A new moradisaurine captorhinid reptile (Amniota: Eureptilia) from the upper Permian of India

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Upper Permian rocks of the former supercontinent Gondwana record climax late Paleozoic terrestrial vertebrate faunas that were dominated numerically and ecologically by therapsid synapsids. Older faunal elements of earlier Paleozoic faunas, such as captorhinid reptiles, are rare and scattered components of the first amniote faunas to inhabit high-latitude regions. Here we describe a new genus and species of moradisaurine captorhinid that represents an archaic faunal element of the high-fibre herbivore fauna of the late Permian of what is now peninsular India. The presence of a relatively broad parietal and three rows of conical teeth on the maxilla and the dentary distinguishes *Indosauriscus kuttyi* gen. et sp. nov. from other moradisaurines. The hypodigm of *I. kuttyi* comprises skulls that range in length from 39 mm to 54 mm, and high ossification of the braincase elements and well developed skull-roof sutures, indicate that *I. kuttyi* adults were smaller than those of most moradisaurines. Results of our phylogenetic analyses suggest that moradisaurines, despite appearing first in the paleotropics, dispersed into temperate, high-latitude regions of Pangea early in their evolutionary history. Moradisaurines in dicynodont-dominated faunas, viz. *Indosauriscus kuttyi* and *Gansurhinus naobaogouensis*, were the smallest high-fibre herbivores in their respective faunas. This suggests that small body size may have evolved in these moradisaurines as they co-evolved with the more numerous and diverse dicynodont therapsids.

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17

18 Abstract

19

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21 terrestrial vertebrate faunas that were dominated numerically and ecologically by therapsid

22 synapsids. Older faunal elements of earlier Paleozoic faunas, such as captorhinid reptiles, are

23 rare and scattered components of the first amniote faunas to inhabit high-latitude regions. Here

24 we describe a new genus and species of moradisaurine captorhinid that represents an archaic

25 faunal element of the high-fibre herbivore fauna of the late Permian of what is now peninsular

26 India. The presence of a relatively broad parietal and three rows of conical teeth on the maxilla

27 and the dentary distinguishes *Indosauriscus kuttyi* gen. et sp. nov. from other moradisaurines.

28 The hypodigm of *I. kuttyi* comprises skulls that range in length from 39 mm to 54 mm, and high

29 ossification of the braincase elements and well developed skull-roof sutures, indicate that *I.*

30 *kuttyi* adults were smaller than those of most moradisaurines. Results of our phylogenetic

31 analyses suggest that moradisaurines, despite appearing first in the paleotropics, dispersed into

32   temperate, high-latitude regions of Pangea early in their evolutionary history. Moradisaurines in

33   dicynodont-dominated faunas, viz. *Indosauriscus kuttyi* and *Gansurhinus naobaogouensis*, were

34   the smallest high-fibre herbivores in their respective faunas. This suggests that small body size

35   may have evolved in these moradisaurines as they co-evolved with the more numerous and

36   diverse dicynodont therapsids.

37

38

39   **Subjects** Anatomy, Evolutionary Studies, Paleontology

40   **Keywords** Captorhinidae, Moradisaurinae, high-fibre herbivory, Reptilia

41

42   Introduction

43

44   Captorhinid reptiles are one of the great success stories of early amniote evolutionary history.

45   These reptiles arose near the end of the Carboniferous Period (Müller & Reisz, 2005; Reisz,

46   Haridy & Müller, 2016), approximately 300 million years ago, and over the next 40+ million

47   years they diversified into a variety of faunivorous, omnivorous, and herbivorous forms (Clark &

48   Carroll, 1973; Dodick & Modesto, 1995; Sumida et al., 2010; Modesto, Scott & Reisz, 2018).

49   The last surviving captorhinids were contemporaneous to, or minor faunal elements of, late

50   Permian terrestrial vertebrate faunas that were dominated by therapsid synapsids (Taquet, 1969;

51   Kutty, 1972; Gaffney & McKenna, 1979; Modesto & Smith, 2001). Over the course of their

52   evolutionary history, captorhinids seemingly dispersed from the crucible of amniote origins in

53   paleotropical Euramerica across the world, with captorhinid remains reported from all continents

54   except Australia and Antarctica (Vjushkov & Chudinov, 1957; Kutty, 1972; Heaton, 1979; Gow,

55   2000; Reisz, Haridy & Müller, 2016; Cisneros et al., 2020).

56   One of the hallmarks of evolutionary history of these early reptiles is the acquistion of high-

57   fibre herbivory in the captorhinid clade Moradisaurinae (de Ricqlès & Taquet, 1982; Dodick &

58   Modesto, 1995; Reisz et al., 2011). Phylogenetic studies suggest that moradisaurines arose

59   during the Cisuralian (early Permian) in the paleotropics of what is now North America (Dodick

60   & Modesto, 1995; Modesto et al., 2016), dispersed during by the Guadalupian (middle Permian)

61   throughout what is now Europe and Asia (Vjushkov & Chudinov, 1957; Reisz et al., 2011; Liu,

62 2023; Matamales-Andreu et al., 2021, 2023), and by the early Lopingian (late Permian) had

63 reached paleo-high-latitude areas in what is now India (Mueller et al., 2007).

64   The presence of captorhinids in India was reported first by Kutty (1972) in a brief description

65 of a therapsid-dominated fauna from upper Permian rocks of the Pranhita-Godavari Valley.

66 Although this captorhinid material represents the only non-dicynodont member of the Pranhita-

67 Godavari fauna, it generated little interest apart from its biostratigraphic value (Ray, 1999, 2000;

68 Ray & Bandyopadhyay, 2003), and it was recognized as moradisaurine only relatively recently

69 (Mueller et al., 2007). This material comprises five skulls and associated elements of the anterior

70 part of the postcranial skeleton. In light of recent advancements in our knowledge of the anatomy

71 of moradisaurine captorhinids (Reisz et al., 2011; Modesto, Lamb & Reisz, 2014; Modesto et al.,

72 2019; LeBlanc et al., 2015; Sidor et al., 2022; Liu, 2023; Matamales-Andreu et al., 2023), we

73 describe the Indian moradisaurine in detail here, investigate its phylogenetic relationships, and

74 discuss its implications for moradisaurine evolution.

75

76 Materials and Methods

77

78 **Materials**

79

80 ISIR 232, ISIR 233, ISIR 234, ISIR 235, and ISIR 236, all reposited in the Geology

81 Museum, Indian Statistical Institute, Kolkata, India, were prepared using standard mechanical

82 methods.

83

84 **Geological setting**

85

86 The Gondwana succession in the Pranhita-Godavari Valley is represented by thick sequences of

87 fluvial-lacustrine sediments, ranging in age from Permian to Cretaceous (King, 1881). Ray

88 (1997) studied the depositional systems of the Permo-Triassic rocks and recognized three

89 formations in ascending order: Barakar, Kundaram, and Kamthi. The captorhinid material was

90 recovered from the Kundaram Formation in the northwestern part of the valley (Kutty, 1972)

91 near the village of Golet in Adilabad district, Andhra Pradesh (Fig. 1). The Kundaram Formation

92 is a typical redbed sequence of fluvial deposits consisting of intercalated layers of red mudstone,

93 sandstone, and ferruginous shale. As in all fluvial deposits, the cross-bedded sandstone unit of

94 the Kundaram Formation represents the channel-related facies, whereas the finer siltstone and

95 mudstone units represent the overbank facies accumulated in floodplain environments (Ray,

96 1997). The ferruginous mudstone units are generally fossiliferous and have yielded exclusively

97 terrestrial amniotes such as dicynodonts. The fossils are mostly found enclosed in hard ironstone

98 nodules scattered on the surface (Kutty, 1972).

99

100 **Nomenclatural act**

101

102 The electronic version of this article in Portable Document Format (PDF) will represent a

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

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

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

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

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

108 through any standard web browser by appending the LSID to the prefix http://zoobank.org/.

109 Publication LSID is urn:lsid:zoobank.org:pub:47E6FA4C-AF21-40C3-8925-84B3CC374357.

110 The online version of this work is archived and available from the following digital repositories:

111 PeerJ, PubMed Central SCIE and CLOCKSS.

112

113 **Source of phylogenetic tree**

114

115 We used the data matrix of Sidor et al. (2022), which is the most recent cladistic evaluation of

116 moradisaurine interrelationships. Mesquite (Maddison & Maddison, 2023) was used to score the

117 Indian moradisaurine for the 76 phylogenetic characters of Sidor et al. (2022). To this we added

118 Albright, Sumida & Jung's (2021) character 1 (Adult/mature skull length), enumerated here as

119 character 77, and two new characters (78 and 79, see Supplemental File 2). The Mesquite file

120 (available as Supplemental File 1) was then imported into PAUP* (Swofford, 2021) and the

121 matrix was processed by a heuristic search. Multistate taxa were interpreted as uncertainty,

122 starting tree(s) were obtained via stepwise addition, and tree-bisection-reconnection was

123 employed as the branch-swapping algorithm. We ordered 7 characters (see Supplemental File 2).

124   following the suggetion of Rineau et al. (2015) that ordering 'clinal' characters increases the

125   resolving power of the analysis. A bootstrap analysis of 1,000 iterations was also conducted, and

126   Bremer decay values were determined by rerunning heuristic searches after adding a single step

127   to the shortest tree, instructing PAUP* to calculate the strict consensus tree for the resulting

128   trees; this procedure was repeated until there was no phylogenetic resolution in the ingroup, and

129   then the number of steps required to collapse each clade was determined by comparing this series

130   of consensus trees with the shortest tree.

131

132   Systematic Paleontology

133

134   EUREPTILIA Olson, 1947

135   CAPTORHINIDAE Case, 1911

136   MORADISAURINAE de Ricqlès & Taquet, 1982

137

138   Genus *Indosauriscus* nov.

139   urn:lsid:zoobank.org:act:DD1D0B12-FBE7-4A29-9EE7-2C5E772D8C01

140

141   **Diagnosis.** A small species of moradisaurine captorhinid reptile, characterized by the presence of

142   only three rows of conical teeth on the maxilla and the dentary, and a parietal that is relatively

143   broad, with the transverse breadth of the bone measuring three-quarters its anteroposterior

144   length.

