents the clavicle, but nothing more about its morphology can be said. The left

443   scapulocoracoid is preserved almost entirely as impression (there is a small chunk of actual

444   bone from the anterior margin of the procoracoid). This impression shows that the coracoid-

445   procoracoid base of the structure was very anteroposteriorly broad. The scapula is broad

446   ventrally but narrows markedly dorsally, where it curves anteriorly at tip. A prominent ridge on

447   the scapula originates at the posterior margin of this element before curving anteriorly along the

448   length of the scapular spine. An elongate bone preserved in the paratype (Fig. 9) is here

449   identified as a fibula. This element lacks the curvature seen in the cervical-thoracic ribs on this

450   block and in KPM 347, and is too long to be a lumbar rib. Additionally, it is expanded at both

451   ends, unlike a rib. The morphology of this element is identical to the fibula in other

452   therocephalians, in which it is usually a narrow, simple bone (Fourie & Rubidge, 2009).

453

454   **PHYLOGENETIC ANALYSIS**

455   *Gorynychus masyutinae* was coded into the most recent analysis of therocephalian

456   interrelationships, that of Huttenlocker & Smith (2017). This analysis includes 57 taxa (including

457   the newly-added *Gorynychus*) and 136 discrete-state characters (available as Supplemental

458   Data). Analysis was undertaken using heuristic searching in PAUP* (Swofford, 2002) v.4.0a

459   (build 159), treating *Biarmosuchus tener* as the outgroup. All characters were treated as

460   unordered following Huttenlocker & Smith (2017). Bootstrap analysis was done using "fast"

461   stepwise addition for 1000 replicates.

462   1260 most parsimonious trees of length 389 were recovered (consistency index=0.429,

463   retention index=0.785). The strict consensus tree recovers *Gorynychus masyutinae* as the

464   sister-taxon of Eutherocephalia (i.e., Akidnognathidae+Whaitsioidea+Baurioidea) (Fig. 11). The

465   addition of *Gorynychus* adds substantial instability to the analysis of Huttenlocker & Smith

466   (2017), notably with the complete collapse of Whaitsioidea (although a core Hofmeyriidae

467   composed of *Hofmeyria*, *Ictidostoma*, and *Mirotenthes* is retained). Unusually, *Perplexisaurus*

468   falls outside of Eutherocephalia in the current analysis, occupying the node between

469   Scylacosauridae and (*Gorynychus*+Eutherocephalia). This is probably attributable to the

470   extremely fragmentary nature of *Perplexisaurus*, which otherwise is very similar to *Karenites*

471   and probably closely related.

472   The breakdown of one of the major eutherocephalian clades (Whaitsioidea) as the sole

473   result of adding *Gorynychus* to the dataset indicates remarkably poor support for a group that,

474   on a strictly gestalt basis, seems to be very well-characterized. This problem can likely be

475   blamed on extensive homoplasy in Eutherocephalia, as well as the need for additional sources

476   of phylogenetic data. Only 19/136 characters in Huttenlocker & Smith's (2017) analysis are

477   postcranial, for instance. Although cranial-focused analyses are standard for Therapsida (an

478   artifact in part of preferential collecting of skulls by Karoo paleontologists during most of the 20th

479   century), recent analyses of synapsid relationships (e.g., Benson, 2012) have highlighted the

480   importance of bringing more robust sets of postcranial data to bear on phylogenetic problems in

481   this clade. More basic descriptive work on therocephalian postcrania is needed; although

482   skeletons are now known for a wide array of taxa, anatomical descriptions are currently

483   available for only a select few (e.g., Kemp, 1986; Fourie & Rubidge, 2009; Botha-Brink &

484   Modesto, 2011; Fourie, 2013).

485

486   **DISCUSSION**

487   At roughly 20 cm in skull length, *Gorynychus* is the largest predatory component of the

488   Kotelnich tetrapod assemblage. Co-occurring gorgonopsians are substantially smaller, with skull

489   lengths less than 10 cm (Kammerer & Masyutin, in review). The only (inferred) predators

490   approaching *Gorynychus* in size are the burnetiamorph *Proburnetia* (known only from the

491   holotypic mould, of uncertain stratigraphic origin within the Kotelnich series) and the

492   eutherocephalian *Viatkosuchus* (Ivakhnenko, 2011). This situations parallels that of middle–

493   earliest late Permian faunas in South Africa (the *Tapinocephalus* and *Pristerognathus* AZs),

494   wherein the only gorgonopsians are small animals and therocephalians are the larger-bodied

495   predators (Kammerer, 2014). The Kotelnich predatory fauna is particularly comparable to that of

496   the *Pristerognathus* AZ; in the middle Permian *Tapinocephalus* AZ, although large-bodied

497   therocephalians were abundant, the apex predators were gigantic anteosaurian dinocephalians.

498   The extinction of anteosaurs at the end of the Capitanian left a depauperate fauna with

499   therocephalians momentarily atop the food chain (Day et al., 2015). It was only following the

500   later extinction of these basal therocephalians that gorgonopsians began to diversify and

501   cemented their position as the dominant large-bodied therapsid predators (Kammerer et al.,

502   2015).

503   Although the presence of a therocephalian apex predator and relatively small

504   gorgonopsians in Kotelnich indicates that the earliest South African records may accurately

505   reflect ancestral body size in these clades (rather than regional peculiarities), in other regards

506   the Kotelnich fauna differs markedly from that of the Karoo. The dominant herbivorous taxon in

507   the Kotelnich fauna, and most abundant tetrapod of any kind, is the pareiasaur *Deltavjatia*

508   (Tsuji, 2013). This pattern is in stark contrast to that of South Africa, where dicynodont

509   therapsids are numerically dominant in all middle–late Permian faunas (Smith et al., 2012).

510   Furthermore, this does not seem to be an isolated oddity, as the best-sampled later Permian

511   Russian tetrapod fauna (North Dvina, a.k.a. Sokolki) also has pareiasaurs (*Scutosaurus*) as the

512   dominant component (although there the top predator is the giant gorgonopsian *Inostrancevia*;

513   this inferred predator-prey pair represents the 'oligobiomorph community' of Ivakhnenko [2008]).

514   The therocephalian fauna in Kotelnich is also unusual even by comparison to the

515   *Pristerognathus* AZ. Although eutherocephalian fossils have been found in the *Pristerognathus*

516   AZ, they are rarer than scylacosaurids/lycosuchids and are relatively poorly-known

517   (Huttenlocker & Smith, 2017). By contrast, eutherocephalians are the most abundant and

518   species-rich theriodonts at Kotelnich. As such, the Kotelnich fauna seems to capture a phase in

519   therocephalian evolution not well-represented in the South African record: the initial

520   diversification of Eutherocephalia. The recovery of *Gorynychus* as a taxon just outside of

521   Eutherocephalia, rather than a lycosuchid or scylacosaurid, adds another wrinkle to this

522   interpretation. The few eutherocephalians known from the *Pristerognathus* AZ belong to well-

523   known groups (the whaitsioid family Hofmeyriidae and baurioid family Ictidosuchidae) deeply

524   nested within Eutherocephalia and appear in the record seemingly without precedent. In

525   Kotelnich, however, there is a combination of taxa at the base of Eutherocephalia (*Gorynychus*,

526   possible *Perplexisaurus*) and potential early representatives of known eutherocephalian families

527   (e.g., *Viatkosuchus*). This indicates substantial therocephalian diversification occurring in

528   Laurasia at the time, and suggest that eutherocephalians originated outside of the Karoo and

529   only later migrated to the basin.

530

531   **CONCLUSIONS**

532   Based on the remains of two individuals, a new therocephalian taxon, *Gorynychus masyutinae*,

533   is described from the (probably) earliest late Permian Kotelnich locality of Russia. *Gorynychus* is

534   the largest known predatory tetrapod in the Kotelnich assemblage, and demonstrates that

535   therocephalians acted as top predators in Russian as well as South African assemblages during

536   the transition between typical middle and late Permian terrestrial communities. Although falling

537   outside of Eutherocephalia, *Gorynychus* is more closely related to eutherocephalians than to the

538   large-bodied therocephalian predators of southern Africa (and possibly earlier Permian

539   assemblages in Russia, if *Porosteognathus* from the middle Permian Isheevo fauna truly is a

540   scylacosaurid). The Kotelnich therocephalian fauna shows greater diversity of

541   eutherocephalians than probable coeval faunas in South Africa, and suggests that initial

542   diversification in this clade probably was not occurring in the Karoo Basin.

