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

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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.

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

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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.

26   **INTRODUCTION**

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

28   non-mammalian therapsids. Whereas other non-mammalian therapsid groups remained

29   relatively static in terms of niche occupation through time, therocephalians 'reinvented'

30   themselves several times in their history, each time following mass extinctions. The earliest

31   known therocephalians (Lycosuchidae and Scylacosauridae, historically united in the

32   paraphyletic group "Pristerosauria" [Boonstra, 1953]), which are best represented in middle

33   Permian sediments of the Karoo Basin of South Africa, were large-bodied (skull length up to 40

34   cm) predators (Boonstra, 1969; van den Heever, 1980, 1994). Following the extinction of

35   dinocephalians (including the gigantic, carnivorous anteosaurs) at the end of the Capitanian,

36   therocephalians briefly served as the apex predators of the Karoo during the middle–late

37   Permian transition represented by the *Pristerognathus* Assemblage Zone (AZ) (Kammerer,

38   2011; Abdala et al., 2014; Day et al., 2015). However, by the end of the *Pristerognathus* AZ

39   lycosuchids and scylacosaurids were extinct, and the saber-toothed gorgonopsians had taken

40   over as the dominant large-bodied therapsid predators (Smith et al., 2012; Kammerer et al.,

41   2015). The surviving late Permian therocephalians all belong to the subclade Eutherocephalia,

42   which were predominantly small-bodied animals (skull length ≤10 cm), many of which were

43   likely insectivores (Mendrez, 1975; Kemp, 1986; Huttenlocker, 2009). A few eutherocephalians

44   re-evolved large size and inferred macropredatory habits by the end of the Permian (e.g., the

45   whaitsiid *Theriognathus* and the akidnognathid *Moschorhinus*), but these taxa died out as a

46   result of the end-Permian mass extinction (*Moschorhinus* survived the main extinction pulse, but

47   disappears from the record shortly thereafter, making it an example of a 'dead clade walking';

48   Jablonski, 2002; Huttenlocker & Botha-Brink, 2013; Huttenlocker, 2014). Remarkably, despite

49   major losses in the end-Permian mass extinction, therocephalians managed to reinvent

50   themselves yet again, with a moderately successful third act as small-bodied herbivores (the

51   Bauriamorpha) in the Early–Middle Triassic (Sigogneau-Russell & Sun, 1981; Abdala et al.,

52   2014) before the clade was finally lost for good.

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

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

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

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

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

58   and parareptiles from the middle Permian of China and Russia (Li, 2001; Ivakhnenko, 2003). No

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

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

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

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

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

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

65   known only from isolated skull bones).

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

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

68   spectacularly-complete pareiasaurs (Hartmann-Weinberg, 1937), therocephalians were not

69   described from Kotelnich until the 1990s (Tatarinov, 1995a, 1995b, 1997, 1999a, 1999b). Now,

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

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

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

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

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

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

76   age is considered most likely, possibly equivalent with the South African *Tropidostoma* AZ

77   based on anomodont comparisons (Kurkin, 2011). Benton et al. (2012) instead suggested

78   equivalency between the Kotelnich assemblage and the *Pristerognathus* AZ. However, the

79   described therocephalian fauna of Kotelnich is composed entirely of eutherocephalians (which

80   other than *Viatkosuchus* are very small, i.e., <10 cm skull length), not the large scylacosaurids

81   or lycosuchids characteristic of the *Pristerognathus* AZ in South Africa.

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

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

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

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

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

87

88   **Nomenclatural acts**

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

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

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

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

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

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

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

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

97   40DD-A464-621AC01421B6. The online version of this work is archived and available from the

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

99

100   **Institutional abbreviation**

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

102

103 **GEOLOGICAL CONTEXT**

104 The Kotelnich locality is a rich, tetrapod-bearing fossil assemblage in the Kirov Region of

105 European Russia. The first fossils found at this locality were two pareiasaur skeletons collected

106 by the hydrogeologist S. G. Kashtanov in 1933 (Kashtanov, 1934). Subsequent expeditions by

107 A. P. Hartmann-Weinberg (in 1935) and Kashtanov (in 1936) recovered additional pareiasaur

108 material (today all considered referable to *Deltavjatia rossica*; Benton et al., 2012; Tsuji, 2013).

109 Further expeditions by staff of the Paleontological Institute in Moscow occurred between the

110 1940s–1960s, collecting mostly *Deltavjatia* specimens (see, e.g., Efremov & Vjuschkov, 1955).

111 Fossil collection at Kotelnich was renewed in the 1990s and has continued to the present day,

112 most recently through the efforts of the Vyatka Paleontological Museum in Kirov. These more

113 recent (1990s–present) excavations have revealed a substantially more diverse fauna than was

114 previously known, adding an array of anomodont, gorgonopsian, and therocephalian therapsids

115 as well as non-pareiasaurian parareptiles to the list of Kotelnich tetrapods (although *Deltavjatia*

116 remains the numerically dominant taxon; Benton et al., 2012).

117 Several fossiliferous layers are present at Kotelnich; the lowest red beds represent a

118 lacustrine or floodplain system which famously preserves numerous complete, fully articulated

119 skeletons of the mid-sized pareiasaur *Deltavjatia rossica*. This level (the Vanyushonki Member

120 of Coffa [1999]) has also produced the majority of synapsid finds, including spectacular

121 examples such as the complete, articulated specimen of the small gorgonopsian *Viatkogorgon*

122 *ivakhnenkoi* (Tatarinov, 1999a) and a block containing 15 skeletons of the arboreal anomodont

123 *Suminia getmanovi* (Fröbisch and Reisz, 2011). Although most Kotelnich tetrapods are found in

124 the red-brown mudstones at the base of the succession, plants, fish, and highly fragmentary

125 tetrapod remains (primarily isolated teeth) are also present in lenses of later deposition at the

126 top of the section (Benton et al., 2012).

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

128 red beds (Vanyushonki Member). The holotype was discovered in 2008 by I. Shumov, 10.15

129 meters below the marker bed and 413 meters upstream from the village of Nizhnaya Vodskaya.

130 These specimens were mechanically prepared by O. Masyutina and are housed in the

131 collections of the Vyatka Paleontological Museum in Kirov.

132

133 **SYSTEMATIC PALEONTOLOGY**

134 **Synapsida** Osborn, 1903

135 **Therapsida** Broom, 1905

136 **Therocephalia** Broom, 1903

137

138 *Gorynychus* gen. nov.

139

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

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

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

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

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

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

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

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

148

149 *Gorynychus masyutinae* sp. nov.

150 (Figs. 1–11)

151

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

153   **Holotype:** KPM 346–349 (Figs. 1–9), a single individual (skull and cervical vertebrae in

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

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

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

157 347, postcranial elements including remaining half of fifth cervical (precise break, originally

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

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

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

161   **Referred material:** KPM 291 (Figs. 10, 11A–C), a block of fragmentary, disarticulated

162 elements including the anterior portion of a partial right dentary, an isolated incisor, a jugal, at

163 least four vertebrae, several ribs, a fibula, and various indeterminate bone fragments. KPM

164 448/1 (Fig. 11D), an isolated incisor with damaged root.

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

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

167 locality.

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

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

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

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

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

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

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

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

176

177 **DESCRIPTION**

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

179 ornamentation and sutural boundaries on most of the snout and palate (Figs. 2–7). However,

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

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

182 not exposed as prepared), but the subsequent members of the series are badly worn (Fig. 8).

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

184 as an impression (Fig. 9). The more extensive of the two referred specimens is a single block of

185 disarticulated, fragmentary elements (Fig. 10), although most of these elements show good

186 bone preservation (Fig. 11A–C). One of these elements, an isolated incisor with intact crown,

187 can confidently be referred to *Gorynychus masyutinae* based on the presence of very large,

188 curved denticles on its mediodistal edges. The dentary fragment also has a tall, robust

189 symphysis identical to that of the holotype; although it is possible this could represent a

190 gorgonopsian, the only gorgonopsians known from this locality are much smaller and actually

191 have weakly-developed dentary symphyses. Given the absence of any other material that is not

192 consistent with identification as *Gorynychus* and the lack of overlapping elements, this set of

193 fossils is interpreted to be the remains of a single *Gorynychus* individual. An additional isolated

194 tooth (KPM 448/1; Fig. 11D) exhibits the same denticulation and general morphology as those

195 of KPM 348 and KPM 291 (Figs. 2C, 11C) and can also be referred to *Gorynychus masyutinae*.