145

146   **Etymology.** After the Republic of India; the Ancient Greek σαῦρος, for 'lizard'; and the

147   diminutive Latin suffix '*-iscus*'. The gender is masculine.

148

149   *Indosauriscus kuttyi* sp. nov.

150   urn:lsid:zoobank.org:act:853DC754-A6F3-4AE0-BE95-3C4C40334C36

151

152   **Holotype.** ISIR 233, skull with maxillae and lower jaw attached.

153

154   **Referred specimens.** ISIR 232, partial skull (Kutty, 1972); ISIR 234, skull fragment showing

155   tooth battery; ISIR 235, partial skull and mandible slightly distorted; ISIR 236, skull and

156   mandible with some postcranial elements attached; ISIR 237, snout portion only.

157

158   **Horizon and locality.** Near the village of Golet, Adilabad district, Andhra Pradesh, India (Fig.

159   1). Kundarum Formation; upper Permian; homotaxial to the *Tropidostoma-Gorgonops* and/or

160   *Cistecephalus* assemblage zones of the Karoo Basin, South Africa (Ray, 1999; Smith et al.,

161   2020), which together range in age from 259.3 to 255.2 Ma (Rubidge et al., 2013).

162

163   **Diagnosis.** As for genus, this being the only known species.

164

165   **Etymology.** The specific epithet honours T. S. Kutty, in recognition of his contributions to

166   vertebrate palaeontology.

167

168   Description

169

170   *Indosauriscus kuttyi* has the typical captorhinid apomorphies of the procumbent snout with large

171   premaxillary dentition, the tranversely expanded temporal region, the large occipital flange of the

172   squamosal, the absence of the tabular bone and the transversely expanded postparietal bone, the

173   greatly reduced supratemporal bone, and the large stapes. The Indian captorhinid shares

174   distinctive ridge-and-pit sculpturing of the skull roof and mandible with well documented taxa

175   such as *Captorhinus laticeps*, *Captorhinus aguti*, *Labidosaurus hamatus*, *Labidosaurikos*

176   *meachami*, *Moradisaurus grandis*, and *Tramuntanasaurus tiai* (Heaton, 1979; de Ricqlès &

177   Taquet, 1982; Dodick & Modesto, 1995; Modesto et al., 2007; Matamales-Andreu et al., 2023).

178   Assignment to Moradisaurinae is based on the presence of multiple rows of bullet-shaped teeth

179   on the maxilla and the dentary (Reisz et al., 2011). The reduction in palatal dentition, the

180   enlarged contact between the parasphenoid and the stapes, the increased height of the

181   quadratojugal bone, and the contribution of the postparietal bone to the skull roof are all

182   apomorphies shared with *Labidosaurikos meachami*, *Moradisaurus grandis*, and/or *Rothianiscus*

183   *multidontus* among moradisaurines, and suggest that *Indosauriscus* is nested more deeply in

184   Moradisaurinae than *Captorhinikos valensis* and *Sumidadectes chozaensis* (formerly

185 "*Captorhinikos chozaensis*": Jung & Sues, 2024). A reconstruction of the skull of *Indosauriscus*

186 *kuttyi* is shown in Fig. 2. It is based mainly on ISIR 233 with supplementary information from

187 ISIR 232.

188

189 **Ontogenetic age**

190 The skulls range in length from 39 mm to 54 mm. These skulls are remarkably small for

191 moradisaurines, which regularly exceeded 250 cm in total length, e.g. 265 mm in *Rothianiscus*

192 *multidontus*, 410 mm in *Moradisaurus grandis*, and 280 mm in *Labidosaurikos meachami*

193 (Olson & Beerbower, 1953; de Ricqlès & Taquet, 1982; Dodick & Modesto, 1995). The

194 absolutely small size of the Indian captorhinids might, therefore, be indicative of a young

195 ontogenetic age. There is, however, a suite of features that support the inference of skeletal

196 maturity. One of these is the level of suture development on the skull roof, particularly the

197 conspicuous interfingering contacts between the frontals and the nasals, between the frontals and

198 the parietals, and between the two frontals in the largest skull, ISIR 233 (skull length of 54 mm),

199 are highly suggestive that this specimen is an adult individual. The second item of evidence for

200 skeletal maturity is the observation of ISIR 233 that the premaxillary process of the nasal extends

201 ventrally along the dorsal process of the premaxilla and forms the anterior margin of the external

202 naris. This distinctive morphology is seen also in large specimens of *Captorhinus laticeps* (figure

203 12 in Heaton, 1979) and in *Labidosaurus hamatus* (figure 3a in Modesto et al., 2007), and we

204 have seen the same in large specimens of *Captorhinus* sp. from Richards Spur, Oklahoma

205 (R.R.R. and S.P.M., pers. obsv.); we have not found this morphology in smaller, subadult

206 specimens of these species. The presence of this morphology in ISIR 233, the largest specimen

207 in the hypodigm of *Indosauriscus kuttyi*, is the third feature that indicates that this specimen is

208 skeletally mature. Finally, ISIR 232 preserves a well-ossified braincase with well developed

209 sutures among the opisthotics and the basi- and exoccipitals; the supraoccipital, which is well

210 ossified, is detached from the rest of the braincase, but ISIR 232 has been compressed obliquely,

211 and this element appears that it would fit firmly in its expected position dorsal to the opisthotics

212 and the basi- and exoccipitals. Related to this observation, the recent description of a small skull

213 of *M. grandis* suggests that the braincase is the last region of the skull to coalesce in that

214 moradisaurine (Sidor et al., 2022). Accordingly, the superb ossification of the braincase of ISIR

215 233 is another feature that suggests strongly that the largest specimens of *Indosauriscus kuttyi*

216 are skeletally mature.

217

218 **Skull and mandible**

219 The premaxillae of ISIR 233 are well preserved and in perfect articulation with neighboring

220 elements (Fig. 3). They show that the premaxilla of *Indosauriscus kuttyi* is similar to that of

221 *Captorhinus aguti* and many other captorhinids in exhibiting is anteroventrally-inclined alveolar

222 ridge that houses a conspicuously large tooth in the first tooth position. Three smaller teeth are

223 present posterior to the first tooth. All premaxillary teeth are slightly recurved posteriorly. The

224 dorsal process contacting the nasal bears an acute alary process that is subequal in length to the

225 midline process (Fig. 3D).

226 The septomaxilla is an irregularly shaped element that is set into the posterior half of the

227 external naris (Figs. 3B, 3C and 3D). It contacts the lacrimal and the nasal dorsally and the

228 maxilla ventrally, and with the lacrimal and the maxilla forms the septomaxillary foramen (Fig.

229 3D). The free anterior edge of the septomaxilla is deeply incised, producing a keyhole-shaped

230 profile for the deeper part of the external naris.

231 The nasal is a slightly curved sheet of bone that forms most of the roof of the snout. In dorsal

232 aspect it is much shorter and wider than the frontal. Anteriorly it forms a blunt snout tip and

233 articulates with the premaxilla with a deeply serrate suture. The anterolateral corner of the bone

234 has a narrow extension that extends directly ventrally anterior to the external naris to the level of

235 the ventral margin of this opening (Figs. 3B, 3C and 3D). Posteriorly and ventrally the nasal

236 contacts the frontal and the lacrimal along broad, interdigitating sutures. The contact with the

237 prefrontal is unusual in that the posterolateral margin of the nasal is deeply incised by an anterior

238 process of the prefrontal.

239 The lacrimal extends between the external nares and the orbit (Fig. 3). It forms the posterior

240 margin of the former and the antorbital margin of the latter. From its highest point just anterior to

241 the anterolateral corner of the orbit, the lacrimal decreases in height via weakly meandering

242 sutures with the prefrontal and the nasal to the posterolateral corner of the external naris, where it

243 forms a rim for that opening and contacts the septomaxilla slightly deep to the facial surface. The

244 ventral margin of the lacrimal forms a low, sigmoidal contact with the dorsal surface of the

245 maxilla, but upon contacting the jugal the ventral margin of the lacrimal abruptly changes to a

246 straighter oblique contact with the jugal. The lacrimal terminates posteriorly with a short, acute

247 suborbital process. In dorsal aspect the lacrimal has a smooth, sloping visceral surface that

248 extends medially to contact the palatine. This surface is perforated near the rim of the orbit by a

249 pair of lacrimal puncti (Fig. 3A).

250 The maxilla has a long, low profile in lateral aspect. Anteriorly it extends a narrow, acute

251 process to overlap the alveolar portion of the premaxilla and contributes to the ventral margin of

252 the external naris (Figs. 3B and 3D). Dorsally it features a low, rounded process that forms a

253 sigmoidal contact with the overlying lacrimal. This dorsal process reaches its highest point just

254 anterior to the contact with the jugal, approximately directly dorsal to the sixth or seventh

255 maxillary tooth position. In lateral aspect the maxilla narrows posteriorly to a sharply acute end

256 that terminates at the level of the orbital midpoint (Fig. 3B); in dorsal aspect it is evident that the

257 maxilla actually continues a little farther posteriorly under the palate (Fig. 3A). In lateral aspect

258 the ventral or alveolar margin is a weakly convex edge that extends from the last premaxillary

259 tooth position to the level of the orbital midpoint, and the right maxilla of ISIR 233 appears to

260 have room for twelve tooth positions. A section through the left maxilla of ISIR 233 suggests

261 that there are at least two rows of maxillary teeth (Fig. 3C). ISIR 234 is preserved as a section

262 through the maxillary tooth-plate dentition (Fig. 4A) and confirms that the maxilla of

263 *Indosauriscus kuttyi* has a multiple rowed region composed of three rows of teeth. As in other

264 moradisaurines, the tooth rows are parallel to the long axis of the tooth plate. The teeth in the

265 multiple rowed (MR) region are subcircular in cross section and conical in profile (e.g. lateral)

266 view. The tooth cross sections in ISIR 234 (Fig. 4A) suggest that there is a gradual increase in

267 the diameter of the MR teeth from anterior to posterior within a tooth row and from lingual-most

268 tooth row to the labial-most tooth row. These are general trends seen also in the MR dentitions of

269 *Labidosaurikos meachami* and *Moradisaurus grandis* (Dodick and Modesto, 1995; Modesto et

270 al., 2019).