543

ACKNOWLEDGEMENTS

We thank director A. Toporov, curator T. Berestova, and the staff members at the Vyatka

Paleontological Museum for all of their help. CFK's research was supported by a grant from the

Deutsche Forschungsgemeinschaft (KA 4133/1-1).

548

REFERENCES

Abdala F, Rubidge BS, van den Heever JA. 2008. The oldest therocephalians (Therapsida,

Eutheriodontia) and the early diversification of Therapsida. *Palaeontology* **51:**1011–1024.

Abdala F, Kammerer CF, Day MO, Jirah S, Rubidge BS. 2014. Adult morphology of the

therocephalian *Simorhinella baini* from the middle Permian of South Africa and the taxonomy,

paleobiogeography, and temporal distribution of the Lycosuchidae. *Journal of Paleontology*

88:1139–1153.

Benson RBJ. 2012. Interrelationships of basal synapsids: cranial and postcranial morphological

parititons suggest different topologies. *Journal of Systematic Palaeontology* **10:**601–624.

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.

Boonstra LD. 1969. The fauna of the *Tapinocephalus* Zone (Beaufort beds of the Karoo).

Annals of the South African Museum **56:**1–73.

568

569 **Botha-Brink J, Modesto SP. 2011.** A new skeleton of the therocephalian synapsid

570 *Olivierosuchus parringtoni* from the Lower Triassic South African Karoo Basin. *Palaeontology*

571 **54:**591–606.

572

573 **Broom R. 1903.** On the classification of the theriodonts and their allies. *Report of the South*

574 *African Association for the Advancement of Science* **1:**286–294.

575

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

577 269.

578

579 **Coffa AA. 1997.** Geology and stratigraphy of the Upper Permian Kotel'nich locality, Vyatka

580 River, Russia. Unpublished PhD thesis, Monash University.

581

582 **Day MO, Ramezani J, Bowring SA, Sadler PM, Erwin DH, Abdala F, Rubidge BS. 2015.**

583 When and how did the terrestrial mid-Permian mass extinction occur? Evidence from the

584 tetrapod record of the Karoo Basin, South Africa. *Proceedings of the Royal Society B*

585 **282:**20150834 DOI 10.1098/rspb.2015.0834.

586

587 **Fourie H. 2013.** The postcranial description of *Ictidosuchoides* (Therapsida: Therocephalia:

588 Baurioidea). *Annals of the Ditsong National Museum of Natural History* **3:**1–10.

589

590 **Fourie H, Rubidge BS. 2009.** The postcranial skeleton of the basal therocephalian

591 *Glanosuchus macrops* (Scylacosauridae) and comparisons of morphological and phylogenetic

592 trends amongst the Theriodontia. *Palaeontologia africana* **44:**27–39.

593

594 **Hartmann-Weinberg AP. 1937.** Pareiasauriden als Leitfossilien. *Problemy Paleontologii*

595 **2/3:**649–712.

596

597 **Huttenlocker AK. 2009.** An investigation into the cladistic relationships and monophyly of

598 therocephalian therapsids. *Zoological Journal of the Linnean Society* **157:**865–891.

599

600 **Huttenlocker AK. 2014.** Body size reductions in nonmammalian eutheriodont therapsids

601 (Synapsida) during the end-Permian mass extinction. *PLoS ONE* **9(2):**e87553 DOI

602 10.1371/journal.pone.0087553.

603

604 **Huttenlocker AK, Botha-Brink J. 2013.** Body size and growth patterns in the therocephalian

605 *Moschorhinus kitchingi* (Therapsida: Eutheriodontia) before and after the end-Permian

606 extinction in South Africa. *Paleobiology* **39:**253–277.

607

608 **Huttenlocker AK, Smith RMS. 2017.** New whaitsioids (Therapsida: Therocephalia) from the

609 Teekloof Formation of South Africa and therocephalian diversity during the end-Guadalupian

610 extinction. *PeerJ* **5:**e3868 DOI 10.7717/peerj.3868.

611

612 **Ivakhnenko MF. 2003.** Eotherapsids from the East European placket. *Paleontological Journal*

613 **37:**S339–2465.

614

615 **Ivakhnenko MF. 2008.** Cranial morphology and evolution of Permian Dinomorpha

616 (Eotherapsida) of Eastern Europe. *Paleontological Journal* **42:**859–995.

617

618 **Ivakhnenko MF. 2011.** Permian and Triassic therocephals (Eutherapsida) of Eastern Europe.

619 *Paleontological Journal* **45:**981–1144.

620

621 **Jablonski D. 2002.** Survival without recovery after mass extinctions. *Proceedings of the*

622 *National Academy of Sciences of the United States of America* **99:**8139–8144 DOI

623 10.1073/pnas.102163299

624

625 **Jenkins FA, Jr. 1971.** The postcranial skeleton of African cynodonts. *Peabody Museum Bulletin*

626 **36**:1–216.

627

628 **Kammerer CF. 2011.** Systematics of the Anteosauria (Therapsida: Dinocephalia). *Journal of*

629 *Systematic Palaeontology* **9:**261–304.

630

631 **Kammerer CF. 2014.** A redescription of *Eriphostoma microdon* Broom, 1911 (Therapsida,

632 Gorgonopsia) from the *Tapinocephalus* Assemblage Zone of South Africa and a review of

633 Middle Permian gorgonopsians. In: Kammerer CF, Angielczyk KD, Fröbisch J, eds. *Early*

634 *Evolutionary History of the Synapsida*. Dordrecht: Springer, 171–184, 337 pp. DOI 10.1007/978-

635 94-007-6841-3_11.

636

637 **Kammerer CF. 2015.** Cranial osteology of *Arctognathus curvimola*, a short-snouted

638 gorgonopsian from the Late Permian of South Africa. *Papers in Paleontology* **1:**41–58.

639

640 **Kammerer CF, Smith RMH, Day MO, Rubidge BS. 2015.** New information on the morphology

641 and stratigraphic range of the mid-Permian gorgonopsian *Eriphostoma microdon* Broom, 1911.

642 *Papers in Palaeontology* **1:**201–221.

643

644 **Kemp TS. 1986.** The skeleton of a baurioid therocephalian from the Lower Triassic

645 (*Lystrosaurus* Zone) of South Africa. *Journal of Vertebrate Paleontology* **6:**215–232.

646

647   **Kurkin, AA. 2011.** Permian anomodonts: paleobiogeography and distribution of the group.

648   *Paleontological Journal* **45:**432–444.

649

650   **Li J. 2001.** The most primitive lower tetrapod fauna in China. *Science in China (Series D)*

651   **44:**47–51.

652

653   **Mendrez CH. 1975.** Principales variations du palais chez les thérocéphales sud-africains

654   (Pristerosauria et Scaloposauria) au cours du Permien supérieur et du Trias inférieur.

655   *Problémes Actuels de Paléontologie—Évolution des Vertébrés. Colloques internationaux du*

656   *Centre national de la recherche scientifique* **218:**379–408.

657

658   **Osborn HF. 1903.** On the primary division of the Reptilia into two sub-classes, Synapsida and

659   Diapsida. *Science* **17:**275–276.

660

661   **Sigogneau-Russell D, Sun A-L. 1981.** A brief review of Chinese synapsids. *Geobios* **14:**275–

662   279.

663

664   **Smith RMH, Rubidge BS, van der Walt M. 2012.** Therapsid biodiversity patterns and

665   environments of the Karoo Basin, South Africa. In: Chinsamy A, ed. F*orerunners of mammals:*

666   *radiation, histology, biology*. Bloomington and Indianapolis: Indiana University Press, 223–246,

667   330 pp.

668

669   **Swofford DL. 2002.** PAUP*. Phylogenetic analysis using parsimony (*and other methods).

670   Version 4. Sinauer Associates, Sunderland, Massachusetts.

671

672 **Tatarinov LP. 1995a.** *Viatkosuchus sumini,* a new Late Permian therocephalian from the Kirov

673 Region. *Paleontological Journal* **29:**111–128.

674

675 **Tatarinov LP. 1995b.** A new ictidosuchid *Karenites ornamentatus* (Theriodontia) from the

676 Upper Permian of the Kotel'nich Locality in the Kirov Region. *Russian Journal of Herpetology*

677 **2:**18–33.