196

197 *Cranium*

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

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

200 tip of snout to edge of temporal fenestra).

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

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

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

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

205 348 and 349) preserved in association with the skull have root proportions identical to the empty

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

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

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

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

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

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

212   same specimen. The cutting edges of KPM 348 are heavily worn, but this wear is asymmetrical.

213   As shown in Figure 2C, one side of the tooth (it is uncertain whether this is the mesial or distal

214   side) has more of its margin worn down than the other. The same style of asymmetrical wear,

215   but with the sides reversed, is present on KPM 448/1 (Fig. 11D). The isolated incisor of KPM

216   291, by contrast, is relatively unworn (Fig. 11C). It is uncertain whether this is simply due to

217   recent eruption before the death of the animal or from occupying a different position in the tooth

218   row (its crown is shorter and slightly more curved than in KPM 348 or KPM 448/1, which could

219   be because it represents a more posterior tooth position or a lower incisor).

220   The facial surface of the premaxilla is overlain by the maxilla posteriorly, near the point

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

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

223   three foramina are situated in a distinct channel that originates vertically beneath the internarial

224   bar then curves posterolaterally (Fig. 2B). The first and third foramina in this channel are small

225   (<1 mm diameter), but the second is large (1 mm diameter) and situated deep inside the

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

227   the premaxilla. The internarial bar is angled somewhat anteriorly, such that it overhangs the

228   alveolar portion of the premaxilla in lateral view (Fig. 4). The ascending ramus of the premaxilla

229   frames the anterodorsal border of the external naris and terminates near the posterodorsal

230   narial border.

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

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

233   nasal (Figs. 2, 4, 5). The ventral plate of the septomaxilla is situated immediately dorsal to the

234   premaxillary-maxillary suture. Immediately ventral to this plate is a large, ovoid foramen (1.5 mm

235   diameter) that spans the premaxillary-maxillary suture. A weak groove extends anterior to this

236   foramen for the length of the ventral plate of the septomaxilla. The constricted intranarial portion

237   of the septomaxilla separates the main portion of the external naris from the maxillo-

238   septomaxillary foramen. It has a pointed, anteromedially-directed anterior process as is typical

239   of therocephalians, but not an expanded transverse lamina as in gorgonopsians.

240   Posterodorsally, the septomaxilla makes a broad, irregular contribution to the facial portion of

241   the snout. This facial process notably does not make up the entire posterior margin of the

242   external naris—the nasal occupies the posterodorsal narial corner (Fig. 2B).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

258   both mesial and distal edges (Fig. 6). Although these denticles are not as large or exaggeratedly

259   curved as those on the incisors, they still show distinct curvature (unlike the finer, straight

260   serrations on the canine). As for the premaxilla, the palatal surface of the maxilla is for the most

261   part not visible in this specimen.

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

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

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

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

266   anterior margin of the orbit.

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

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

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

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

271   prefrontal terminates in a short process extending between the maxilla and nasal. The prefrontal

272   makes up a large portion (roughly half) of the anterior face of the orbital wall, and appears to

273   exclude the frontal from contacting the lacrimal.

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

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

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

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

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

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

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

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

282   attenuate process terminating below the lacrimal, posterior to the anterior lacrimal margin. This

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

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

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

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

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

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

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

290   postorbital bar, an ascending process of the jugal extends dorsally behind the postorbital.

291   Posterior to the postorbital bar the jugal makes a tall contribution to the subtemporal bar,

292   narrowing posteriorly and curving downwards. In the posterior half of the subtemporal bar, the

293   jugal is bifurcated by an anterior process of the squamosal. The ventral portion of the jugal

294   extends nearly to the back of the skull, and has a weakly bulbous terminus. In addition to being

295   preserved in the holotype, an isolated jugal is present on the referred block (Fig. 10), identifiable

296   by the characteristic subtemporal curvature and well-developed process contributing to the

297   postorbital bar.

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

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

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

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

302   by the jugal).

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

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

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

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

307   the frontal and postorbital is poorly preserved and difficult to interpret, but it appears that the

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

309   den Heever, 1994).

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

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

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

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

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

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

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

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

318   occipital condyle (Fig. 5).

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

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

321   *Lycosuchus* (Fig. 7). The vomer is paired—a distinct mid-vomerine suture is visible in the

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

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

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

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

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

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

328   The palatine is the largest bone of the palate (Fig. 7). It is a topologically complex

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

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

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

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

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

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

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

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

337   palatal, transverse, and quadrate (Fig. 7). The palatal portion of the pterygoid has an

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

365 rostrum.

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

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

368 (Fig. 7). Although tall and blade-like posteriorly, the anterior two-thirds of this complex are

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

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

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

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

373 bone interpreted as the orbitosphenoid, which extends dorsally to contact the frontal-postorbital

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

375 footplate ventrally that sits atop the pterygoid. The ascending process of the epipterygoid

376 narrows dorsally before expanding again at its contact with the ventral face of the parietal. The

377 basal tubera are broadly separated by a median depression (Fig. 7). They are relatively slender

378 and angled medially at their posterior end. The left stapes is preserved in place, extending from

379 the basal tuber to near the quadrate. The stapes is dorsoventrally narrow but anteroposteriorly

380 broad, although narrowing along its length laterally (similar to *Lycosuchus*). No foramen or

381 dorsal process is visible, but these could be obscured by matrix. The basioccipital forms a plate

382 posterior to the basal tubera and terminates in the occipital condyle, which is similar to that of

383 other therocephalians.

384   The dentary is a massive, robust bone with a tall, well-developed, unfused symphysis

385 more similar to that of gorgonopsians than other early therocephalians (Figs. 2, 4, 5, 11A). The

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

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

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

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

390   preserved in the disarticulated dentary fragment in KPM 291 (Figs. 10, 11A). The lower canine

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

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

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

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

395   lower postcanine is exposed on the right mandibular ramus anterior to the upper PC1 in the

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

397   length, versus 4 mm in the uppers) but is otherwise similar in morphology, being 'spade'-shaped

398   with well-developed denticulation. The dentary is constricted behind the symphysis, then

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

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

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

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

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

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

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

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

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

408   rounded, in *Gorynychus* this edge is nearly straight (slightly concave).

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

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

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

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

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

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

415   gorgonopsians in which it is usually widely separated from the articular). The surface structure

416   of the reflected lamina is typical of early therocephalians: an anterodorsal depression becoming

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

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

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

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

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

422   tall, 'ribbon'-like bone occupying the medial face of the anterior portion of the jaw ramus (Fig. 7).

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

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

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

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

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

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

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

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

431   quadrate can be discerned in medial view on the left side (Figs. 4, 7). Although mostly worn off,

432   the base of a large retroarticular process is present.

433

434   *Postcranium*

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

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

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

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

439   and 4 are well-preserved and exposed on both sides (Fig. 8). The cervical vertebrae are

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

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

442   preserved on the right side of the specimen in association with (but disarticulated from) vertebra

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

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

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

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

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

448   immediately above their point of origin but expand dorsally into broad, rounded tips

449   (anteroposteriorly 11 mm long in C3). The axial neural spine is definitely anteroposteriorly

450   broader than that of the subsequent vertebrae (Fig. 8), but its exact dimensions (including

451   height relative to subsequent neural spines) are uncertain due to crushing. An isolated vertebra

452   interpreted as the axis in the referred specimen KPM 291 preserves a tall, broad neural spine

453   (Fig. 10), suggesting that the axial spine was substantially taller and longer than subsequent

454   neural spines, as is typical for theriodonts (Jenkins, 1971). The other vertebrae preserved in

455   KPM 291 have relatively lower, longer centra and shorter neural spines (Fig. 11B) than those of

456   C3 and 4 in the holotype. They likely represent dorsals or even anterior caudals, although most

457   are too poorly preserved to identify with any confidence.