271 In relative proportions, the prefrontal of *Indosauriscus kuttyi* is similar to those of

272 *Captorhinus aguti*, *Labidosauriscus richardi*, and *Captorhinus kierani* (e.g. Modesto, 1998;

273 Modesto, Scott & Reisz, 2018; deBraga, Bevitt & Reisz, 2019), but is distinctive in exhibiting a

274 sharp, triangular process anteromedially that incises the the posterolateral corner of the nasal

275 (Fig. 3A). This anteromedial process of the prefrontal resembles a similar extension on the

276 prefrontals of *Labidosaurikos meachami* and *Tramuntanasaurus tiai* (Dodick and Modesto,

277   1995; Matamales-Andreu et al., 2023). The prefrontals of *Captorhinus aguti*, *Captorhinus*

278   *kierani*, *Reiszorhinus olsoni*, and *Labidosauriscus richardi* exhibit incipient anteromedial

279   processes (Modesto, 1998; Sumida et al., 2010; Modesto, Scott & Reisz, 2018; deBraga, Bevitt

280   & Reisz, 2019).

281   The frontals are rectangular sheets that together roof the interorbital portion of the skull table

282   (Fig. 3A). The anterior portion of each frontal, i.e. the part of the frontal that lies medial to the

283   prefrontal, is narrower and slightly longer than the posterior portion, i.e. the part of the frontal

284   that lies directly medial to the postfrontal. With respect to the posterior part, the anterior part of

285   the frontal is relatively longer than that of *Captorhinus aguti* (Modesto, 1998), but not as long as

286   those in *Labidosaurus hamatus* and *Labidosaurikos meachami* (Dodick and Modesto, 1995;

287   Modesto et al., 2007).

288   The jugal most closely resembles those of *Labidosaurus hamatus* and *Labidosaurikos*

289   *meachami* in exhibiting a relatively deep, wedge-like profile in lateral aspect (Dodick and

290   Modesto, 1995; Modesto et al., 2007) compared to the more slender, slightly crescentic jugals of

291   *C. aguti* and *C. kierani* (Modesto, 1998; deBraga, Bevitt & Reisz, 2019). The jugal of

292   *Indosauriscus kuttyi* is approximately 40% deeper than that of *Captorhinus kierani* as measured

293   vertically at the posterior end of the jugal-lacrimal suture and compared to the total length of the

294   jugal. The depth of the jugal of of *Indosauriscus kuttyi* also appears to be increased posteriorly

295   with a ventral extension of the temporal margin, manifesting as a low, convex ridge that extends

296   from a point just anterior to the orbital midpoint posteriorly to a few millimetres of the posterior

297   end of the quadratojugal (Fig. 3B and 3D). This ventral extension of the temporal margin also

298   results in a quadratojugal that is relatively tall anteriorly. In dorsal aspect (Fig. 3A) the jugal can

299   be seen to exhibit a medially-directed alary process, which would have contacted the palatine

300   and the pterygoid. Together with the palatine and the lacrimal, the jugal forms a large,

301   anteroposteriorly elongate suborbital foramen, which is comparable in relative size with the

302   suborbital foramen of *Moradisaurus grandis* recently described by Sidor et al. (2022).

303   The quadratojugal is a slightly arched, quadrangular element forming the posterolateral corner

304   of the temporal region (Figs. 3A, 3B and 3D). It is a relatively long, extending slightly farther

305   anteriorly than the squamosal. The quadratojugal is also a relatively tall element for a

306   captorhinid, extending dorsally to a level even with the ventral-most point of the orbit, a

307   distinction that it shares with *Labidosaurikos meachami* and *Rothianiscus multidontus*. Part of

308   the height of the quadratojugal can be attributed to the low, rounded ventral extension of the

309   temporal region manifest in both the quadratojugal and the jugal. In ISIR 233 the quadratojugal-

310   jugal suture is longer than the squamosal-jugal suture (Figs. 3B and 3D), but this does not seem

311   the case in ISIR 236, in which the sutures are subequal. The difference in sutural proportions

312   here may represent individual variation or sexual dimorphism; a greater sample size is needed to

313   discern between these two possibilities.

314   The postorbital forms the posterior-most rim of the orbit and extends occipitally halfway

315   across the temporal region and forms the anterodorsal portion of the temple (Figs. 3A, 3B, and

316   3D). Medially it contacts the postfrontal anteriorly and the parietal posteriorly via a broadly

317   convex suture. Laterally it overlies the jugal along a shorter convex contact, and posteriorly the

318   postorbital overlaps the anterodorsal corner of the squamosal with a broad tongue of flat bone in

319   the usual captorhinid manner.

320   In dorsal aspect the postfrontal (Fig. 3) resembles more closely that of *Labidosaurikos*

321   *meachami* (Dodick and Modesto, 1995) than other captorhinids, e.g. *Captorhinus aguti*,

322   *Captorhinus kierani*, and *Labidosaurus hamatus* (Modesto, 1998; Modesto et al., 2007; deBraga,

323   Bevitt & Reisz, 2019), in exhibiting a transversely broad posterior process. This transverse

324   expansion of the postfrontal may be related to the relatively greater breadth of the parietal in

325   *Indosauriscus kuttyi* (see below).

326   The parietals are large quadrangular bones that form the posterior portion of the skull table

327   (Fig. 3A). Each parietal is relatively wide, with the transverse width ca. 75% the (total)

328   anteroposterior length of the bone. This greatly exceeds the figures for its closest relatives (58%:

329   deBraga et al. 2019), *Labidosaurikos meachami* (56%: Dodick & Modesto 1995), and

330   *Labidosaurus hamatus* (58%: Modesto et al., 2007). The pineal foramen is a subcircular opening

331   that is positioned immediately anterior to the midpoint of the inter-parietal suture. With respect

332   to total parietal length, the anteroposterior diameter of the pineal foramen is the same relative

333   size as that of its close relatives *Labidosaurus hamatus* and *Labidosaurikos meachami* (ca. 8%

334   and 9%, respectively: Dodick & Modesto, 1995), compared to the slightly larger openings in

335   *Captorhinus magnus* and *Captorhinus kierani* (both ca. 17%: Kissel et al., 2002; deBraga et al.,

336   2019). There are no large pits that exceed in size all other pits in the honeycombing ridge-and-pit

337   ornamentation, as described for the parietals of both *Labidosaurus hamatus* and *Labidosaurikos*

338   *meachami* (Dodick & Modesto, 1995; Modesto et al., 2007).

339   The supratemporal is a small, asymmetrical splint of bone that spans the boundary between

340   the skull table and the occiput (Fig. 3A). It is angled with respect to the occipital margin such

341   that its long axis is aligned with the pineal foramen. The narrow, occipital part of the

342   supratemporal is nestled between the postparietal medially and the the squamosal laterally,

343   whereas the skull-table portion is slightly broader and occupies a small notch in the

344   posterolateral corner of the parietal.

345   The posterior margin of the skull table is formed by the paired postparietals (Figs. 3A, 3C and

346   5B). These are most similar to those of *Labidosaurikos meachami* in having distinct skull-table

347   and occipital regions. As in that moradisaurine, the skull-table region extends the entire

348   transverse breadth of the element and bears ornamentation of ridges and pits that continue

349   posteriorly from the parietal, with which the postparietal shares a broadly meandering suture. At

350   the occipital margin the postparietal drops directly ventrally to form a smoothly surfaced

351   occipital flange. In occipital (posterior) aspect the occipital flange of the postparietal is claw-

352   shaped, deepest medially where it contacted the other postparietal and the supraoccipital and

353   tapering and curving gradually throughout its length to an acute lateral tip that made contact with

354   the squamosal. In its claw-like profile the occipital flange of the postparietal of *Indosauriscus*

355   *kuttyi* resembles more the occipital flanges of *Captorhinus aguti* and *Labidosaurus hamatus*

356   (Modesto, 1998; Modesto et al., 2007) than the distinctly shelf-like occipital flange of

357   *Labidosaurikos meachami* (Dodick & Modesto, 1995).

358   In dorsal and lateral aspects the squamosal (Figs. 3 and 5B) more closely resembles those of

359   *Captorhinus aguti* and other non-moradisaurines in featuring a posteroventral-sloping occipital

360   flange; this is in contrast to the condition in *Labidosaurikos meachami*, in which the occipital

361   flange is orthogonal to the temporal portion of the bone and, as such, is not visible in lateral

362   aspect. The external surface of occipital flange of the squamosal of *Indosauriscus kuttyi*, like that

363   of the postparietal, is smoothly finished and in strong contrast to the ridge-and-pit ornamentation

364   on the temporal portion of the bone. In lateral aspect the squamosal closely resembles that

365   documented for other small captorhinids (e.g. Modesto, 1998) except that the length of the

366   squamosal-jugal suture is equal to, or slightly shorter than, that between the quadratojugal and

367   the jugal (rather than vice versa), and the observation that the squamosal-quadratojugal suture

368   slopes posteroventrally (rather than parallel to the ventral margin of the posterior cheek).