678

679 **Tatarinov LP. 1997.** A new scaloposaur (Reptilia, Theriodontia) with an unusual sensory

680 system, from the Upper Permian of the Kirov Region. *Paleontological Journal* **31:**655–661.

681

682 **Tatarinov LP. 1999.** New theriodonts (Reptilia) from the Late Permian fauna of the Kotelnich

683 Locality, Kirov Region. *Paleontological Journal* **33:**550–556.

684

685 **Tatarinov LP. 2000.** New material of scaloposaurians (Reptilia, Theriodontia) from the Upper

686 Permian of the Kotelnich Locality, Kirov Region. *Paleontological Journal* **34:**S187–S202.

687

688 **Tsuji LA. 2013.** Anatomy, cranial ontogeny and phylogenetic relationships of the pareiasaur

689 *Deltavjatia rossicus* from the Late Permian of central Russia. *Earth and Environmental Science*

690 *Transactions of the Royal Society of Edinburgh* **104:**81–122.

691

692 **Van den Heever JA. 1980.** On the validity of the therocephalian family Lycosuchidae (Reptilia:

693 Therapsida). *South African Journal of Science* **81:**111–125.

694

695 **Van den Heever JA. 1987.** *The comparative and functional cranial morphology of the early*

696 *Therocephalia (Amniota: Therapsida).* Unpublished PhD Thesis, University of Stellenbosch, 659

697 pp.

698

699 **Van den Heever JA. 1994.** The cranial anatomy of the early Therocephalia (Amniota:

700 Therapsida). *Universiteit van Stellenbosch Annale* **1994:**1–59.

701

702 **Vjuschkov BP. 1955.** [Theriodonts of the Soviet Union]. *Trudy Paleontologicheskogo Instituta,*

703 *Akademiya Nauk SSSR* **49:**128–175. [in Russian]

704   FIGURE CAPTIONS

705

706   **Figure 1.** Holotype of *Gorynychus masyutinae*. The two blocks (KPM 346 and 347) making up

707   the majority of the holotype shown in articulation. Holotype also includes two incisor teeth (KPM

708   348 and 349) disarticulated from the skull but found in association (see Figs. 2C and 10D).

709   [planned for page width]

710

711   **Figure 2.** Anterior snout and dentition of *Gorynychus masyutinae*. (A) Photograph and (B)

712   interpretive drawing of the skull (KPM 346) in anterior view. (C) Disarticulated incisor (KPM 348)

713   associated with skull in presumed anterior or anterolateral view. Abbreviations: apc, anterior

714   premaxillary channel; mx, maxilla; na, nasal; nr, naris; pmx, premaxilla; smx, septomaxilla. Gray

715   coloration indicates matrix. Scale bar equals 5 cm. [planned for page width]

716

717   **Figure 3.** Holotype of *Gorynychus masyutinae* in dorsal view. (A) Photograph and (B)

718   interpretive drawing of skull (KPM 346). Abbreviations: d, dentary; fr, frontal; j, jugal; la, lacrimal;

719   mx, maxilla; na, nasal; pmx, premaxilla; po, postorbital; prf, prefrontal; qpt, quadrate ramus of

720   pterygoid; smx, septomaxilla; sq, squamosal. Gray coloration indicates matrix, patterning

721   indicates eroded or broken bone surface. Scale bar equals 1 cm. [planned for page width]

722

723   **Figure 4.** Holotype of *Gorynychus masyutinae* in right lateral view. (A) Photograph and (B)

724   interpretive drawing of skull (KPM 346). Abbreviations: ar, articular; C, upper canine; co,

725   coronoid process of dentary; d, dentary; fr, frontal; i, lower incisor; j, jugal; la, lacrimal; mx,

726   maxilla; na, nasal; pmx, premaxilla; prf, prefrontal; PC, upper postcanine; po, postorbital; q-qj,

727   quadrate-quadratojugal complex; rla, reflected lamina of angular; sa, surangular; smx,

728   septomaxilla; sq, squamosal; ss, squamosal sulcus. Gray coloration indicates matrix, patterning

729   indicates eroded or broken bone surface. Scale bar equals 1 cm. [planned for page width]

730

731   **Figure 5**. Holotype of *Gorynychus masyutinae* in left lateral view. (A) Photograph and (B)

732   interpretive drawing of skull (KPM 346). Abbreviations: C, upper canine; co, coronoid process of

733   dentary; d, dentary; ept, epipterygoid; fr, frontal; j, jugal; la, lacrimal; mx, maxilla; na, nasal; os,

734   orbitosphenoid; pa, parietal; pmx, premaxilla; prf, prefrontal; PC, upper postcanine; po,

735   postorbital; qpt, quadrate ramus of pterygoid; rla, reflected lamina of angular; sa, surangular;

736   smx, septomaxilla. Gray coloration indicates matrix, patterning indicates eroded or broken bone

737   surface. Scale bar equals 1 cm. [planned for page width]

738

739   **Figure 6.** Holotype of *Gorynychus masyutinae* in ventral view. (A) Photograph and (B)

740   interpretive drawing of skull (KPM 346). Abbreviations: an, angular; ar, articular; bt, basal tuber;

741   C, upper canine; d, dentary; j, jugal; mx, maxilla; oc, occipital condyle; pl, palatine; pra,

742   prearticular; ps, parabasisphenoid; pt, palatal portion of pterygoid; q, quadrate; qpt, quadrate

743   ramus of pterygoid; ri, rib; rla, reflected lamina of angular; sf, suborbital fenestra; sp, splenial;

744   sq, squamosal; st, stapes; tpt, transverse process of pterygoid; v, vomer. Gray coloration

745   indicates matrix. Scale bar equals 1 cm. [planned for page width]

746

747   **Figure 7.** Cervical vertebrae of *Gorynychus masyutinae* (KPM 346–347). (A) Photograph and

748   (B) interpretive drawing. Abbreviations: as, axial neural spine; c, cervical vertebra; cr, cervical

749   rib; ic, intercentrum; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; sf?,

750   possible skull fragment; tp, transverse process. Gray coloration indicates matrix. Scale bar

751   equals 5 cm. [planned for page width]

752

753   **Figure 8.** Postcranial elements of *Gorynychus masyutinae* (KPM 347). (A) Photograph and (B)

754   interpretive drawing. Abbreviations: ?, unknown bone; c, cervical vertebra; cl?, possible clavicle;

755 ri, rib; sc, scapulocoracoid; ve, vertebra. Gray coloration indicates matrix. Scale bar equals 5

756 cm. [planned for page width]

757

758 **Figure 9.** KPM 291, a block containing disarticulated elements referred to *Gorynychus*

759 *masyutinae* gen. et sp. nov. (A) Photograph and (B) interpretive drawing. Abbreviations: ax, axis

760 vertebra; d, dentary; i, incisor; po?, postorbital?; r, rib; ve, vertebra. Elements marked with

761 asterisks are shown in greater detail in Figure 10. Scale bar equals 5 cm. [planned for page

762 width]

763

764 **Figure 10**. Disarticulated elements from the specimen KPM 291. (A) Anterior portion of right

765 dentary preserving lower canine; (B) ?dorsal vertebra; (C) incisor tooth compared with (D)

766 incisor from the holotype (KPM 349). Scale bars equal 1 cm. [planned for page width]

767

768 **Figure 11.** Cladogram showing phylogenetic position of *Gorynychus masyutinae*. Strict

769 consensus of 1260 most parsimonious trees. Numbers at nodes represent bootstrap values,

770 major clades labeled at nodes. [planned for page width]

Figure 1

Holotype of *Gorynychus masyutinae*.

The two blocks (KPM 346 and 347) making up the majority of the holotype shown in articulation. Holotype also includes two incisor teeth (KPM 348 and 349) disarticulated from the skull but found in association (see Figs. 2C and 10D).

Figure 2

Anterior snout and dentition of *Gorynychus masyutinae*.