458   The non-vertebral postcranial elements in the holotype are mostly damaged (Fig. 9) The

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

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

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

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

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

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

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

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

467   length of the scapular spine. An elongate bone preserved as part of KPM 291 (Fig. 10) is here

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

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

470   ends, unlike a rib. The morphology of this element is similar to the fibula of other

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

472

473   **PHYLOGENETIC ANALYSIS**

474   *Gorynychus masyutinae* was coded into a recent analysis of therocephalian interrelationships,

475   that of Huttenlocker & Smith (2017). This analysis (available as Supplemental Information)

476   includes 136 discrete-state characters and 58 taxa, including two newly added to the analysis:

477   *Gorynychus masyutinae*, coded based on personal examination of all known specimens, and

478   *Shiguaignathus wangi*, coded based on the figures in Liu & Abdala (2017). Analysis was

479   undertaken using heuristic searching in PAUP* (Swofford, 2002) v.4.0a (build 159), treating

480   *Biarmosuchus tener* as the outgroup. All characters were treated as unordered following

481   Huttenlocker & Smith (2017). Bootstrap analysis was done using "fast" stepwise addition for

482   1000 replicates.

483   1260 most parsimonious trees of length 383 were recovered (consistency index=0.420,

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

485   sister-taxon of Eutherocephalia (i.e., Akidnognathidae+Whaitsioidea+Baurioidea) (Fig. 12). A

486   position outside of Eutherocephalia is supported by the presence of a paired vomer, serrations

487   on all marginal teeth, and teeth on the transverse process of the pterygoid in *Gorynychus* (all of

488   which are typically absent in eutherocephalians) and the absence of a well-developed

489   mandibular fenestra penetrating the jaw in lateral view. The absence of the postfrontal in

490   *Gorynychus* is a character shared with eutherocephalians to the exclusion of lycosuchids and

491   scylacosaurids (although this element is still variably present in some hofmeyriids). The addition

492   of *Gorynychus* adds substantial instability to the analysis of Huttenlocker & Smith (2017),

493   notably with the complete collapse of Whaitsioidea (although a core Hofmeyriidae composed of

494   *Hofmeyria*, *Ictidostoma*, and *Mirotenthes* is retained). Another Kotelnich taxon, *Perplexisaurus*,

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

496   Scylacosauridae and (*Gorynychus*+Eutherocephalia). In previous analyses, *Perplexisaurus* was

497   a highly unstable taxon generally occupying a position somewhere near the base of

498   Eutherocephalia (Huttenlocker & Sidor, 2016; Huttenlocker & Smith, 2017), so its continued

499   lability is not especially surprising.

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

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

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

503   blamed on extensive homoplasy in Eutherocephalia, the mosaic of features present in

504   *Gorynychus*, as well as the need for additional sources of phylogenetic data. Existing

505   phylogenetic data sets for Therocephalia are heavily skewed towards craniodental characters;

506   for example, only 19/136 characters in Huttenlocker & Smith's (2017) analysis are postcranial.

507   Although cranial-focused analyses are typical for Therapsida (an artifact, in part, of preferential

508   collection of skulls by Karoo paleontologists during most of the 20th century), recent analyses of

509   synapsid relationships (e.g., Benson, 2012) have highlighted the importance of bringing more

510   robust sets of postcranial data to bear on phylogenetic problems in this clade. Before such data

511   can be incorporated into therocephalian analyses, however, more basic descriptive work on

512   therocephalian postcrania is needed. Although skeletons are now known for a wide array of

513   taxa, anatomical descriptions are currently available for only a select few (e.g., Kemp, 1986;

514   Fourie & Rubidge, 2009; Botha-Brink & Modesto, 2011; Fourie, 2013).

515

516   **DISCUSSION**

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

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

519   lengths less than 10 cm. The only other Kotelnich predators approaching *Gorynychus* in size

520   are the eutherocephalian *Viatkosuchus* (co-occurring with *Gorynychus* in the Vanyushonki

521   Member) and the burnetiamorph *Proburnetia* (known only from the holotypic mould from the

522   younger Sokol'ya Gora site) (Ivakhnenko, 2011; Benton et al., 2012). This situations parallels

523   that of middle–earliest late Permian faunas in South Africa (the *Tapinocephalus* and

524   *Pristerognathus* AZs), wherein the only gorgonopsians are small animals and therocephalians

525   are the larger-bodied predators (Kammerer, 2014). The Kotelnich predatory fauna is particularly

526   comparable to that of the *Pristerognathus* AZ; in the middle Permian *Tapinocephalus* AZ,

527   although large-bodied therocephalians were abundant, the apex predators were gigantic

528   anteosaurian dinocephalians. The extinction of anteosaurs at the end of the Capitanian left a

529   depauperate fauna with therocephalians momentarily atop the food chain (Day et al., 2015). It

530   was only following the later extinction of these basal therocephalians that gorgonopsians began

531   to diversify and cemented their position as the dominant large-bodied therapsid predators

532   (Kammerer et al., 2015).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

556   possibly *Perplexisaurus*) and potential early representatives of known eutherocephalian families

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

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

559   only later migrated to the basin.

560

561   **CONCLUSIONS**

562   Based on a complete skull and partial skeleton and two additional, fragmentary specimens, a

563   new therocephalian taxon, *Gorynychus masyutinae*, is described from the (probably) earliest

564   late Permian Kotelnich locality of Russia. *Gorynychus* is the largest known predatory tetrapod in

565   the Kotelnich assemblage, and demonstrates that therocephalians acted as top predators in

566   Russian as well as South African assemblages during the transition between typical middle and

567   late Permian terrestrial communities. Although falling outside of Eutherocephalia, *Gorynychus* is

568 more closely related to eutherocephalians than to the large-bodied therocephalian predators of

569 southern Africa (and possibly earlier Permian assemblages in Russia, if *Porosteognathus* from

570 the middle Permian Isheevo fauna truly is a scylacosaurid). The Kotelnich therocephalian fauna

571 shows greater diversity of eutherocephalians than probable coeval faunas in South Africa, and

572 suggests that initial diversification in this clade probably was not occurring in the Karoo Basin.

573

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578

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757   FIGURE CAPTIONS

758

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

760   up the majority of the holotype shown in articulation. Holotype also includes two incisor teeth

761   (KPM 348 and 349) disarticulated from the skull but found in association (see Figs. 2C and

762   10D). Scale bar equals 5 cm. Photograph by Christian F. Kammerer. [planned for page width]

763

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

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

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

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

768   coloration indicates matrix. Scale bars equal 1 cm. Photographs and drawing by Christian F.

769   Kammerer. [planned for page width]

770

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

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

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

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

775   indicates eroded or broken bone surface. Scale bar equals 1 cm. Photograph and drawing by

776   Christian F. Kammerer. [planned for page width]

777

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

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

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

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

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

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

784 indicates eroded or broken bone surface. Scale bar equals 1 cm. Photograph and drawing by

785 Christian F. Kammerer. [planned for page width]

786

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

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

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

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

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

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

793 surface. Scale bar equals 1 cm. Photograph and drawing by Christian F. Kammerer. [planned

794 for page width]

795

796 **Figure 6. Postcanine morphology of *Gorynychus masyutinae*.** Left PC1–3 in lateral view.

797 PC2 is in the process of erupting. Scale bar equals 1 cm. Photograph by Christian F.

798 Kammerer. [planned for column width]

799

800 **Figure 7. Holotype of *Gorynychus masyutinae* in ventral view.** (A) Photograph and (B)

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

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

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

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

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

806 indicates matrix. Scale bar equals 1 cm. Photograph and drawing by Christian F. Kammerer.