369   The palate of ISIR 233 partially preserved and the surface is overprepared, and so the

370   following description of palatal morphology is based on mostly the better preserved ISIR 232

371   (Fig. 5A). Only the posterior end of the vomer is exposed in both ISIR 233 and ISIR 232 because

372   of occlusion of the mandible. What is visible of this element is not distinguishable from the

373   vomers of other captorhinids such as *Captorhinus aguti* or *Labidosaurus hamatus*. In ventral

374   aspect, the palatine resembles most closely that of *Labidosaurikos meachami* in having a

375   transversely compressed exposure between the pterygoid and the medially expanded dental plate

376   of the maxilla. The ventral surface appears edentulous, but surface preservation is not

377   sufficiently well preserved to rule out the possibility that small teeth may have been present

378   posteromedially where there is a slight swelling. The suture between the palatine and the

379   pterygoid is deeply serrate (i.e. in the region where these two elements form a pterygopalatine

380   patch of teeth, as seen in *Labidosaurus hamatus* and small captorhinids such as *Captorhinus*

381   *aguti*). The dorsal surface of the palatine is exposed in ISIR 233 (Fig. 3A), seen through the right

382   orbit, where it is little more that a flat plate of bone that overlies the maxilla and contacts the

383   lacrimal and the jugal laterally. The palatine and the jugal are slightly disarticulated in ISIR 233,

384   but we infer that the two bones formed a relatively large suborbital foramen when reconstructed

385   (see description for the jugal). In general morphology the pterygoid resembles most closely that

386   of *Labidosaurikos meachami*, except that teeth are present along the medial margin, on the

387   pterygopalatine swelling, and as a narrow cluster along the posteroventral edge of the transverse

388   flange. Most of the teeth are preserved as stumps, but the well-preserved tooth crowns are small,

389   slightly bulbous cones.

390   The quadrate is present in those skulls that preserve the jaw-joint region but is not well

391   exposed because it is mostly covered by the skull roof, by the adducted mandible, and by

392   braincase elements. The right quadrate of ISIR 232 (Fig. 5) is the best exposed and what can be

393   seen of this bone is not remarkably different from those of other captorhinids.

394   The left epipterygoid is exposed in lateral aspect in ISIR 232, where is preserved in perfect

395   articulation atop the dorsal edge of the quadrate flange of the left pterygoid (Fig. 4B). It is a

396   triangular structure with a flange-like base and a finger-like dorsal process. Although the

397   anteroventral-most part of the bone is obscured by matrix left to bolster the superficial portions

398   of the left side of the skull, the remainder of the bone resembles more closely the epipterygoid

399   that Heaton (1979, figure 25a) reconstructed for small captorhinids than the relatively robust

400   element preserved in *Labidosaurikos meachami*, (Dodick & Modesto, 1995, figure 10a).

401   The braincase is best preserved in ISIR 232, in which it is preserved in situ and almost

402   entirely articulated (Fig. 5). The parabasisphenoid closely resembles in morphology and

403   proportions that of *Labidosaurikos meachami*, particularly in the extensive overlapping contact

404   with the head of the stapes seen in palatal aspect. The parabasisphenoid resembles that of

405   *Captorhinus aguti* and *Captorhinus kierani* in exhibiting cristae ventrolaterales that feature

406   sharp, thin ridges that extend from the level of the basipterygoid processes posteriorly to the

407   level where the cristae flatten out and extend laterally to make contact with the stapes (Fig. 5A).

408   Both opisthotics are preserved in ISIR 232. Each consists of a medial, irregularly shaped region

409   from which a relatively short paroccipital process extends laterally. The medial portion of the

410   opisthotic forms with the exoccipital a small vagus foramen (Fig. 5B). The basioccipital is

411   mostly covered by surrounding elements, but what is visible in ventral aspect is not

412   distinguishable from the morphology of this element in other captorhinids. The exoccipitals are

413   preserved in ISIR 232, but each is covered to a different extent by surrounding elements. The left

414   is the better exposed of the two, and shows that the dorsal portion of the exoccipital is crescentic

415   and forms the lateral margin of the foramen magnum. Unlike other captorhinids, however, the

416   dorsal tip of this bone is narrowly acute. The supraoccipital, exposed only in posterior aspect, is

417   typically captorhinid in construction, consisting of a plate-like body from which a median dorsal

418   process and paired dorsolateral processes extend from its dorsal margin. The supraoccipital is

419   deeply incised ventrally where it forms the dorsal margin of the foramen magnum. The stapes is

420   characteristically captorhinid in being composed of a conspicuously large stapedial head,

421   relatively long columella, and short, but distinct, medially curving dorsal process.

422   In all specimens the upper and lower jaws are tightly occluded to the skull, prohibiting a

423   detailed description of the dorsal part of the mandible (Figs. 3, 4B and 5). What is discernible

424   indicates the general morphology of the mandible of *Indosauriscus kuttyi* closely resembles that

425   of other small captorhinids, such as *Captorhinus aguti* and *Captorhinus laticeps*. The lateral

426   surfaces of the dentary, the surangular, and the angular are ornamented with the same ridge-and-

427   pit sculpturing seen on the skull, and the ventral surfaces of the dentary, the splenial, the angular,

428   the prearticular, and the articular are smooth and devoid of ornamentation. Like the mandibular

429   rami of its close relatives *Labidosaurus hamatus* and *Labidosaurikos meachami*, that of

430 *Indosauriscus kuttyi* is sigmoidal in ventral aspect, and the mandibular ramus is relatively broad

431 transversely (ca. 12% total mandible length, closer to the 14% of *Labidosaurus hamatus* and

432 *Labidosaurikos meachami* than more basal captorhinids, e.g. ca. 8% in *Captorhinus aguti*). A

433 slight lingual swelling of the splenial in both ventral aspect and in the cross section through the

434 left mandibular ramus of ISIR 233 (Fig. 3C) indicates that a lingual shelf (sensu Modesto et al.,

435 2019) is present on the dentary, as in other moradisaurines in which this region of the mandible

436 is preserved. Whereas we have no direct evidence of multiple rows of teeth on the dentary in the

437 available specimens, the presence of a lingual shelf on the dentary is known only in

438 moradisaurines among captorhinids, and it is associated with the presence of a mandibular

439 (dentary) tooth plate. Considering that the dentary tooth plate exhibits one fewer row of teeth

440 than the corresponding upper tooth plate (e.g., *Labidosaurikos meachami*: Dodick & Modesto,

441 1995), we estimate that the dentary supports two rows of teeth.

442 The splenial and the post-dentary bones, apart from the coronoid, which is not exposed in any

443 of the specimens available to us, resemble in general morphology those of other captorhinids.

444 The only remarkable aspect is the slit-like posterior Meckelian foramen ("foramen

445 intermandibularis caudalis" of Heaton, 1979), seen in the medial view of the right mandibular

446 ramus of ISIR 232 (Fig. 5B): the height of the foramen is only about 15% of its length.

447 Otherwise, the posterior Meckelian foramen appears normally developed, being roughly 7.7%

448 the length of the mandible ramus, which in relative terms is slightly shorter than those of

449 *Labidosaurikos meachami* and *Moradisaurus grandis*, in which the same figures are 10.4% and

450 11.6% (Dodick & Modesto, 1995; Modesto et al., 2019).

451 A single hyoid element, the first ceratobranchial, is preserved in ISIR 232 (Fig. 5A). It is a

452 relatively elongate, slightly curved rod of bone with a spatulate anterior end. The head is slightly

453 smaller and the shaft is slightly longer than the first ceratobranchial of *Captorhinus laticeps*

454 (figure 12 in Heaton, 1979).

455

456 **Postcranial skeleton**

457 ISIR 236 is the only specimen with preserved postcrania (Fig. 6). In dorsal aspect there are two

458 large flat bones that may be scapulocoracoids and what appears to be the proximal end of the left

459 humerus, but the margins of the former are broken along the edges of the specimen, and the

460 surface preservation of all these elements is poor (Fig. 6A). In ventral aspect the preservation is

461   much better and the dermal elements of the pectoral girdle are present in perfect articulation,

462   although smaller disarticulated elements obscure details of the margins of these bones (Fig. 6B).

463   The ventral portions of the clavicles are bifurcated as in those of the small captorhinids (Holmes,

464   1977), and the anterior, larger process of each clavicle approaches the midline along the anterior

465   margin of the interclavicle; overlying material precludes confident determination whether the

466   clavicles actually make contact with each other medially as they do in small captorhinids

467   (Holmes, 1977). The tongue-like posterior process of the main plate of the clavicle is relatively

468   much larger than in *Captorhinus aguti* (figure 2d in Holmes, 1977). The greater part of the right

469   humerus is preserved in association with the pectoral girdle. It is preserved in anterodorsal view,

470   with the deltopectoral crest oriented posteriorly. The left humerus distal to the origin for the

471   supinator, across to the entepicondylar foramen, is missing. Numerous disarticulated, vertebral

472   elements and ribs are preserved on and around the pectoral bones, and what is visible of these

473   conforms with general captorhinid morphology and is not otherwise remarkable.

474

475   Phylogenetic analysis

476

477   The phylogeny of captorhinid reptiles is complicated by the inbalance between the number of

478   taxa that have been described and the available potential synapomorphies that can be used to

479   determine patterns of relationships. The majority of taxa are based on cranial materials or

480   fragmentary cranial remains, with differences in dental anatomy and size distinguishing the

481   various species of *Captorhinus*. Captorhinids therefore appear to be notoriously conservative in

482   their anatomy in this regions of the skeleton, with dental anatomy and the evolution of multiple

483   rows of teeth weighing heavily on the overall list of characters. In addition, size appears to be a

484   major factor, with smaller taxa being more slender and gracile, while younger and larger

485   members being stocky and massive postcranially. Overall, there are more than 25 named taxa,

486   and only 79 characters to evaluate their interrelationships. Of these, 16 characters are related to

487   dentition and only 10 are available postcranially. Excluding some of the poorly known taxa, such

488   as *Hecatogomphius* and *Riabininus*, both known only from maxillary dentary bones (Vjushkov

489   & Chudinov, 1957; Ivakhnenko, 1990), does relatively little to help resolve the pattern of

490   relationships. Our phylogenetic analysis of 24 captorhinid taxa with *Protorothyris* and

491   *Paleothyris* as outgroups yielded 4 equally parsimonious trees, each with a tree length of 236

492   steps (CI 0.445; RI 0.689; HI 0.555). The strict consensus of these trees is shown in Fig. 7.