(A) Photograph and **(B)** interpretive drawing of the skull (KPM 346) in anterior view. **(C)** Disarticulated incisor (KPM 348) associated with skull in presumed anterior or anterolateral view. **Abbreviations:** apc, anterior premaxillary channel; mx, maxilla; na, nasal; nr, naris; pmx, premaxilla; smx, septomaxilla. Gray coloration indicates matrix. Scale bar equals 5 cm.
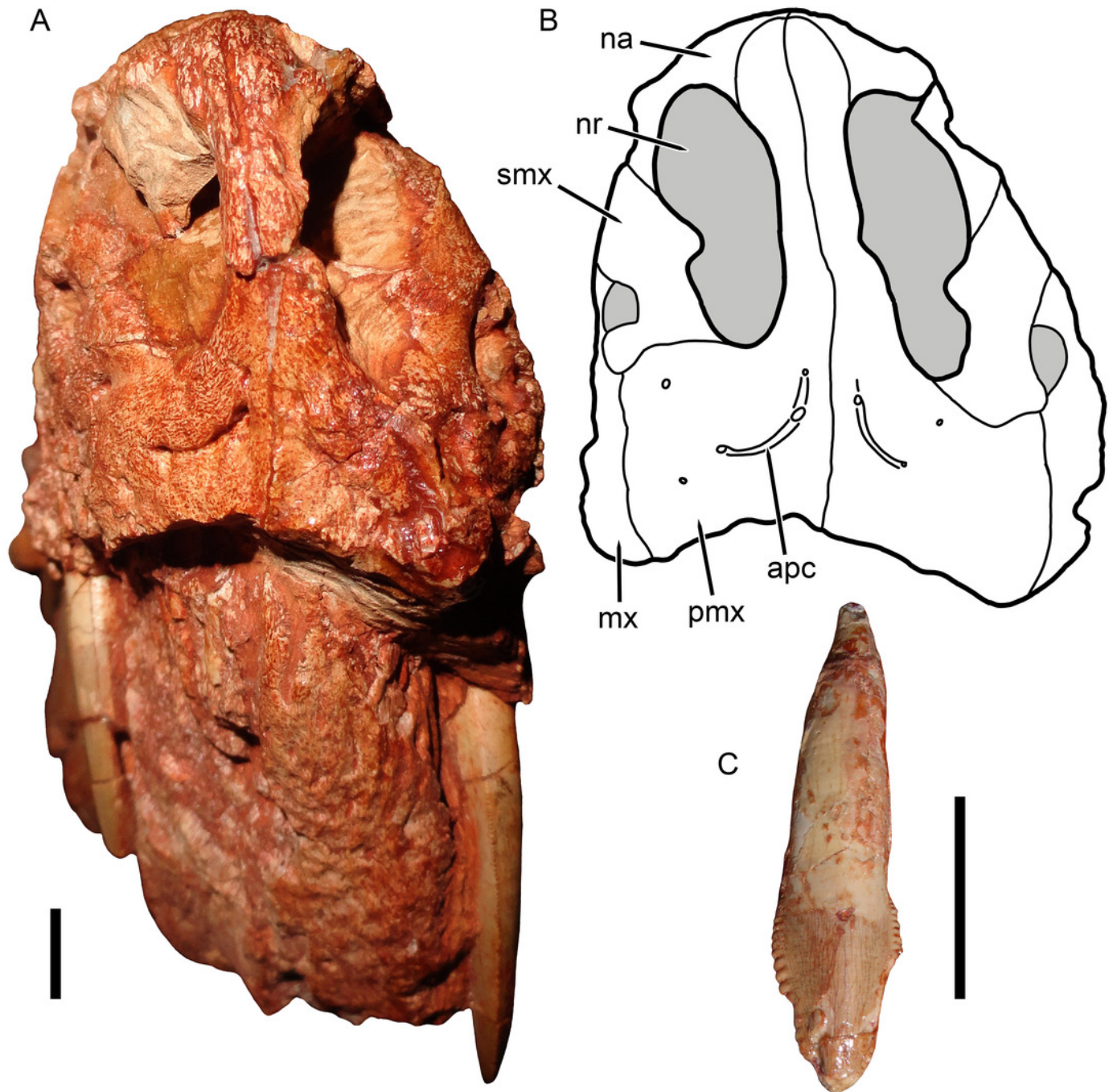
Figure 3

Holotype of *Gorynychus masyutinae* in dorsal view.

(A) Photograph and **(B)** interpretive drawing of skull (KPM 346). **Abbreviations:** d, dentary; fr, frontal; j, jugal; la, lacrimal; mx, maxilla; na, nasal; pmx, premaxilla; po, postorbital; prf, prefrontal; qpt, quadrate ramus of pterygoid; smx, septomaxilla; sq, squamosal. Gray coloration indicates matrix, patterning indicates eroded or broken bone surface. Scale bar equals 1 cm.
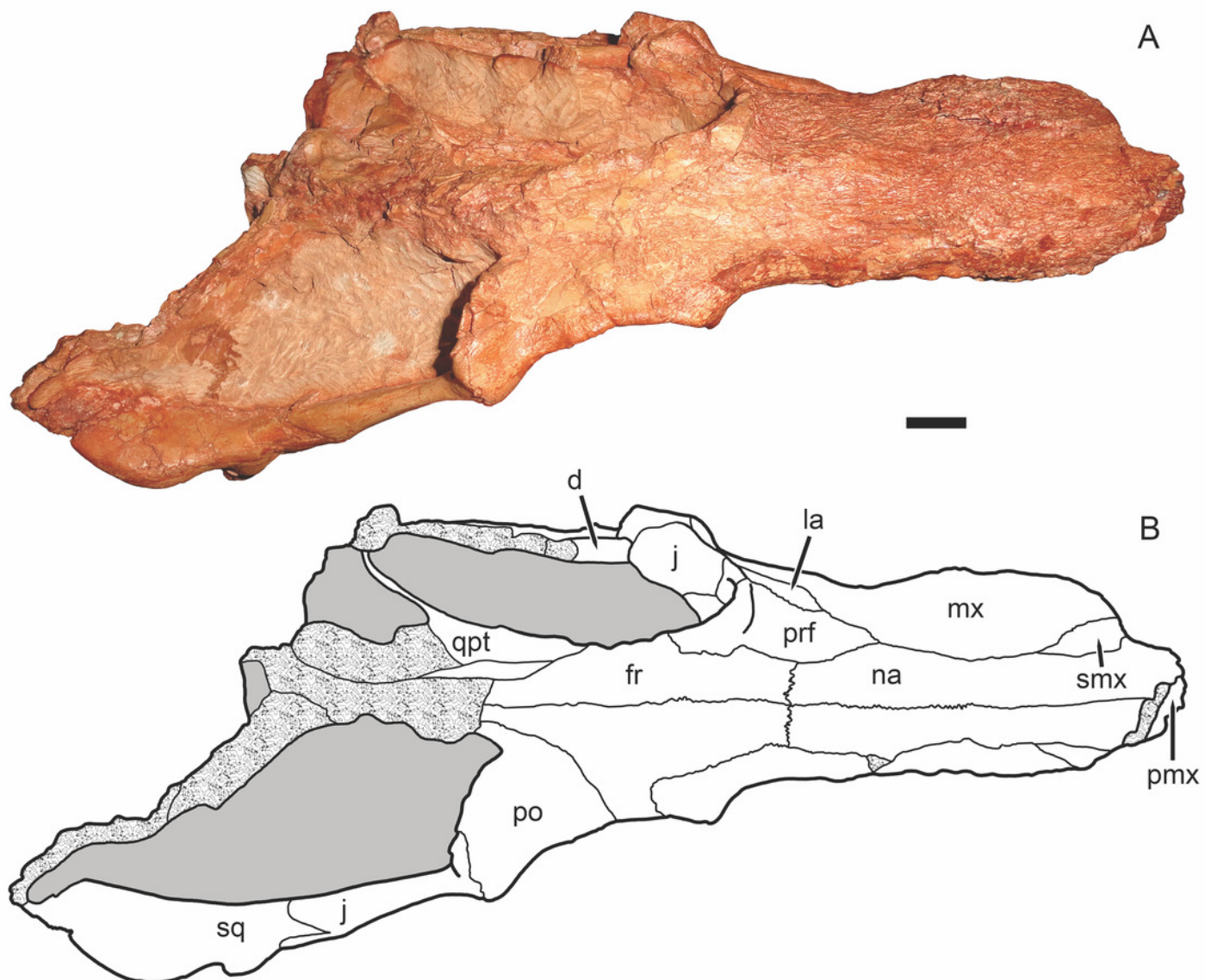
Figure 4

Holotype of *Gorynychus masyutinae* in right lateral view.