807 [planned for page width]

808

809 **Figure 8. Cervical vertebrae of *Gorynychus masyutinae* (KPM 346–347).** (A) Photograph

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

811 cervical rib; ic, intercentrum; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis;

812 sf?, possible skull fragment; tp, transverse process. Gray coloration indicates matrix. Scale bar

813 equals 5 cm. Photograph and drawing by Christian F. Kammerer. [planned for page width]

814

815 **Figure 9. Postcranial elements of *Gorynychus masyutinae* (KPM 347).** (A) Photograph and

816 (B) interpretive drawing. Abbreviations: ?, unknown bone; c, cervical vertebra; cl?, possible

817 clavicle; ri, rib; sc, scapulocoracoid; ve, vertebra. Gray coloration indicates matrix. Scale bar

818 equals 5 cm. Photograph and drawing by Christian F. Kammerer. [planned for page width]

819

820 **Figure 10. KPM 291, a block containing disarticulated elements referred to *Gorynychus***

821 ***masyutinae.*** (A) Photograph and (B) interpretive drawing. Abbreviations: ax, axis vertebra; d,

822 dentary; i, incisor; po?, postorbital?; r, rib; ve, vertebra. Elements marked with asterisks are

823 shown in greater detail in Figure 10. Scale bar equals 5 cm. Photograph and drawing by

824 Christian F. Kammerer. [planned for page width]

825

826 **Figure 11**. **Disarticulated elements of *Gorynychus masyutinae.*** (A–C) are highlighted

827 elements of KPM 291 (see Fig. 9): (A) Anterior portion of right dentary preserving lower canine;

828 (B) ?dorsal vertebra; and (C) incisor tooth. (D) is another isolated incisor (KPM 448/1). Scale

829 bars equal 1 cm. Photographs by Christian F. Kammerer. [planned for page width]

830

831 **Figure 12. Cladogram showing phylogenetic position of *Gorynychus masyutinae.*** Strict

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

833 major clades labeled at nodes. Image by Christian F. Kammerer [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). Scale bar equals 5 cm. Photograph by Christian F. Kammerer.

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 bars equal 1 cm. Photographs and drawing by Christian F. Kammerer.

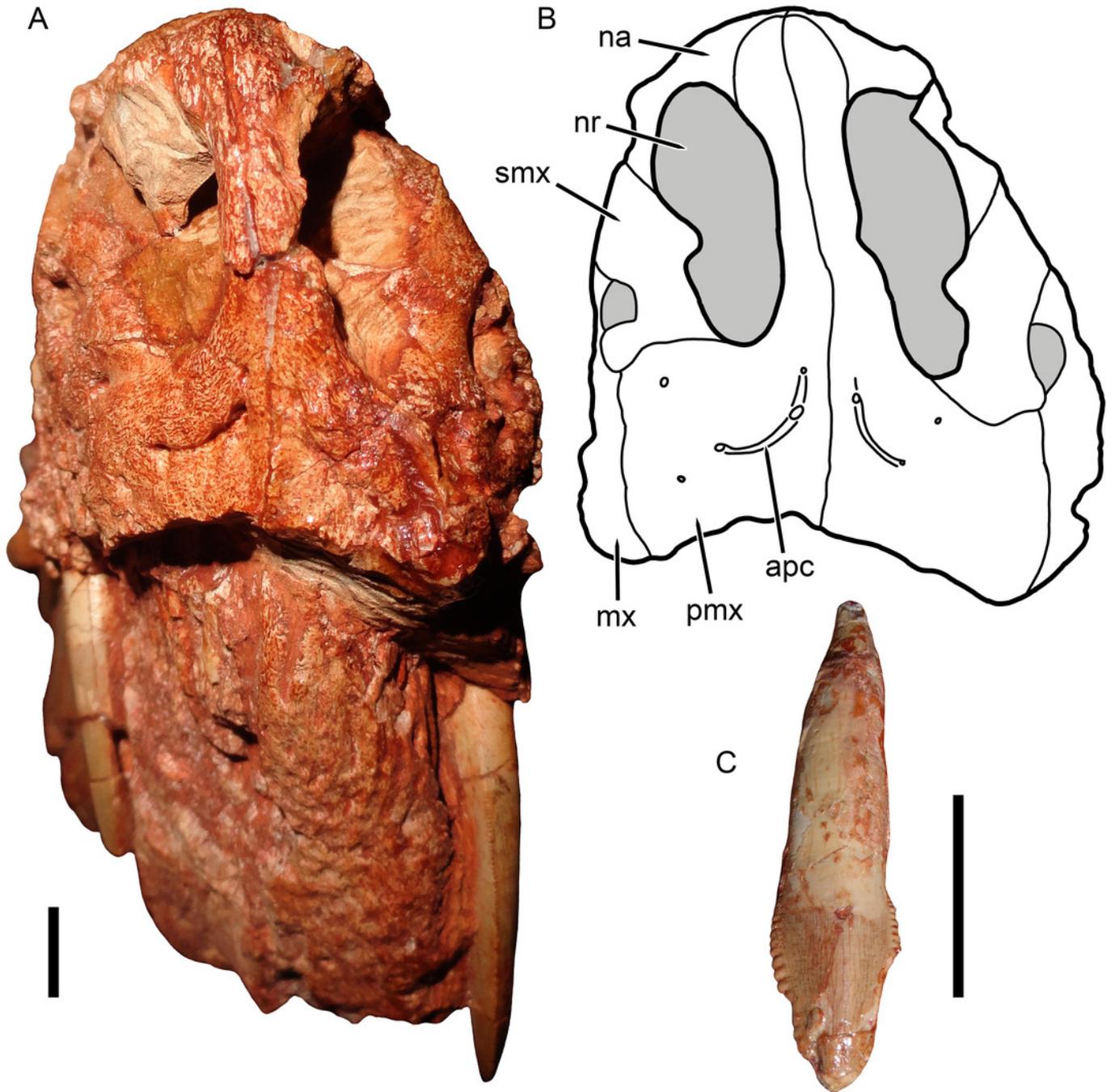



Figure 3

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. Photograph and drawing by Christian F. Kammerer.

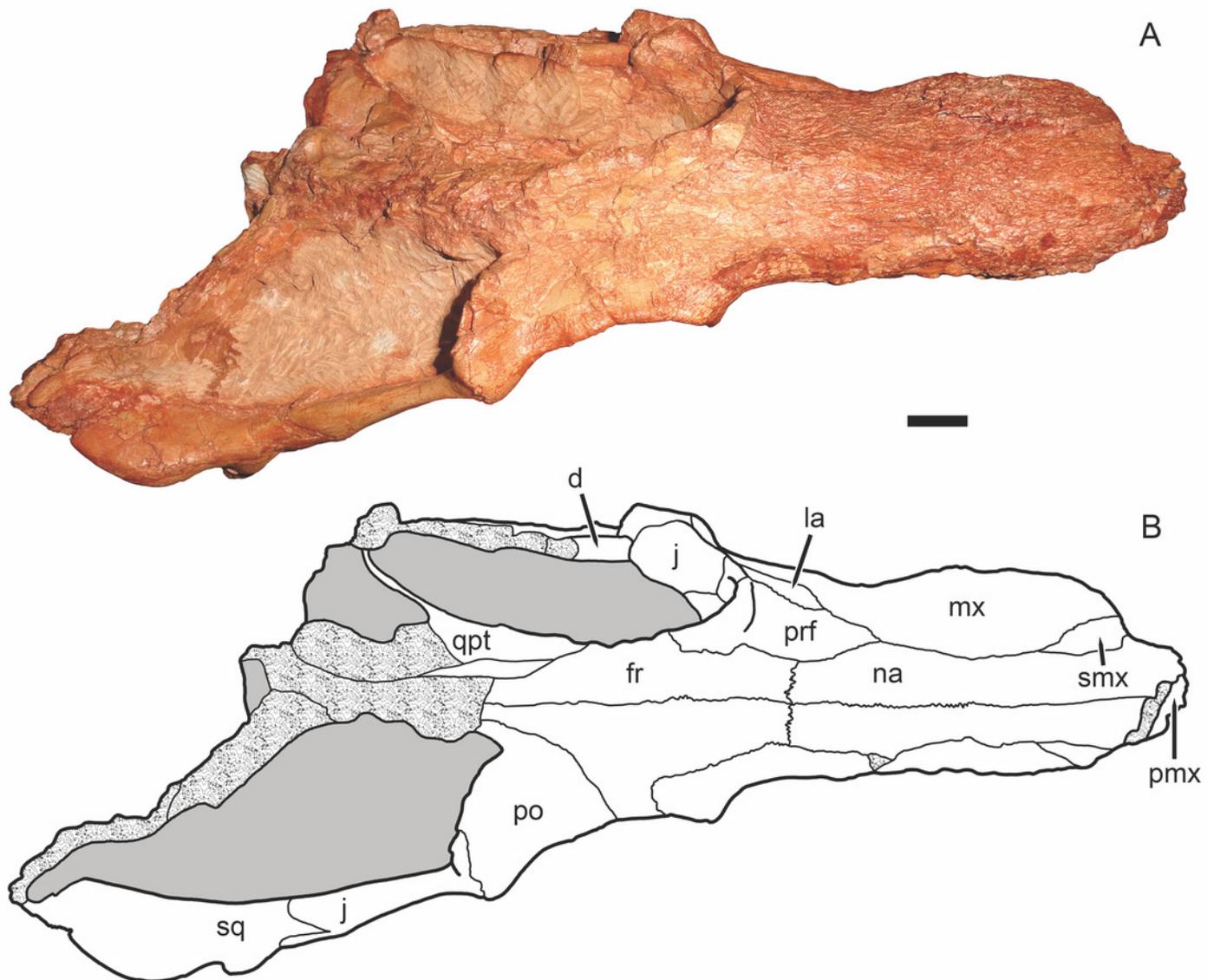



Figure 4

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. Photograph and drawing by Christian F. Kammerer.