493   *Labidosaurus* forms a sister-group relationship with a monophyletic Moradisaurinae, which

494   includes *Rhodotheratus parvus* as its basal-most member. *Indosauriscus* is nested well within

495   Moradisaurinae, as the sister taxon of the clade that includes *Captorhinikos valensis*,

496   *Gansurhinus naobaogouensis, Labidosaurikos meachami, Moradisaurus grandis, Rothianiscus*

497   *multidontus*, and *Sumidadectes chozaensis*. A reduced phylogenetic analysis focusing mainly on

498   Moradisaurinae by removing *Paleothyris, Protorothyris, Thuringothyris, Euconcordia*,

499   *Opisthodontosaurus, Reiszorhinus, Rhodotheratus, Romeria, Protocaptorhinus*, and *Captorhinus*

500   *laticeps*, and using *Rhiodenticulatus* as the outgroup, yielded a single most parsimonious tree

501   (heuristic search with 1,000 iterations, 137 steps long, CI = 0.613, RI = 0.635, RC = 0.389),

502   which recovered the same moradisaurine clades as in the full analysis and further resolved

503   *Gansurhinus naobaogouensis* as the sister of the clade of *Labidosaurikos meachami*,

504   *Moradisaurus grandis, Rothianiscus multidontus*, and *Sumidadectes chozaensis*.

505

506   Discussion

507

508   **Paleogeographic distribution of captorhinids and moradisaurines within a phylogenetic**

509   **framework**

510   The evolutionary history of captorhinids is characterized by an early diversification in the

511   equatorial region of Pangea during the late Carboniferous and early Permian. This diversification

512   includes the likely acquisition of omnivory and herbivory, with associated modifications largely

513   in their dentition for effective oral processing of food and increase in size. Increase in size

514   occurred predominantly within the moradisaurine sub-clade of captorhinids (although

515   *Reiszorhinus* and *Labidosaurus* also reached moderate to large size among non-moradisaurine

516   captorhinids) all within the early Permian equatorial region of Pangea. Overall, the weakness of

517   the phylogeny of Captorhinidae in general and Moradisaurinae in particular makes detailed

518   assessments about patterns of paleogeographic dispersal of the latter group of reptiles somewhat

519   problematic. The well supported sister-group relationship between Moradisaurinae and the North

520   American *Labidosaurus hamatus*, and the basal position of the North American *Rhodotheratus*

521   *parvus*, together support the hypothesis that moradisaurines originated in western Laurasia

522   during the early Permian. According to our tree topology, moradisaurines achieved a wider

523   geographic distribution early in their evolution but these early diverging moradisaurines do not

524   appear until the end of the middle Permian. Thus, there is some basis for an 'out of equatorial

525   Pangea' expansion into middle and late Permian temperate regions including Gondwana, Russia,

526   and China. Interestingly, this dispersal occurred not only among moradisaurines, but there were

527   also separate dispersal events associated with more basal members of the clade. Superficially, the

528   multiple out-of-tropics expansions with no apparent later migration to the equatorial belt

529   conforms to a pattern of biotic diversification by taxon pulses (Erwin, 1979; Folinsbee & Brooks,

530   2007). There is no evidence that captorhinid lineages ever migrated back into the equatorial belt

531   of Pangea because the available temporal information indicates that the western Laurasian

532   *Labidosaurikos* is stratigraphically one of the oldest moradisaurines.

533   The tree topology resulting from our reduced phylogenetic analysis does not allow a decisive

534   reconstruction of the pattern of moradisaurine dispersal out of western Laurasia. This is partly

535   because the ancestor of the clade that contains *Indosauriscus* and *Labidosaurikos* could have

536   dispersed to eastern Laurasia and Gondwana, but despite the early appearance of the latter it is

537   possible that the ancestor of *Labidosaurikos* and its sister taxon *Rothianiscus* do not represent an

538   early diversification of moradisaurines, but rather a secondary dispersal back to western

539   Laurasia. Nevertheless, if the temporal pattern of the fossil record is taken into account, then the

540   ancestors of the two clades, one containing *Moradisaurus* and *Gansurhinus* and the other

541   containing *Indosauriscus* and *Tramuntanasaurus*, likely represent separate dispersal events out

542   of western Laurasia. Our current knowledge of the fossil record is problematic and neither

543   scenario is particularly satisfactory. *Labidosaurikos* is one of the stratigraphically oldest

544   moradisaurines, but it is one of the phylogenetically youngest Moradisaurines, at least according

545   to the results of our weakly supported reduced phylogenetic analysis. Although the evidence

546   does support an "out of equatorial Pangea" hypothesis, a more confident reconstruction of the

547   pattern(s) of moradisaurine dispersals out of western Laurasia must await new fossil materials

548   and more robust phylogenetic results.

549

550   **Evolution of multiple rows of teeth in captorhinid reptiles**

551   In recovering *Rhodotheratus parvus* as a moradisaurine, our phylogenetic results contrast with

552   those of recent work on captorhinid interrelationships (Albright, Sumida & Jung, 2021;

553   Matamales-Andreu et al., 2023), which proposed that multiple tooth rows (MTRs) evolved

554   independently at least three times within Captorhinidae, i.e, in (1) *Rhodotheratus parvus*, (2)

555   *Captorhinus aguti*, and (3) Moradisaurinae. Our work suggests that MTRs evolved only twice in

556   this clade: in (1) *C. aguti* and (2) Moradisaurinae. The recovery of *R. parvus* as a moradisaurine

557   is interesting, because its arrangement of MTRs (with apparently three rows on the maxilla, and

558   two rows of teeth on the dentary: Albright, Sumida & Jung, 2021) is reminiscent of the pattern

559   seen in *C. aguti*, in which the tooth rows are angled with respect to the main axis of the jaw, and

560   which contrasts with the linear, parallel or subparallel organization of the MTRs in

561   *Tramuntanasaurus tiai* and phylogenetically younger moradisaurines. The basal position of *R.*

562   *parvus* in Moradisaurinae suggests the possibility that MTR pattern seen in *T. tiai*, *Indosauriscus*

563   *kuttyi*, and their close moradisaurine relatives is derived from the condition seen in *R. parvus.*

564   Previous studies of *Captorhinus aguti* dentition suggested a mechanism for the ontogenetic

565   development of MTRs through differential, asymmetrical growth of the tooth-bearing maxillary

566   and dentary bones, effectively moving the ontogenetically older teeth labially to such an extent

567   that replacement teeth were able to attach to the alveolar shelf of the respective bones that were

568   formed as the older teeth were displaced labially but not replaced by the next generation of teeth

569   (Bolt & DeMar, 1975; de Ricqlès & Bolt, 1983; LeBlanc & Reisz, 2015). This mechanism

570   allowed for the development of MTRs in *Captorhinus aguti*. Although this ontogenetic

571   asymmetrical growth may explain the mechanism for this species, it is uncertain if this also

572   applies to *R. parvus.* In addition, differences in the configuration of the MTRs in *C. aguti* and in

573   most moradisaurines, together with the emplacement of MTRs on plate-like alveolar bone and

574   evidence of tooth replacement (Modesto et al., 2019), are suggestive of different MTR

575   development in moradisaurines exclusive of *R. parvus*. Histological analyses of the latter may

576   help us resolve the apparent differences between the MTRs of most moradisaurines and those of

577   *C. aguti* and *R. parvus.*

578

579   **Paleobiology**

580   *Indosauriscus kuttyi* is the only reptile known from the Kundarum Formation, the fauna of which

581   is dominated numerically by dicynodont synapsids (Kutty, 1972; Ray, 1999) but includes

582   medium-sized, indeterminate gorgonopsian synapsids (Ray & Bandyopadhyay, 2003). The

583   dicynodonts range in size from small to relatively large herbivores (skull lengths [SLs] 50 mm to

584   350 mm; Ray & Bandyopadhyay, 2003). *Indosauriscus kuttyi*, with a skull length ranging 39 mm

585   to 54 mm, falls at the small end of this spectrum of herbivore body size. Whereas the Kundarum

586   captorhinid was described as omnivorous by Ray & Bandyopadhyay (2003), our identification of

587   *Indosauriscus kuttyi* as a moradisaurine enriches the herbivore component of the Kundarum

588   fauna.

589   In addition to its small size, *Indosauriscus kuttyi* is remarkable because it is one of the last

590   representatives of an older Permian group of herbivorous reptiles that co-occurs with species of a

591   geologically younger group of therapsid herbivores. Interestingly, the late Permian captorhinid

592   *Gansurhinus naobaogouensis* is of interest because it is the only other moradisaurine that occurs

593   with dicynodonts (Liu, 2023). Although approximately twice the size of the Kundarum

594   moradisaurine, *Gansurhinus naobaogouensis*, with a maximum skull length of 110 mm (Liu,

595   2023), is, like *Indosauriscus kuttyi*, the smallest herbivore of its fauna (Naobaogou Formation,

596   China; dicynodont SLs range 143 mm to 330 mm: Liu, 2021; Shi & Liu, 2023). Interestingly,

597   Brocklehurst (2016) found that *Gansurhinus qingtoushanensis* (along with *Captorhinikos*

598   *valensis*) was characterized by an extremely rapid decrease in an ancestral-size-reconstruction

599   analysis of Captorhinidae. The observations that *Gansurhinus naobaogouensis* and

600   *Indosauriscus kuttyi* are the smallest herbivores of their respective faunas contrast with that

601   derived from *Moradisaurus grandis*, the largest and the last late Permian moradisaurine (SK of

602   400 mm: de Ricqlès & Taquet, 1982). *Moradisaurus grandis* occurs in an endemic fauna

603   (Moradi Formation, Niger; Sidor et al., 2005) with only a medium-sized pareisaur as the co-

604   occurring herbivore (Tsuji et al., 2013). Accordingly, the small body sizes of *Indosauriscus*

605   *kuttyi* and *Gansurhinus naobaogouensis* in their respective faunas may have been an

606   evolutionary response on the part of these reptiles to competition from the more numerous, and

607   generally larger, dicynodonts. Testing this hypothesis will require more robust phylogenetic

608   results for moradisaurines, as well as additional field work in the upper Permian continental

609   strata.