(A) Photograph and **(B)** interpretive drawing of skull (KPM 346). **Abbreviations:** ar, articular; C, upper canine; co, coronoid process of dentary; d, dentary; fr, frontal; i, lower incisor; j, jugal; la, lacrimal; mx, maxilla; na, nasal; pmx, premaxilla; prf, prefrontal; PC, upper postcanine; po, postorbital; q-qj, quadrate-quadratojugal complex; rla, reflected lamina of angular; sa, surangular; smx, septomaxilla; sq, squamosal; ss, squamosal sulcus. Gray coloration indicates matrix, patterning indicates eroded or broken bone surface. Scale bar equals 1 cm.

A

B

na

smx

po   fr

prf

ss   sq

j

la

mx

co

sa

q-qj

C

ar

rla

d

PC3

i2

pmx
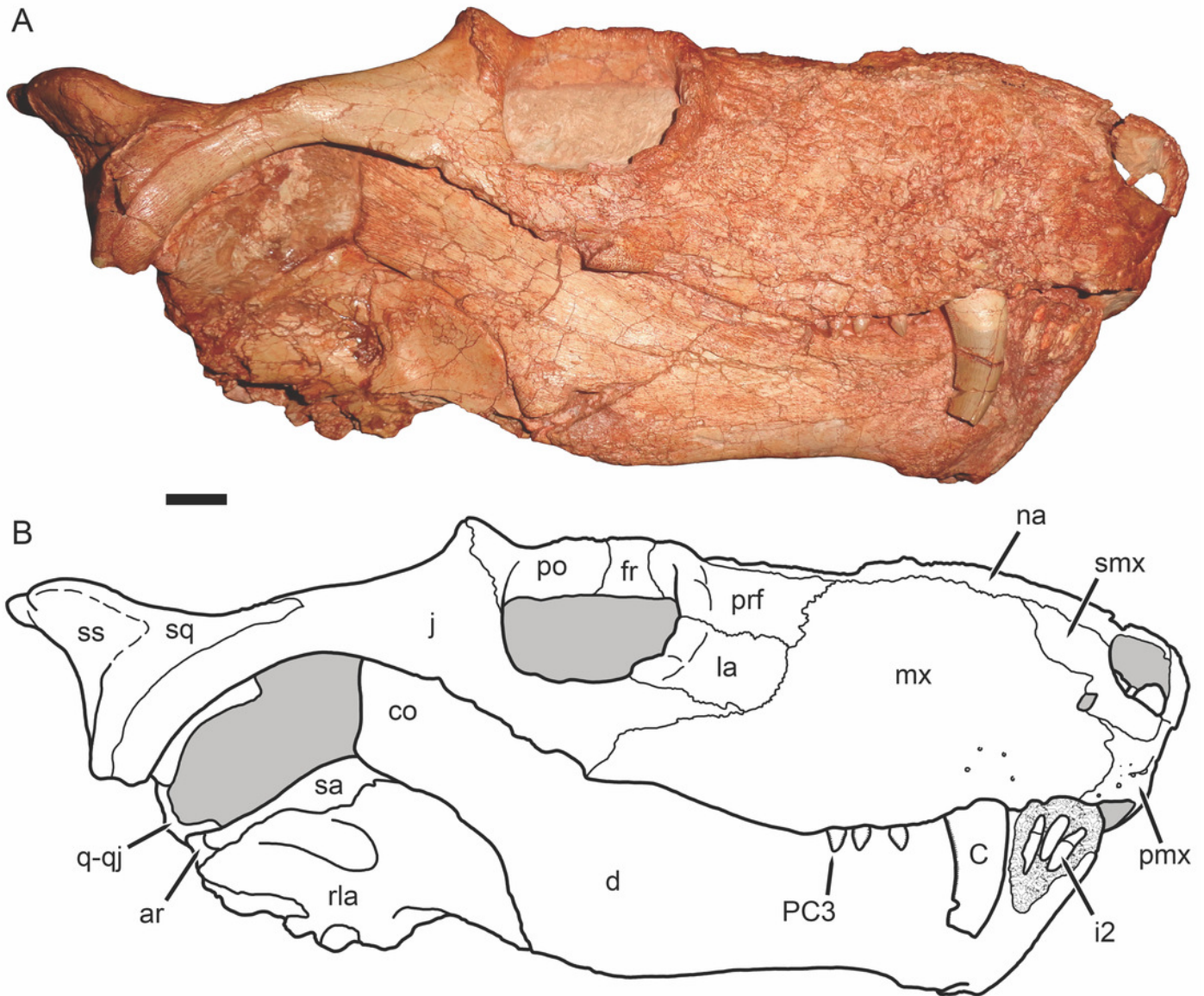
Figure 5

Holotype of *Gorynychus masyutinae* in left lateral view.

(A) Photograph and **(B)** interpretive drawing of skull (KPM 346). **Abbreviations:** C, upper canine; co, coronoid process of dentary; d, dentary; ept, epipterygoid; fr, frontal; j, jugal; la, lacrimal; mx, maxilla; na, nasal; os, orbitosphenoid; pa, parietal; pmx, premaxilla; prf, prefrontal; PC, upper postcanine; po, postorbital; qpt, quadrate ramus of pterygoid; rla, reflected lamina of angular; sa, surangular; smx, septomaxilla. Gray coloration indicates matrix, patterning indicates eroded or broken bone surface. Scale bar equals 1 cm.
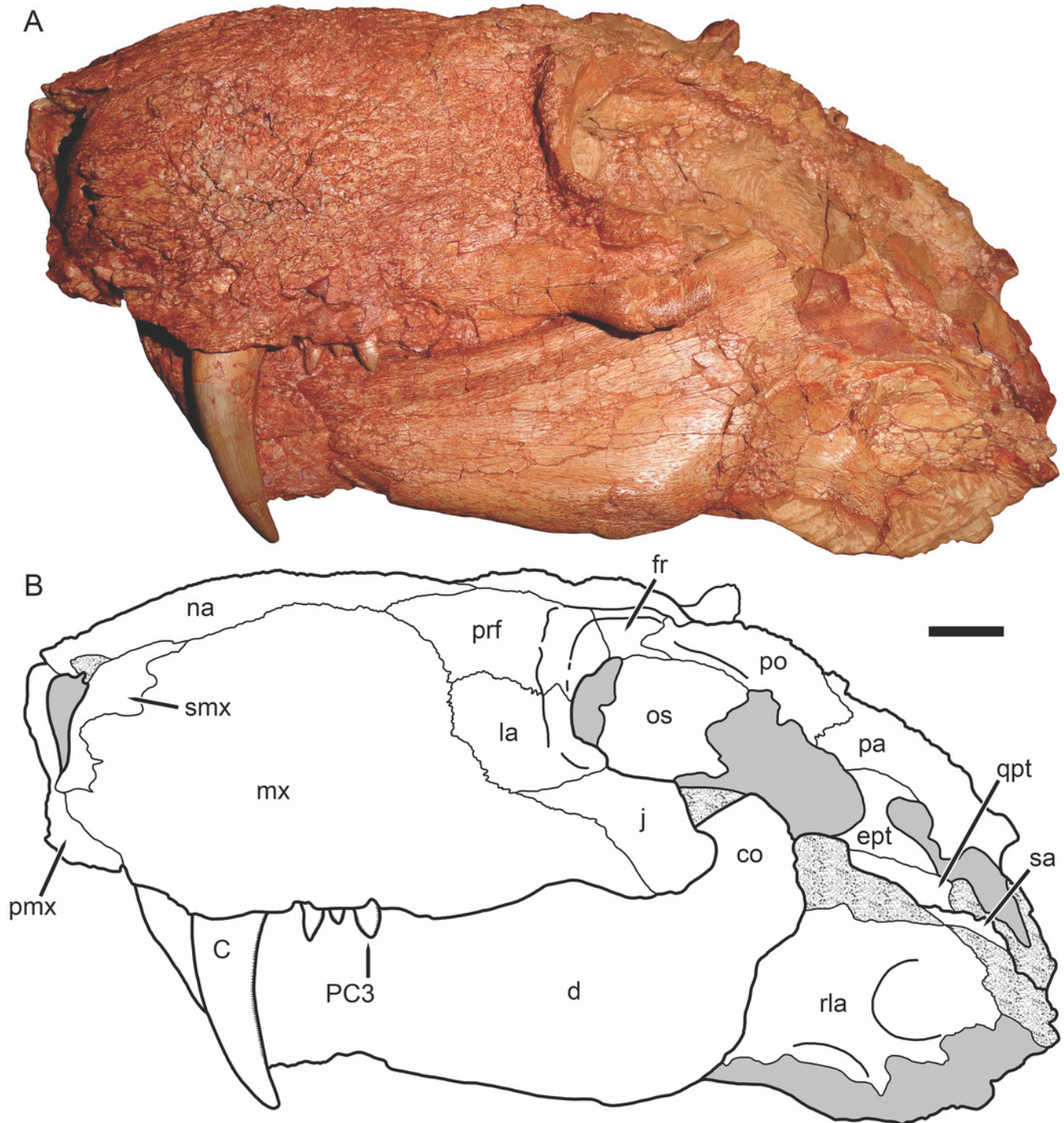
Figure 6