A

B

na

smx

po fr

prf

ss sq

j

la

mx

co

q-qj

sa

C

PC3

pmx

ar

rla

d

i2

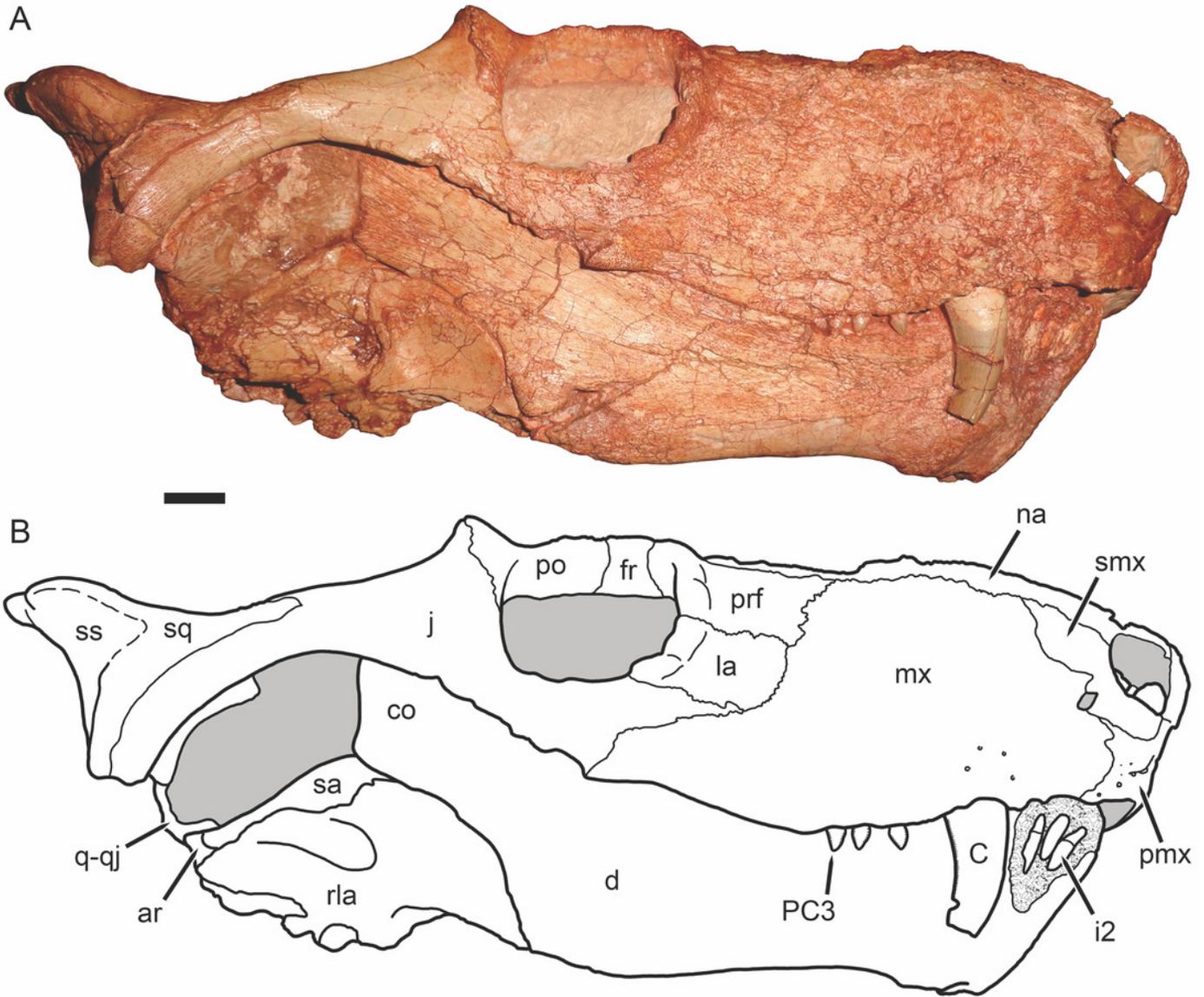



Figure 5

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. Photograph and drawing by Christian F. Kammerer.

A

B

na

fr

prf

po

smx

la

os

pa

mx

qpt

j

ept

pmx

co

sa

C

PC3

d

rla

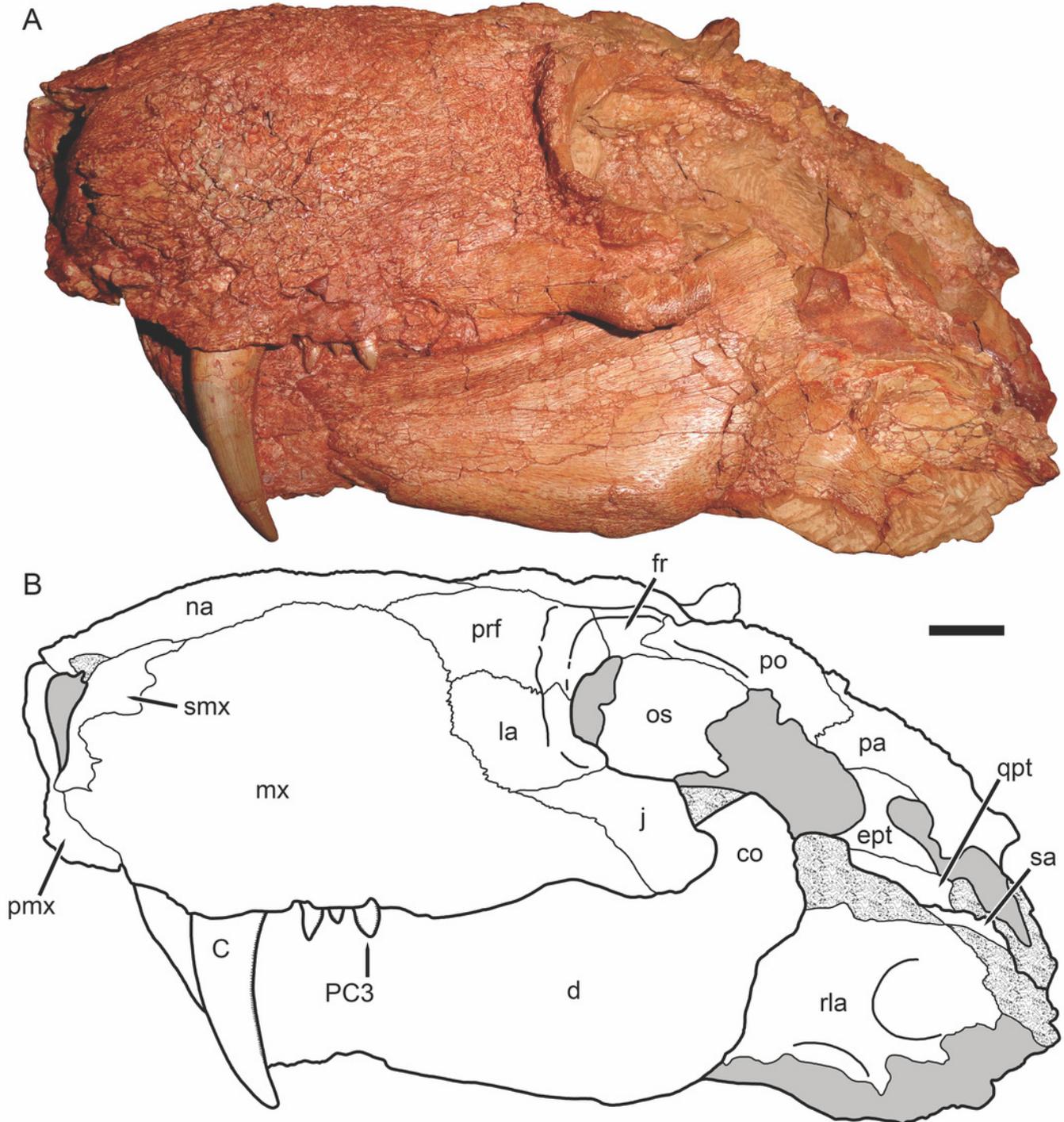



Figure 6

Postcanine morphology of *Gorynychus masyutinae*.