610

611   Conclusions

612

613   We describe a new captorhinid reptile, *Indosauriscus kuttyi*, from the upper Permian Kundarum

614   Formation of India. Phylogenetic analysis of captorhinids positions *Indosauriscus kuttyi* as an

615   early branching moradisaurine. *Indosauriscus kuttyi* is the only herbivorous reptile in the

616 Kundarum Formation, and it is the smallest herbivore in a terrestrial tetrapod fauna that is

617 dominated by dicynodont therapsids. Its small body size may have been an adaptive response to

618 competition with dicynodonts, a possibility hinted at by similar circumstances for *Gansurhinus*

619 *naobaogouensis* in the Naobaogou Formation of China, but further data is needed to examine

620 this hypothesis in detail.

621

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623

628

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630

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632

637

638 Author Contributions

639

640 Robert R. Reisz conceived and designed the experiments, performed the experiments, analysed

641 the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved

642 the final draft.

643

644 Sankar Chatterjee authored or reviewed drafts of the paper, and approved the final draft.

645

646   Sean P. Modesto analysed the data, prepared figures and/or tables, authored or reviewed drafts of

647   the paper, and approved the final draft.

648

649   Data Availability

650

651   The following information was supplied regarding data availability:

652

653   The data matrix employed in the phylogenetic analysis, saved in nexus format, is available as a

654   Supplemental File 1. Supplemental File 2 contains a character list, explaining new characters and

655   character modifications. Specimens described in the manuscript are stored at the Indian

656   Statistical Institute, Kolkata, India. Specimen accession numbers: ISIR 232, ISIR 233, ISIR 234,

657   ISIR 235, and ISIR 236.

658

659   Supplemental Information

660

661   Supplemental information for this article can be found online at

662   http://dx.doi.org/10.7717/peerj.XXXX#supplemental-information.

663

664   References

665

666   **Albright GM, Sumida SS, Jung J. 2021.** A new genus of captorhinid reptile (Amniota:

667   Eureptilia) from the Lower Permian Hennessey Formation of central Oklahoma, and a

668   consideration of homoplasy in the family Captorhinidae. *Annals of Carnegie Museum*

669   **87**:89–116 DOI: 10.2992/007.087.0201.

670   **Bolt JR, DeMar R. 1975.** An explanatory model of the evolution of multiple rows of teeth in

671   *Captorhinus aguti. Journal of Paleontology* **49**:814–832.

672   **Brocklehurst N. 2016.** Rates and modes of body size evolution in early carnivores and

673   herbivores: a case study from Captorhinidae. *PeerJ* **4**:e1555; DOI: 10.7717/peerj.1555

674   **Case EC. 1911**. A revision of the Cotylosauria of North America. *Carnegie Institute of*

675   *Washington Publication* **145**:1–122.

676 **Cisneros JC, Angielczyk K, Kammerer CF, Smith RMH, Fröbisch J, Marsicano CA,**
677   **Richter M. 2020.** Captorhinid reptiles from the lower Permian Pedra de Fogo Formation,
678   Piauí, Brazil: the earliest herbivorous tetrapods in Gondwana. *PeerJ* **8**:e8719 DOI:
679   10.7717/peerj.8719

680 **Clark J, Carroll RL. 1973.** Romeriid reptiles from the Lower Permian. *Bulletin of the Museum*
681   *of Comparative Zoology* **144**:353–407.

682 **deBraga M, Bevitt JJ, Reisz RR. 2019.** A new captorhinid from the Permian cave system near
683   Richards Spur, Oklahoma, and the taxic diversity of *Captorhinus* at this locality.
684   *Frontiers Earth Sciences* **7**, feart.2019.00112 DOI: 10.3389/feart.2019.00112

685 **Dodick JT, Modesto SP. 1995.** The cranial anatomy of the captorhinid reptile *Labidosaurikos*
686   *meachami* from the Lower Permian of Oklahoma. *Palaeontology* **38**:687–711.

687 **Erwin TL. 1979.** Thoughts on the evolutionary history of ground beetles: hypotheses generated
688   from comparative faunal analyses of lowland forest sites in temperate and tropical
689   regions. In: Erwin T. L., et al., ed. *Carabid beetles: their evolution, natural history, and*
690   *classification*. The Hague: Dr W. Junk Publishers, 539–592.

691 **Folinsbee KE, Brooks DR. 2007.** Miocene hominoid biogeography: pulses of dispersal and
692   differentiation. *Journal of Biogeography* **34**: 383–397.

693 **Gaffney ES, McKenna MC. 1979.** A Late Permian captorhinid from Rhodesia. *American*
694   *Museum Novitates* **2688**:1–15.

695 **Gow CE. 2000.** A captorhinid with multiple tooth rows from the Upper Permian of Zambia.
696   *Palaeontologia Africana* **36**:11–14.

697 **Heaton MJ. 1979.** Cranial anatomy of primitive captorhinid reptiles from the Late
698   Pennsylvanian and Early Permian Oklahoma and Texas. *Oklahoma Geological Survey*
699   *Bulletin* **127**:1–84.

700 **Holmes RB. 1977.** The osteology and musculature of the pectoral limb of small captorhinids.
701   *Journal of Morphology* **152**:101–140. DOI: 10.1002/jmor.1051520107.

702 **Ivakhnenko MF. 1990.** Elements of the Early Permian tetrapod faunal assemblages of Eastern
703   Europe. *Paleontological Journal* **24**:104–112.

704 **Jung JP, Sues H-D. 2024.** Reassessment of '*Captorhinikos*' *chozaensis*, an early Permian
705   (Cisuralian: Kungurian) captorhinid reptile from Oklahoma and north-central Texas. *Journal*
706   *of Paleontology* **98** DOI: 10.1017/jpa.2023.85.

707 **King W. 1881.** The geology of the Pranhita-Godavari valley. *Memoir of Geological Survey of*
708   *India*, **18**, 151–311.

709 **Kutty TS. 1972.** Permian reptilian fauna from India. *Nature* **237**:462–463.

710 **Liu J. 2021.** The tetrapod fauna of the upper Permian Naobaogou Formation of China: 6.
711   *Turfanodon jiufengensis* sp. nov. (Dicynodontia). *PeerJ* **9**:e10854 DOI:
712   10.7717/peerj.10854

713 **Liu J. 2023.** The tetrapod fauna of the upper Permian Naobaogou Formation of China: 9. A new
714   species of *Gansurhinus* (Reptilia: Captorhinidae) and a revision of Chinese captorhinids.
715   *Journal of Vertebrate Paleontology* **42**:e2203200 DOI:
716   10.1080/02724634.2023.2203200.

717 **LeBlanc ARH, Reisz RR. 2015.** Patterns of tooth developments and replacement in captorhinid
718   reptiles: A comparative approach for understanding the origin of multiple tooth rows.
719   *Journal of Vertebrate Paleontology* **35**:e919928 DOI: 10.1080/02724634.2014.919928

720 **LeBlanc ARH, Brar AK, May W, Reisz RR. 2015.** Multiple tooth-rowed captorhinids from the
721   early Permian fissure fills of the Bally Mountain Locality of Oklahoma. *Vertebrate Anatomy*
722   *Morphology Palaeontology* **1**:35–49.

723   **Maddison WP, Maddison DR. 2023.** Mesquite: A modular system for evolutionary
724   analysis, version 3.81. http://www.mesquiteproject.org.

725 **Matamales-Andreu R, Roig-Munar FX, Oms O, Galobart À, Fortuny J. 2021.** A
726   captorhinid-dominated assemblage from the palaeoequatorial Permian of Menorca (Balearic
727   Islands, western Mediterranean). *Earth and Environmental Science Transactions of the Royal*
728   *Society of Edinburgh* **112**:125–145 DOI: 10.1017/S1755691021000268.

729 **Matamales-Andreu R, Mujal E, Galobart À, Fortuny J. 2023.** A new medium-sized
730   moradisaurine captorhinid eureptile from the Permian of Mallorca (Balearic Islands, western
731   Mediterranean) and correlation with the co-occurring ichnogenus *Hyloidichnus*. *Papers in*
732   *Palaeontology* **9**(3):e1498 DOI: 10.1002/spp2.1498.

733 **Modesto SP. 1998.** New information on the skull of the Early Permian reptile *Captorhinus*
734   *aguti*. *PaleoBios* **18**:21–35.

735 **Modesto S, Smith RM. 2001.** A new Late Permian captorhinid reptile: a first record from the
736   South African Karoo. *Journal of Vertebrate Paleontology* **21**(3):405–409.

737 **Modesto SP , Lamb AJ, Reisz RR. 2014.** The captorhinid reptile *Captorhinikos valensis* from

738   the lower Permian Vale Formation of Texas, and the evolution of herbivory in eureptiles.

739   *Journal of Vertebrate Paleontology* **34**:291–302 DOI: 10.1080/02724634.2013.809358.

740 **Modesto SP, Scott D, Reisz RR. 2018.** A new small captorhinid reptile from the lower Permian

741   of Oklahoma and resource partitioning among small captorhinids in the Richards Spur fauna.

742   *Papers in Palaeontology* **4**:293–307 DOI: 10.1080/02724634.2013.809358.

743 **Modesto SP, Flear VJ, Dilney MM, Reisz RR. 2016.** A large moradisaurine tooth plate from

744   the Lower Permian of Texas and its biostratigraphic implications. *Journal of Vertebrate*

745   *Paleontology* **36**: e1221832 DOI: 10.1080/02724634.2016.1221832.