Holotype of *Gorynychus masyutinae* in ventral view.

(A) Photograph and **(B)** interpretive drawing of skull (KPM 346). **Abbreviations:** an, angular; ar, articular; bt, basal tuber; C, upper canine; d, dentary; j, jugal; mx, maxilla; oc, occipital condyle; pl, palatine; pra, prearticular; ps, parabasisphenoid; pt, palatal portion of pterygoid; q, quadrate; qpt, quadrate ramus of pterygoid; ri, rib; rla, reflected lamina of angular; sf, suborbital fenestra; sp, splenial; sq, squamosal; st, stapes; tpt, transverse process of pterygoid; v, vomer. Gray coloration indicates matrix. Scale bar equals 1 cm.
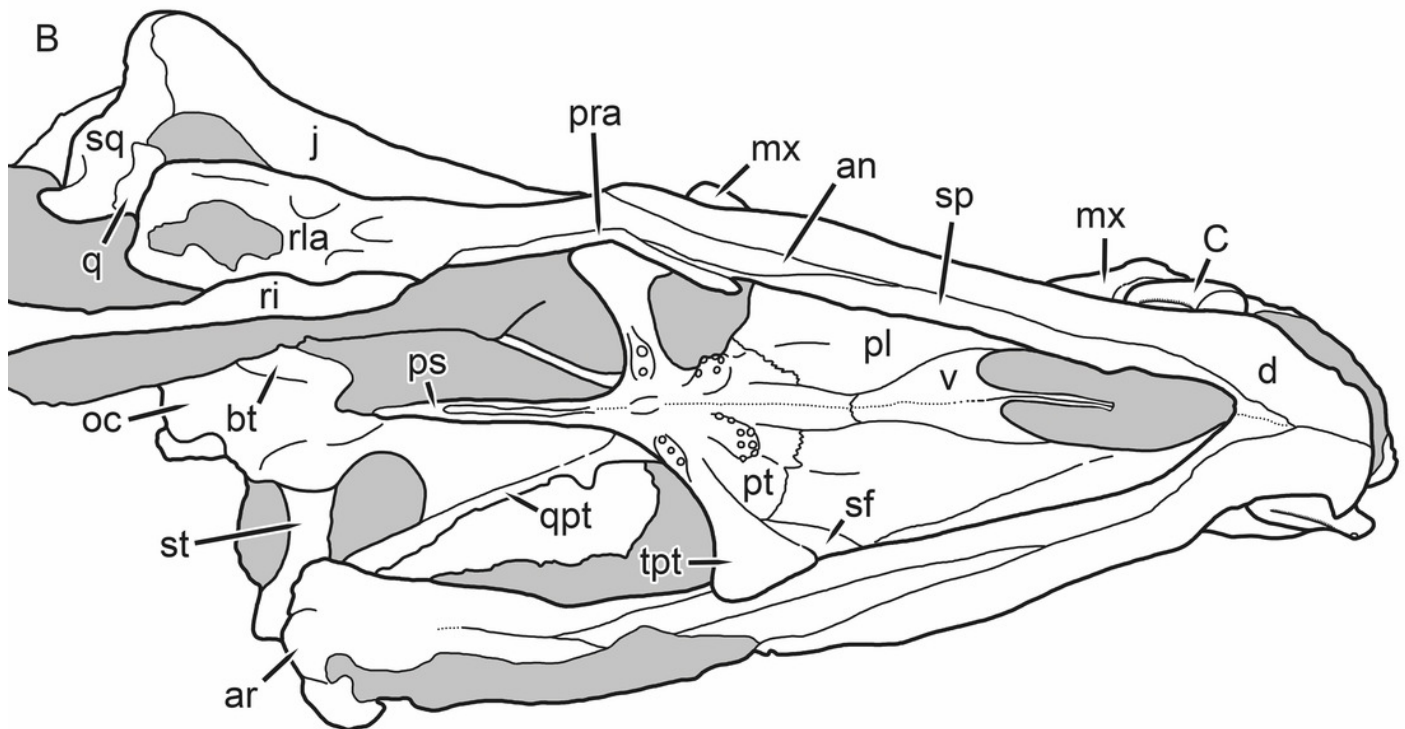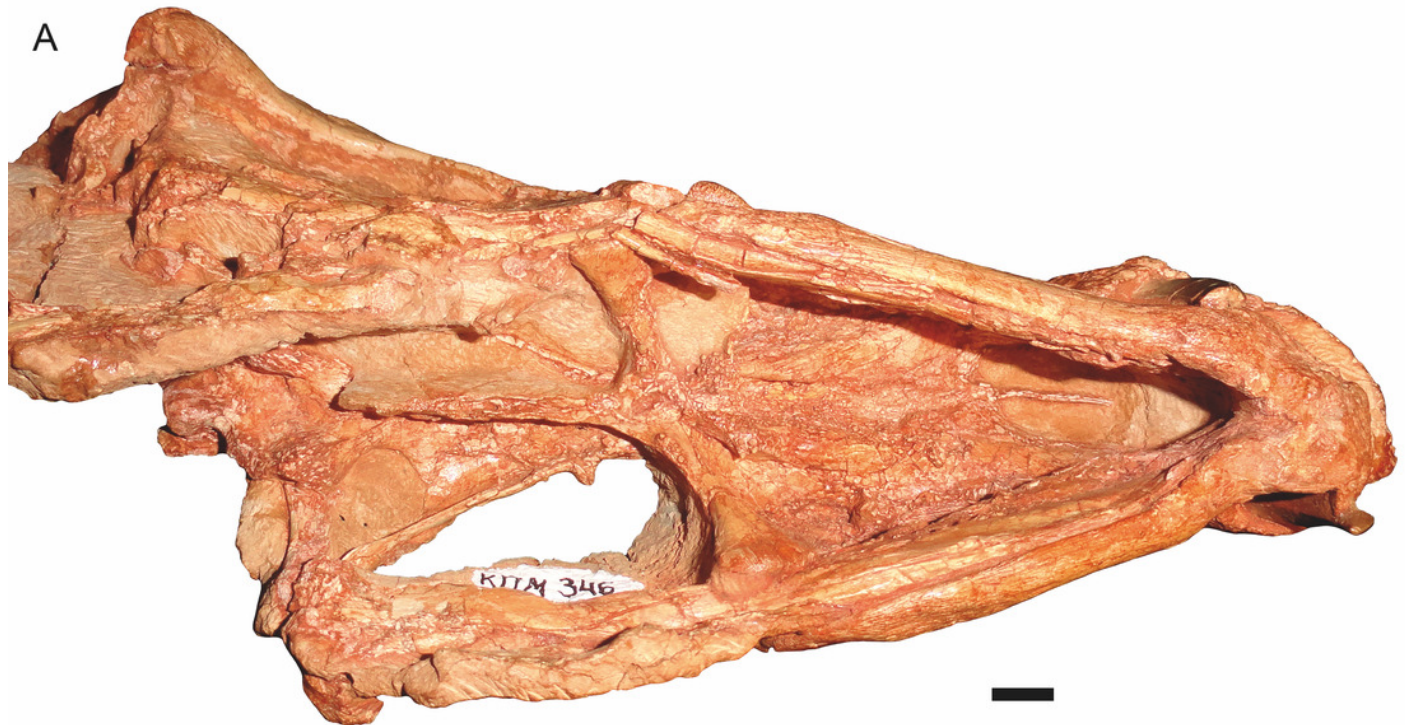
Figure 7

Cervical vertebrae of *Gorynychus masyutinae* (KPM 346–347).