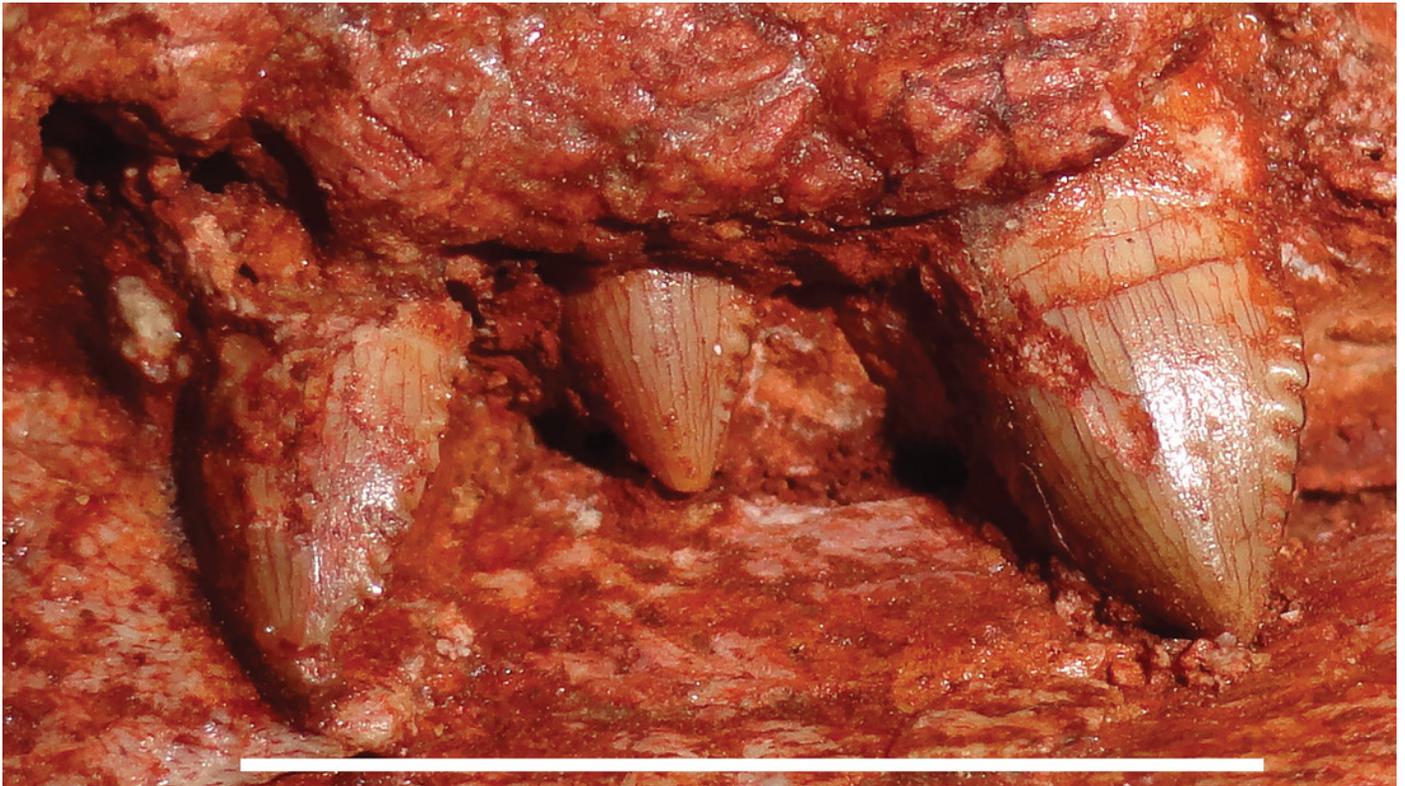
Left PC1–3 in lateral view. PC2 is in the process of erupting. Scale bar equals 1 cm.

Photograph by Christian F. Kammerer.

Figure 7

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. Photograph and drawing by Christian F. Kammerer.

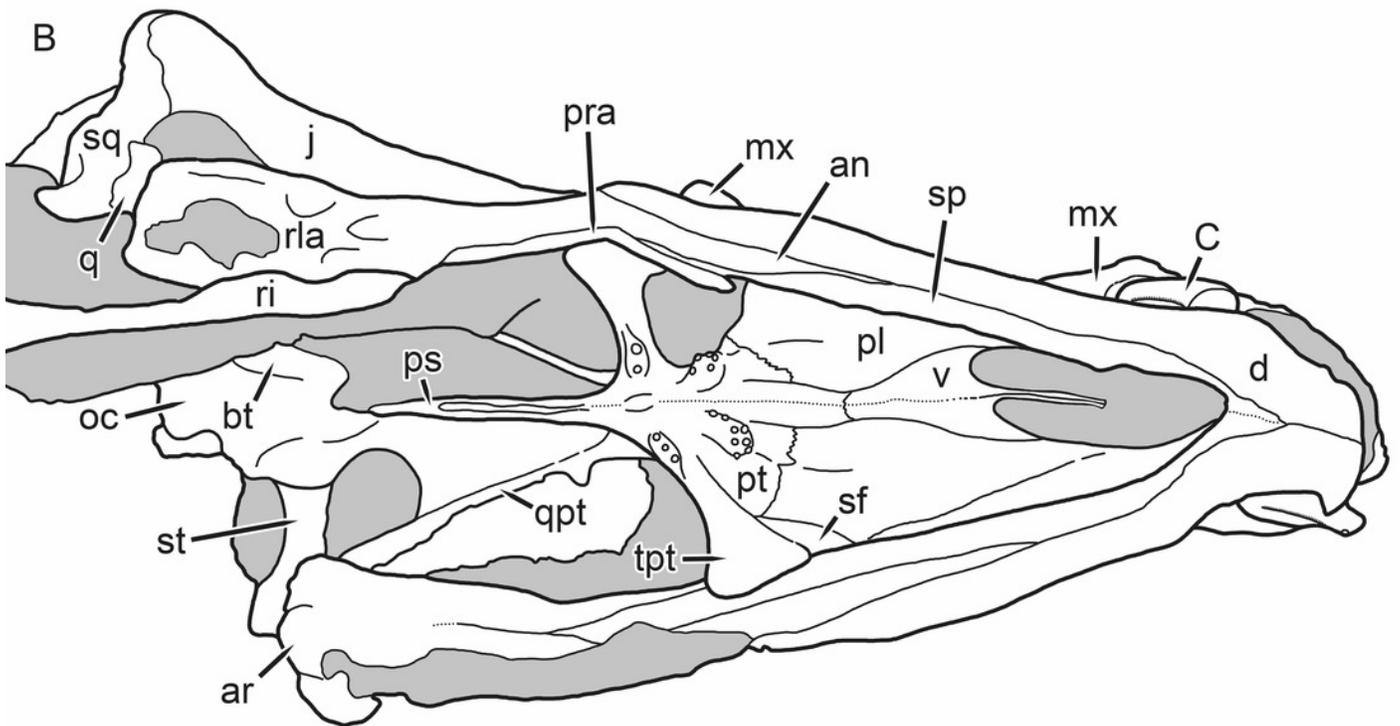
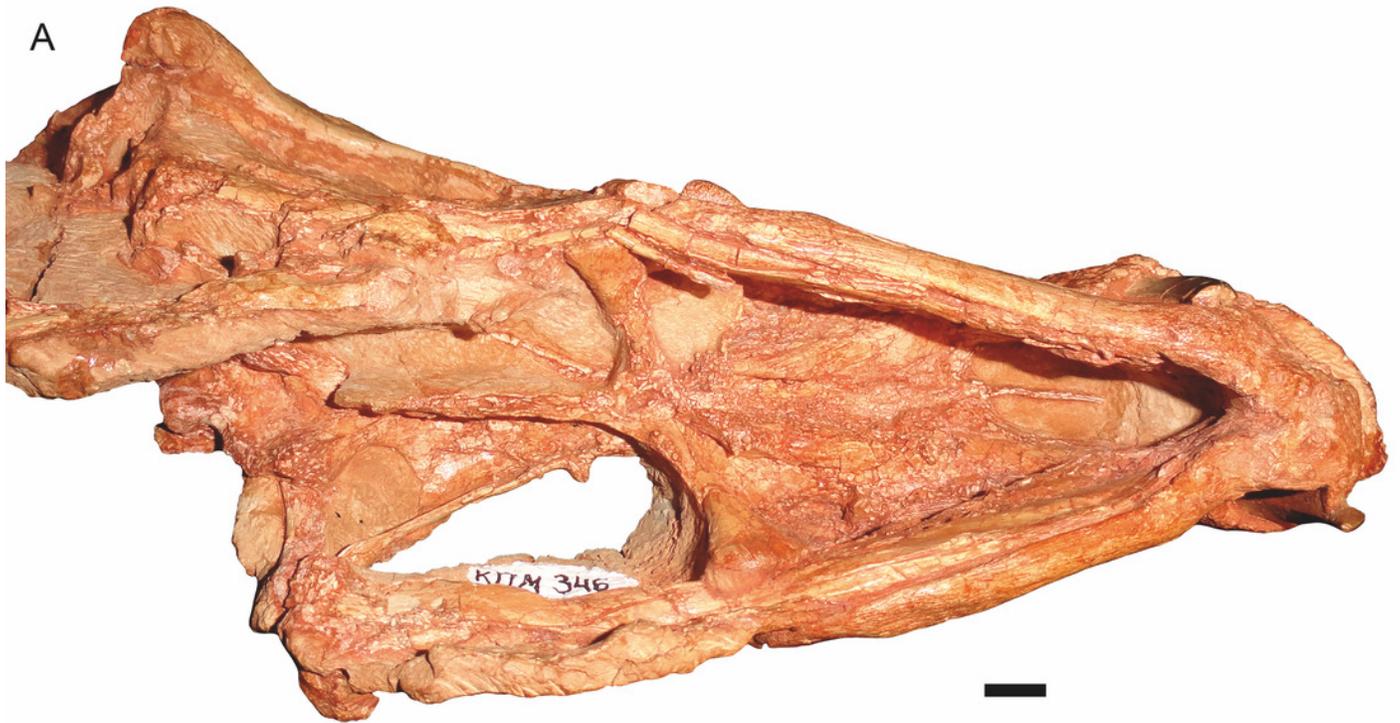