746 **Modesto, SP, Richards CD, Ide O, Sidor CA. 2019.** The vertebrate fauna of the Upper

747   Permian of Niger. X. The mandible of the captorhinid reptile *Moradisaurus grandis*. *Journal*

748   *of Vertebrate Paleontology* **38**:e1531877 DOI: 10.1080/02724634.2018.1531877.

749 **Modesto SP, Scott D, Berman DS, Müller J, Reisz RR. 2007.** The skull and the

750   palaeoecological significance of *Labidosaurus hamatus*, a captorhinid reptile from the Lower

751   Permian of Texas. *Zoological Journal of the Linnean Society* **149**:237–262 DOI:

752   10.1111/j.1096-3642.2007.00242.x.

753 **Mueller J, Reisz R, Chatterjee S, Kutty TS. 2007.** A passage to India: a small captorhinid

754   from the Permian Kundaram Formation and the postglacial dispersal of early reptiles.

755   *Journal of Vertebrate Paleontology* **27**(3 Supplement):121A. DOI:

756   10.1080/02724634.2018.1531877.

757 **Müller J, Reisz R. 2005.** An early captorhinid reptile (Amniota, Eureptilia) from the Upper

758   Carboniferous of Hamilton, Kansas. *Journal of Vertebrate Paleontology* **27**:561–568.

759 **Olson EC. 1947.** The family Diadectidae and its bearing on the classification of reptiles.

760   *Fieldiana Geology* **10**:63–77.

761 **Olson EC, Beerbower JR. 1953.** The San Angelo Formation, Permian of Texas, and Its

762   Vertebrates. *The Journal of Geology* **61**:389–423.

763 **Ray S. 1997.** Some contributions to the Lower Gondwana stratigraphy of the Pranhita-Godavari

764   valley, Deccan India. *Journal Geological Society of India* **50**:633–640.

765 **Ray S. 1999.** Permian reptilian fauna from the Kundaram Formation, Pranhita-Godavari Valley,

766   India. *Journal of African Earth Sciences* **29**:211–218.

767   **Ray S**. **2000.** Endothiodont dicynodonts from the Late Permian Kundaram Formation, India.
768   *Palaeontology* **43**:375–404.

769   **Ray S, Bandyopadhyay S**. **2003.** Late Permian vertebrate community of the Pranhita-Godavari
770   valley, India. *Journal of Asian Earth Sciences* **21**:643–654.

771   **Reisz RR, Jun L, Li J-L, Müller J. 2011.** A new captorhinid reptile *Gansurhinus*
772   *qingtoushanensis* gen. et sp. nov. from the Permian of China. *Naturwissenschaften* **98**:435–
773   441.

774   **Reisz R, Haridy Y, Müller J. 2016.** *Euconcordia* nom. nov., a replacement name for the
775   captorhinid eureptile *Concordia* Müller and Reisz, 2005 (non Kingsley, 1880), with new data
776   on its dentition. *Vertebrate Anatomy Morphology Palaeontology* **3**:1–6 DOI:
777   10.18435/B53W22

778   **Ricqlès A de, Bolt JR. 1983.** Jaw growth and tooth replacement in *Captorhinus aguti* (Reptilia:
779   Captorhinomorpha): a morphological and histological analysis. *Journal of Vertebrate*
780   *Paleontology* **3**:7–24.

781   **Ricqlès A. de, Taquet P. 1982.** La faune de vertébrés du Permien Supérieur du Niger. I. Le
782   captorhinomorphe *Moradisaurus grandis* (Reptilia, Cotylosauria). *Annales de Paléontologie*
783   **68**:33–106.

784   **Rineau V, Grand A, Zaragüeta R, Laurin M. 2015.** Experimental systematics: sensitivity of
785   cladistic methods to polarization and character ordering schemes. *Contributions to Zoology* **84**:
786   129–148 DOI: 10.1163/18759866-08402003

787   **Rubidge BS, Erwin DH, Ramezani J, Bowring SA, de Klerk WJ.** 2013. High-precision
788   temporal calibration of Late Permian vertebrate biostratigraphy: U-Pb zircon constraints from
789   the Karoo Supergroup, South Africa. *Geology* **41**: 363–366.

790   **Shi Y-T, Liu J. 2023.** The tetrapod fauna of the upper Permian Naobaogou Formation of China:
791   10. *Jimusaria monanensis* sp. nov. (Dicynodontia) shows a unique epipterygoid. *PeerJ*
792   **11**:e15783 DOI: 10.7717/peerj.15783

793   **Sidor CA, Ide O, Larsson HCE, O'Keefe FR, Smith RMH, Steyer J-S, Modesto SP. 2022.**
794   The vertebrate fauna of the Upper Permian of Niger—XI. Cranial material of a juvenile
795   *Moradisaurus grandis* (Reptilia: Captorhinidae). *Journal of Vertebrate Paleontology*
796   **41**:e2030345 DOI: 10.1080/02724634.2021.2030345.

797   **Sidor CA, O'Keefe FR, Damiani R, Steyer J-S, Smith RMH, Larsson HCE, Sereno PC,**

798   **Larsson HCE, Ide O, Maga A. 2005.** Permian tetrapods from the Sahara show climate-

799   controlled endemism in Pangaea. *Nature* **434**:886–889.

800   **Smith RMH, Rubidge BS, Day MO, Botha J. 2020.** Introduction to the tetrapod biozonation of

801   the Karoo Supergroup. *South African Journal of Geology* **123**:131–140.

802   **Sumida SS, Dodick J, Metcalf A, Albright G. 2010.** *Reiszorhinus olsoni*, a new single-tooth-

803   rowed captorhinid reptile from the Lower Permian of Texas. *Journal of Vertebrate*

804   *Paleontology* **30**(3):704–714 DOI: 10.1080/02724631003758078.

805   **Swofford DL. 2021.** PAUP*: Phylogenetic Analysis Using PAUP, version 4.0b169.

806   https://paup.phylosolutions.com/.

807   **Taquet P. 1969.** Première découverte en Afrique d'un reptile captorhinomorphe (Cotylosaurien).

808   *Comptes Rendus de l'Académie des Sciences Paris D* **268**:779–781.

809   **Tsuji LA, Sidor CA, Steyer J-S, Smith RMH, Tabor NJ, Ide O. 2013.** The vertebrate fauna of

810   the Upper Permian of Niger—VII. Cranial anatomy and relationships of *Bunostegos*

811   *akokanensis* (Pareiasauria). *Journal of Vertebrate Paleontology* **33**(4):747–773.

812   **Vjushkov BP, Chudinov PK. 1957.** Otkrytie Kaptorinid v verkhnnej Permi SSSR [Discovery of

813   a captorhinid in the upper Permian of the USSR]. *Doklady Akademii Nauk SSSR*

814   **112**:523–536.

815

816   FIGURE CAPTIONS

817

818   Figure 1. **Location and geology maps.** (A) Pranhita-Godavari Valley in India, redrawn from

819   Ray & Bandyopadhyay (2003). (B) Permian fossil localities of the Kundarum Formation, near

820   the village Golet. (C) Republic of India overview.

821

822   Figure 2. **Reconstruction of the skull of *Indosauriscus kuttyi* gen. et sp. nov.** (A) right lateral,

823   (B) dorsal, and (C) ventral views. Abbreviations: ang, angular; bo, basioccipital; d, dentary; f,

824   frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pm, premaxilla; po,

825   postorbital; pp, postparietal; prf, prefrontal; pt, pterygoid; qj, quadratojugal; sm, septomaxilla;

826   sp, splenial; sq, squamosal; st, supratemporal; su, surangular.

827

828 Figure 3. *Indosauriscus kuttyi* **gen. et sp. nov., ISIR 233, holotype.** Illustrations and

829 photographs of partial skull with adducted mandible in (A) dorsal, (B) right lateral, (C) left

830 lateral and (D) anterior views. Abbreviations: ang, angular; d, dentary; f, frontal; j, jugal; l,

831 lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po,

832 postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q,

833 quadrate; qj, quadratojugal; sm, septomaxilla; sp, splenial; sq, squamosal; st, supratemporal; su,

834 surangular.

835

836 Figure 4. *Indosauriscus kuttyi* **gen. et sp. nov., ISIR 232 and 234, referred specimens.** (A)

837 Photograph of ISIR 234, maxillary tooth-plate dentition sections in dorsal view; anterior to the

838 top of image. (B) Photograph of lateral aspect of ISIR 232, skull showing left epipterygoid in

839 lateral view and Meckelian foramen of right mandibular ramus. Abbreviations: ep, epipterygoid;

840 mf, Meckelian foramen.

841

842 Figure 5. *Indosauriscus kuttyi* **gen. et sp. nov., referred specimen.** Illustrations and

843 photographs of ISIR 232, partial skull with braincase, mandible, and atlas-axis complex in (A)

844 palatal and (B) occipital views; an asterisk (*) indicates the quadrate foramen. Abbreviations:

845 ang, angular; ar, articular; atc, atlantal centrum; ati, atlantal intercentrum; atn, atlantal neural

846 arch; ax, axis vertebra; bo, basioccipital; d, dentary; ex, exoccipital; h, hyoid element; m,

847 maxilla; op, opisthotic; pal, palatine; pop, paroccipital process; pp, postparietal; pra, prearticular;

848 ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; so, supraoccipital; sp,

849 splenial; sq, squamosal; su, surangular; v, vomer; X, vagus foramen.

850

851 Figure 6. *Indosauriscus kuttyi* **gen. et sp. nov., ISIR 236, referred specimen.** Postcrania in (A)

852 dorsal and (B) ventral views. Abbreviations: ang, angular; ar, articular.