(A) Photograph and **(B)** interpretive drawing. **Abbreviations:** as, axial neural spine; c, cervical vertebra; cr, cervical rib; ic, intercentrum; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; sf?, possible skull fragment; tp, transverse process. Gray coloration indicates matrix. Scale bar equals 5 cm.
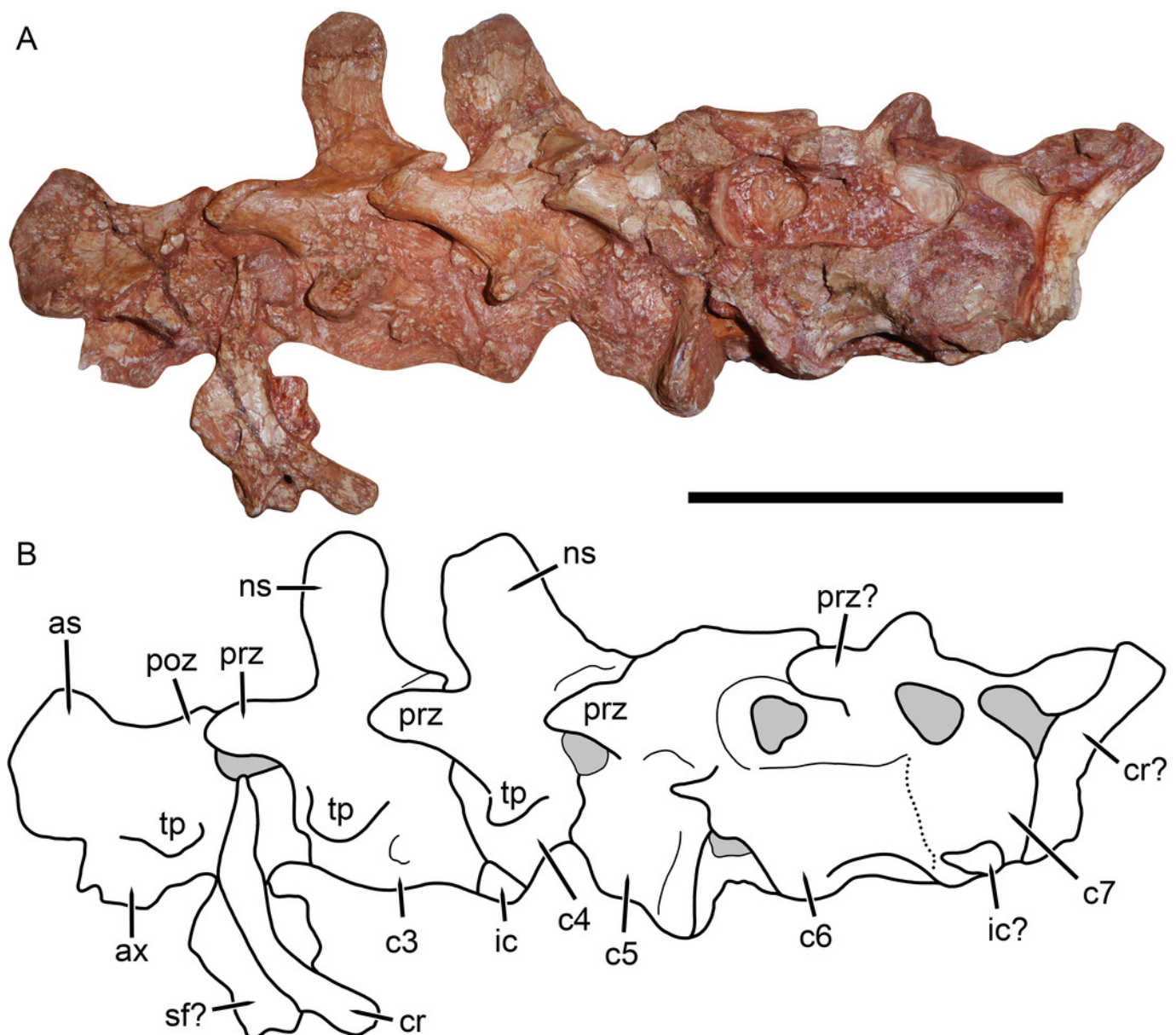
Figure 8

Postcranial elements of *Gorynychus masyutinae* (KPM 347).

(A) Photograph and **(B)** interpretive drawing. **Abbreviations:** ?, unknown bone; c, cervical vertebra; cl?, possible clavicle; ri, rib; sc, scapulocoracoid; ve, vertebra. Gray coloration indicates matrix. Scale bar equals 5 cm.
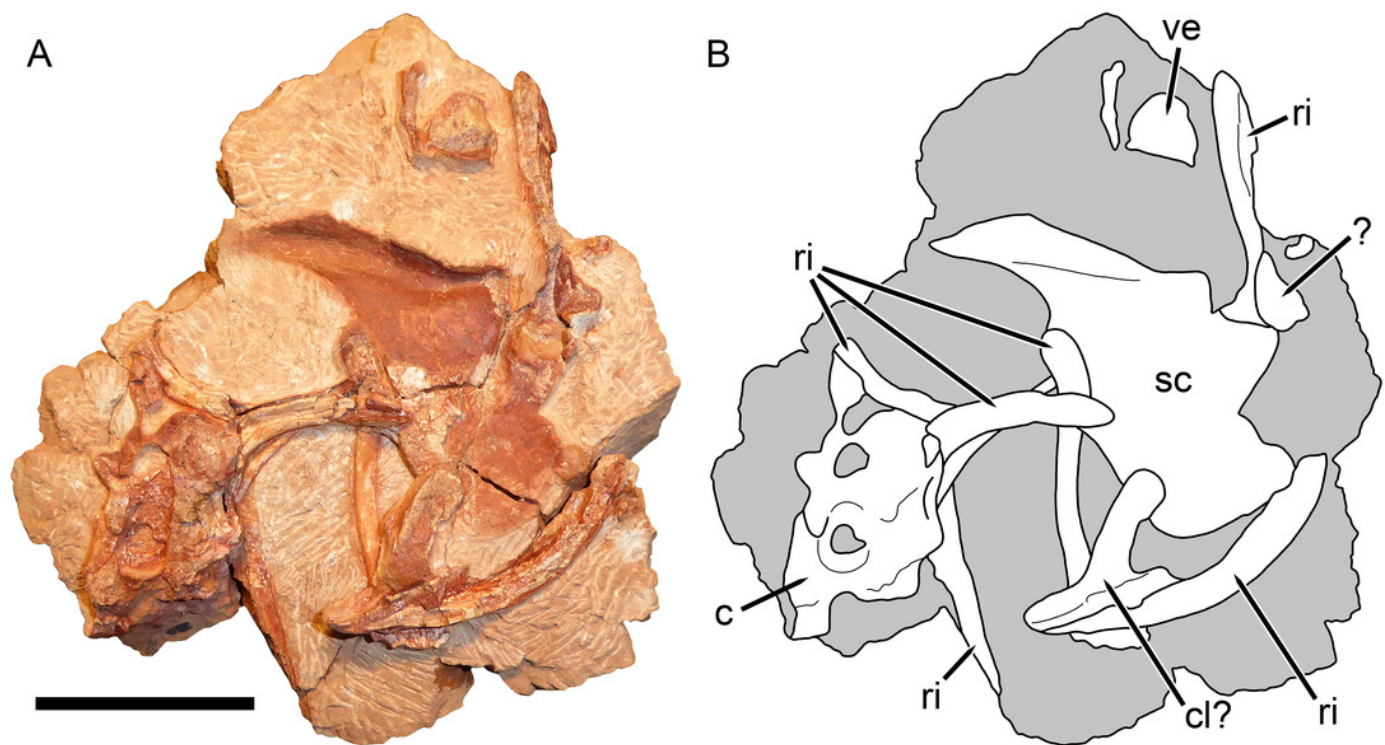
Figure 9

KPM 291, a block containing disarticulated elements referred to *Gorynychus masyutinae* gen. et sp. nov.