Figure 8

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. Photograph and drawing by Christian F. Kammerer.

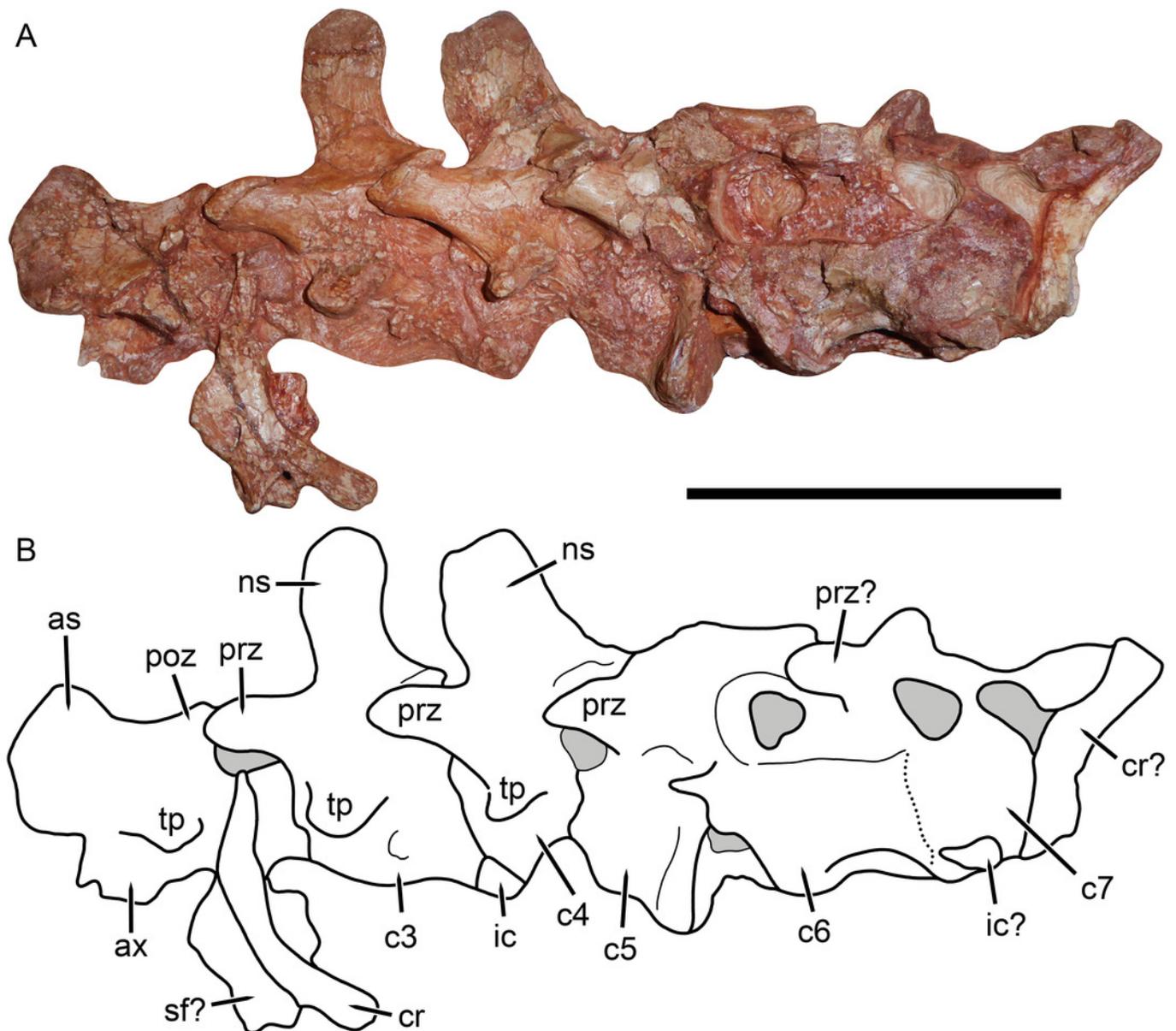



Figure 9

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. Photograph and drawing by Christian F. Kammerer.