(A) Photograph and (B) interpretive drawing. **Abbreviations:** ax, axis vertebra; d, dentary; i, incisor; po?, postorbital?; r, rib; ve, vertebra. Elements marked with asterisks are shown in greater detail in Figure 10. Scale bar equals 5 cm.
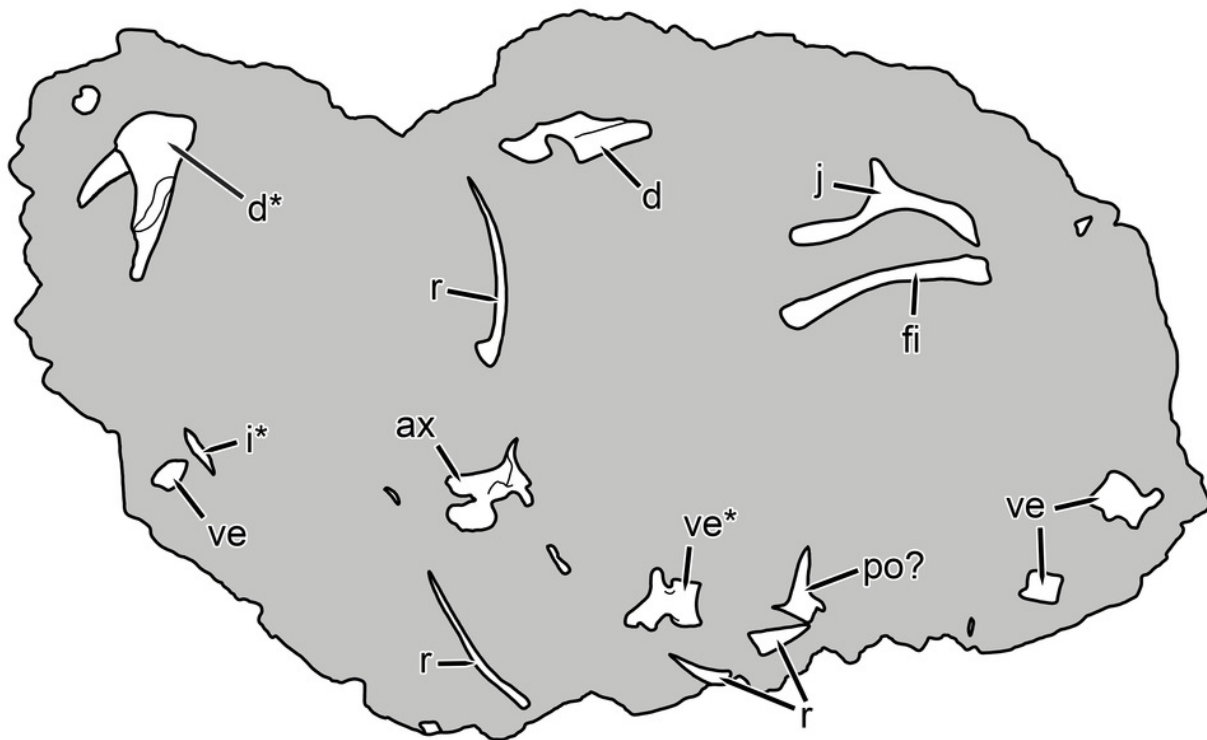
Figure 10

Disarticulated elements from the specimen KPM 291.

(A) Anterior portion of right dentary preserving lower canine; **(B)** ?dorsal vertebra; **(C)** incisor tooth compared with **(D)** incisor from the holotype (KPM 349). Scale bars equal 1 cm.
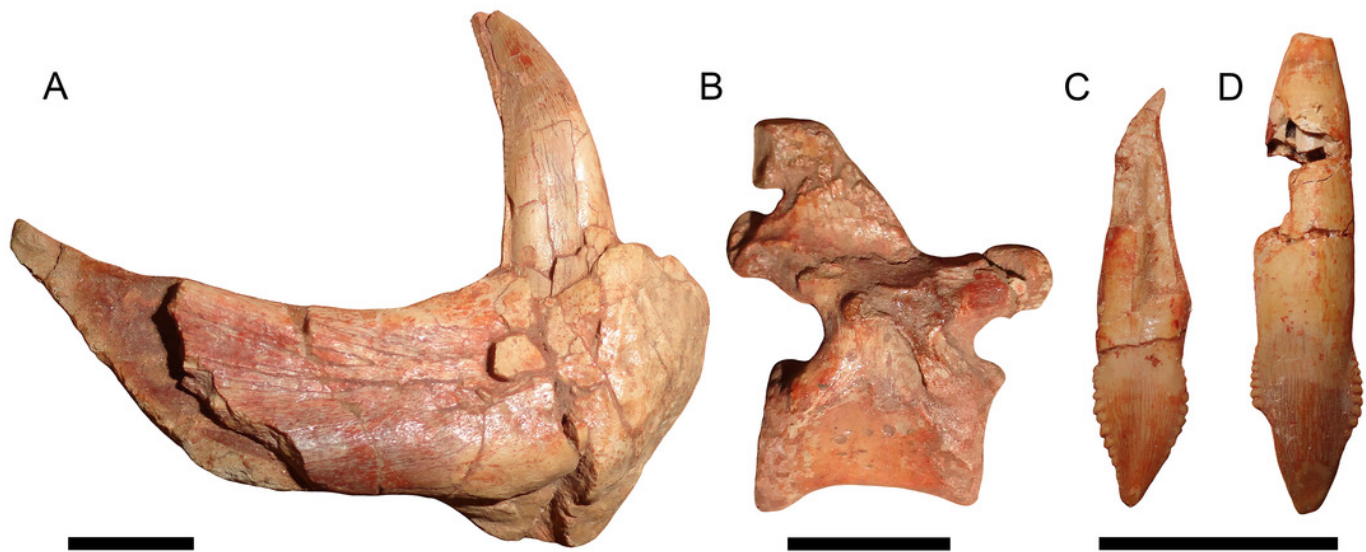
Figure 11

Cladogram showing phylogenetic position of *Gorynychus masyutinae*.

Strict consensus of 1260 most parsimonious trees. Numbers at nodes represent bootstrap values, major clades labeled at nodes.

Biarmosuchus tener
Titanophoneus potens
Gorgonopsia
Anomodontia
Charassognathus gracilis
Dvinia prima
Procynosuchus delaharpeae
Lycosuchus vanderrieti
Glanosuchus macrops
Pristerognathus polyodon
Ictidosaurus angusticeps
Scylacosaurus sclateri
Alopecodon priscus
Pardosuchus whaitsi
Perplexisaurus foveatus
Gorynychus masyutinae
Scylacosuchus orenburgensis
Ophidostoma tatarinovi
Microwhaitsia mendrezi
Ictidochampsa platyceps
Viatkosuchus sumini
Moschowhaitsia vjuschkovi
Theriognathus microps
Chthonosaurus velocidens
Ichibengops munyamadziensis
Hofmeyria atavus
Ictidostoma hemburyi
Mirotenthes digitipes
Annatherapsidus petri
USNM PAL 412421
Akidnognathus parvus
Promoschorhynchus platyrhinus
Olivierosuchus parringtoni
Euchambersia mirabilis
Cerdosuchoides brevidens
Moschorhinus kitchingi
Ictidosuchus primaevus
Ictidosuchoides longiceps
Ictidosuchops rubidgei
Regisaurus jacobi
Urumchia lii
Karenites ornamentatus
Mupashi migrator
Lycideops longiceps
Choerosaurus dejageri
Tetracynodon tenuis
Tetracynodon darti
Scaloposaurus constrictus
Ericiolacerta parva
Silphedosuchus orenburgensis
Nothogomphodon danilovi
Ordosiodon lincheyuensis
Hazhenia concava
Antecosuchus ochevi
Bauria cynops
Traversodontoides wangwuensis
Microgomphodon oligocynus

81
100
EUTHERIODONTIA
99
THEROCEPHALIA
99
96
83
SCYLACOSAURIDAE
52
EUTHEROCEPHALIA
HOFMEYRIIDAE
AKIDNOGNATHIDAE
69
58
91
BAURIOIDEA
70
76
88
55