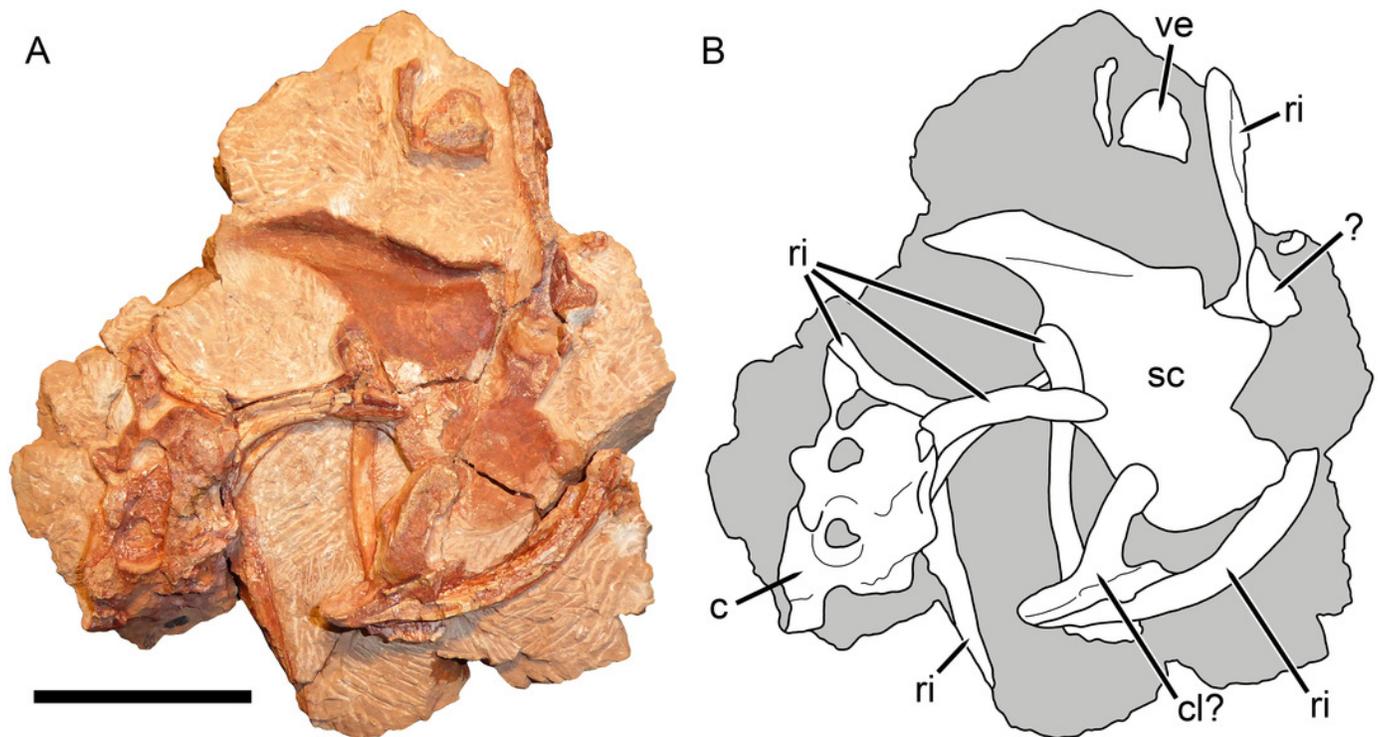



Figure 10

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. Photograph and drawing by Christian F. Kammerer.

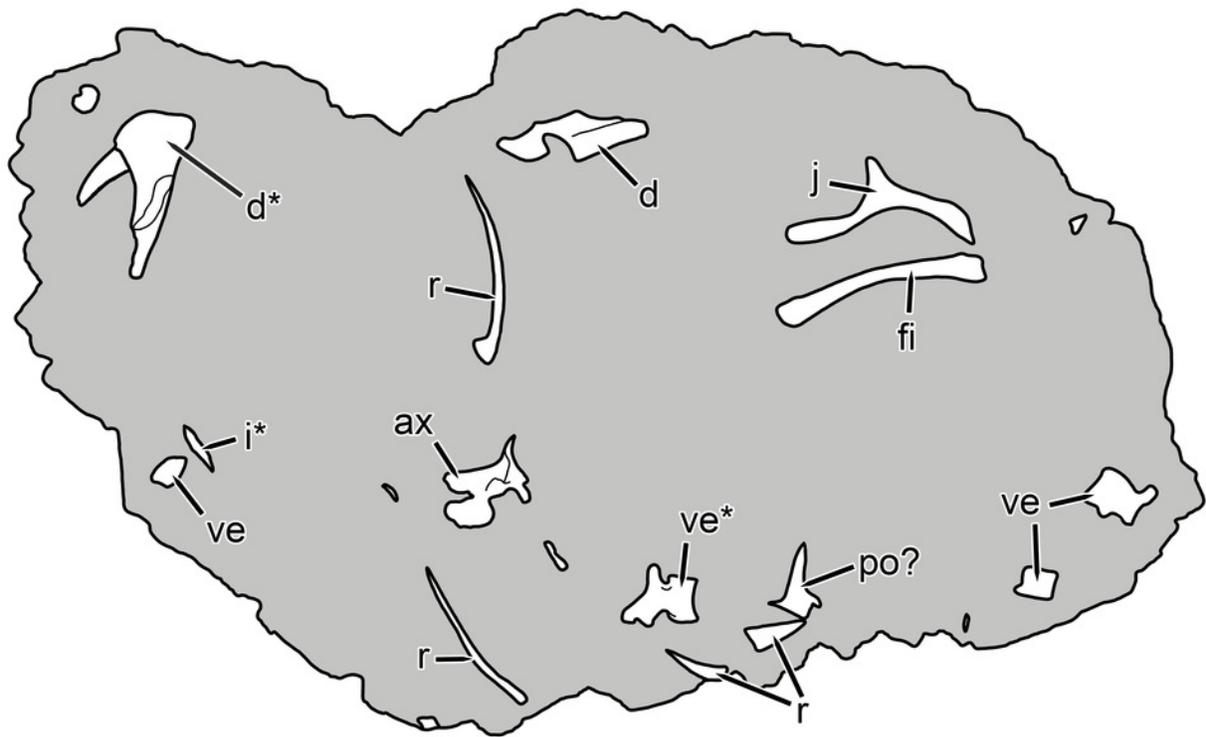



Figure 11

Disarticulated elements of *Gorynychus masyutinae*.

(A–C) are highlighted elements of KPM 291 (see Fig. 9): (A) Anterior portion of right dentary preserving lower canine; (B) ?dorsal vertebra; and (C) incisor tooth. (D) is another isolated incisor (KPM 448/1). Scale bars equal 1 cm. Photographs by Christian F. Kammerer.

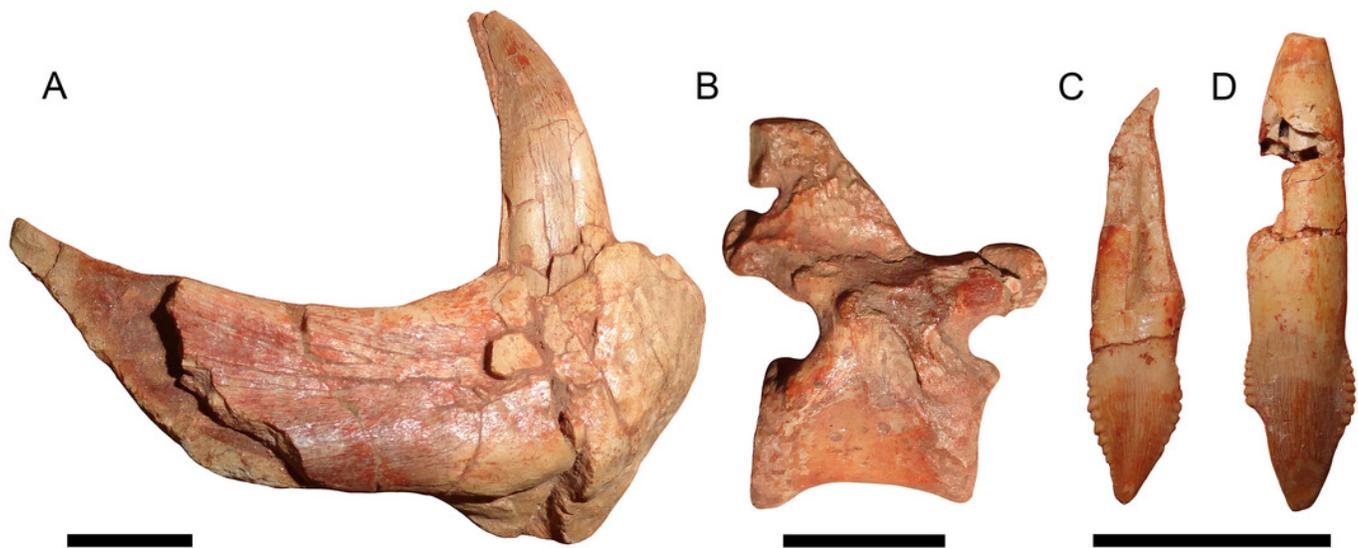



Figure 12

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. Image by Christian F. Kammerer.

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
Shiguaignathus wangi
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

EUTHERIODONTIA

THEROCEPHALIA

SCYLACOSAURIDAE

HOFMEYRIIDAE

EUTHEROCEPHALIA

AKIDNOGNATHIDAE

BAURIOIDEA

100
99
51
96
85
65
53
90
67
79
89
56