853

854 Figure 7. **Moradisaurine captorhinid interrelationships.** (A) Strict consensus of 4 trees

855 following phylogenetic analysis of a data matrix of 24 taxa and 79 characters; moradisaurine

856 branches in green; basal captorhinid branches in blue; outgroup branches in black. (B) Single

857 most parsimonious tree following phylogenetic analysis of reduced number of taxa, with

858 *Rhiodenticulatus heatoni* as the outgroup; basal captorhinid branches in blue; branches of North

859   American moradisaurines in solid green; moradisaurine branches in green. Bremer support

860   (Roman font, above branch) and bootstrap support (italicized font, below branch) values are

861   shown for clades. (C) Resolved moradisaurine topology from tree in C illustrating one

862   biogeographic scenario of two independent dispersals out of tropical western Euramerica;

863   branches of North American moradisaurines in open green; branches of extra-North American

864   moradisaurines in solid green. Arrow 1: dispersal of ancestor of *Labidosaurikos meachami* and

865   *Rothianiscus multidontus* into tropical western Euramerica (i.e. North America [NA]) from

866   extra-NA Pangea. Arrow 2: dispersal of ancestor of *Captorhinikos valensis* and *Sumidadectes*

867   *chozaensis* into NA from extra-NA Pangea. (D) Resolved moradisaurine topology from tree in C

868   illustrating alternate biogeographic scenario; branch colors as in C. Arrow 3: dispersal of

869   ancestor of clade containing *Gansurhinus naobaogouensis*, *L. meachami*, *R. multidontus*, *C.*

870   *valensis* and *S. chozaensis* into NA from extra-NA Pangea. Arrow 4: dispersal of *G.*

871   *naobaogouensis* into extra-NA Pangea from NA.

Figure 1

Location and geology maps

(A) Pranhita-Godavari Valley in India, redrawn from Ray & Bandyopadhyay (2003). (B) Permian fossil localities of the Kundarum Formation, near the village Golet, redrawn from Ray & Bandyopadhyay (2003). (C) Republic of India overview, redrawn from Ray & Bandyopadhyay (2003).
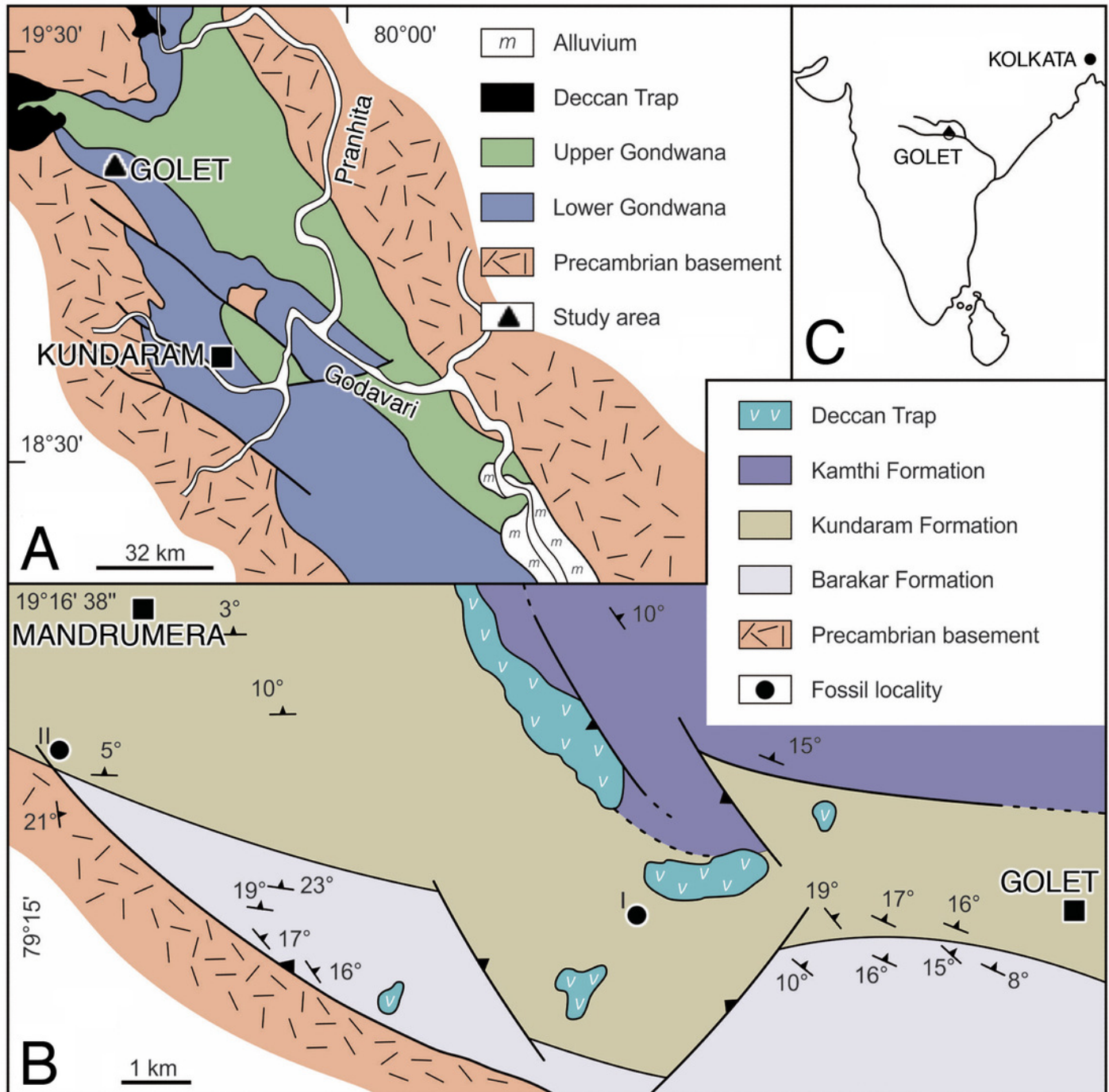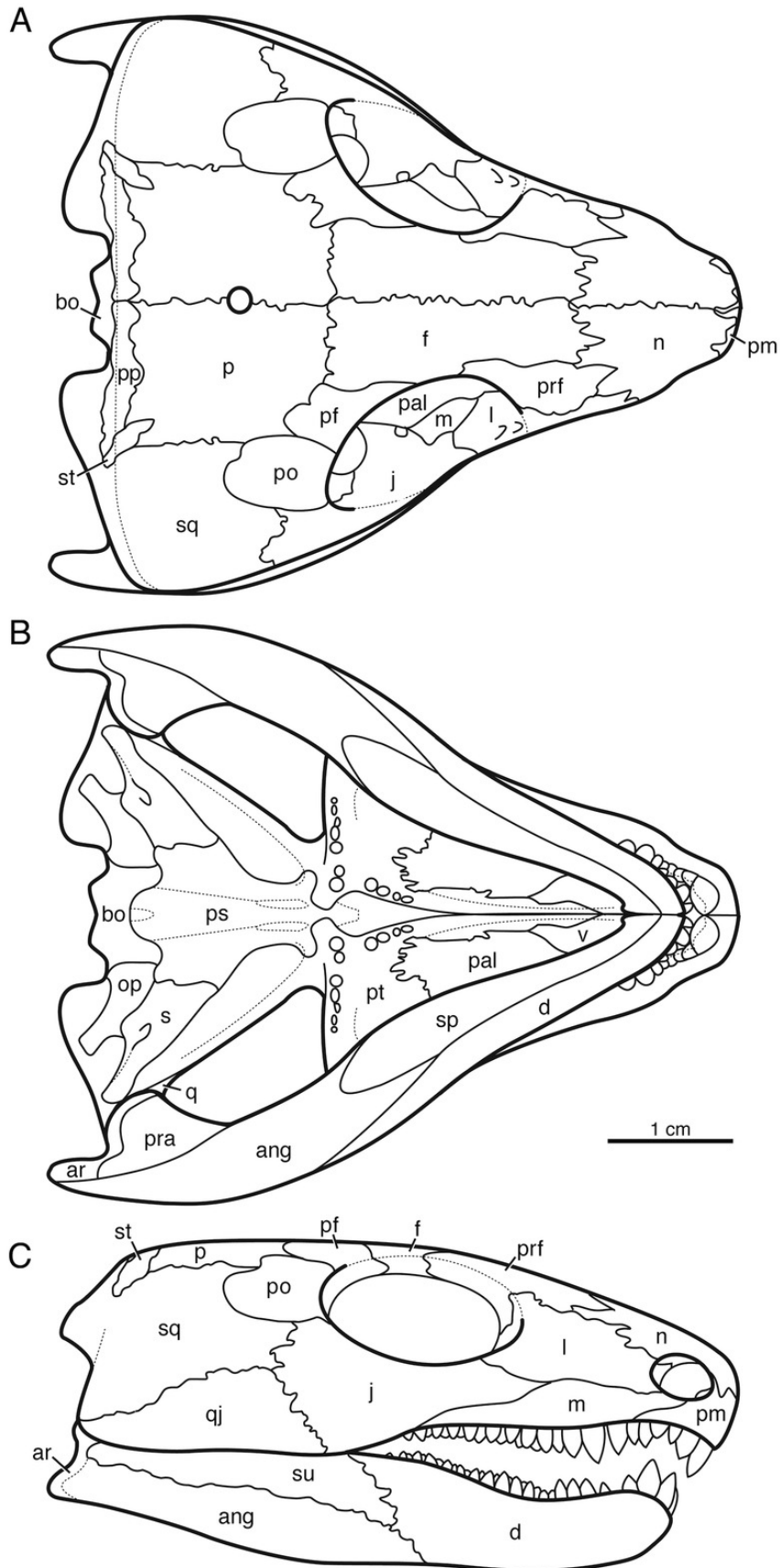
Figure 2

Reconstruction of the skull of *Indosauriscus kuttyi* gen. et sp. nov.

(A) right lateral, (B) dorsal, and (C) ventral views.

Figure 3

Indosauriscus kuttyi gen. et sp. nov., ISIR 233, holotype

~~Illustrations~~ and photographs of partial skull with adducted mandible in (A) dorsal, (B) right lateral, (C) left lateral and (D) anterior views. Abbreviations: ang, angular; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sm, septomaxilla; sp, splenial; sq, squamosal; st, supratemporal; su, surangular
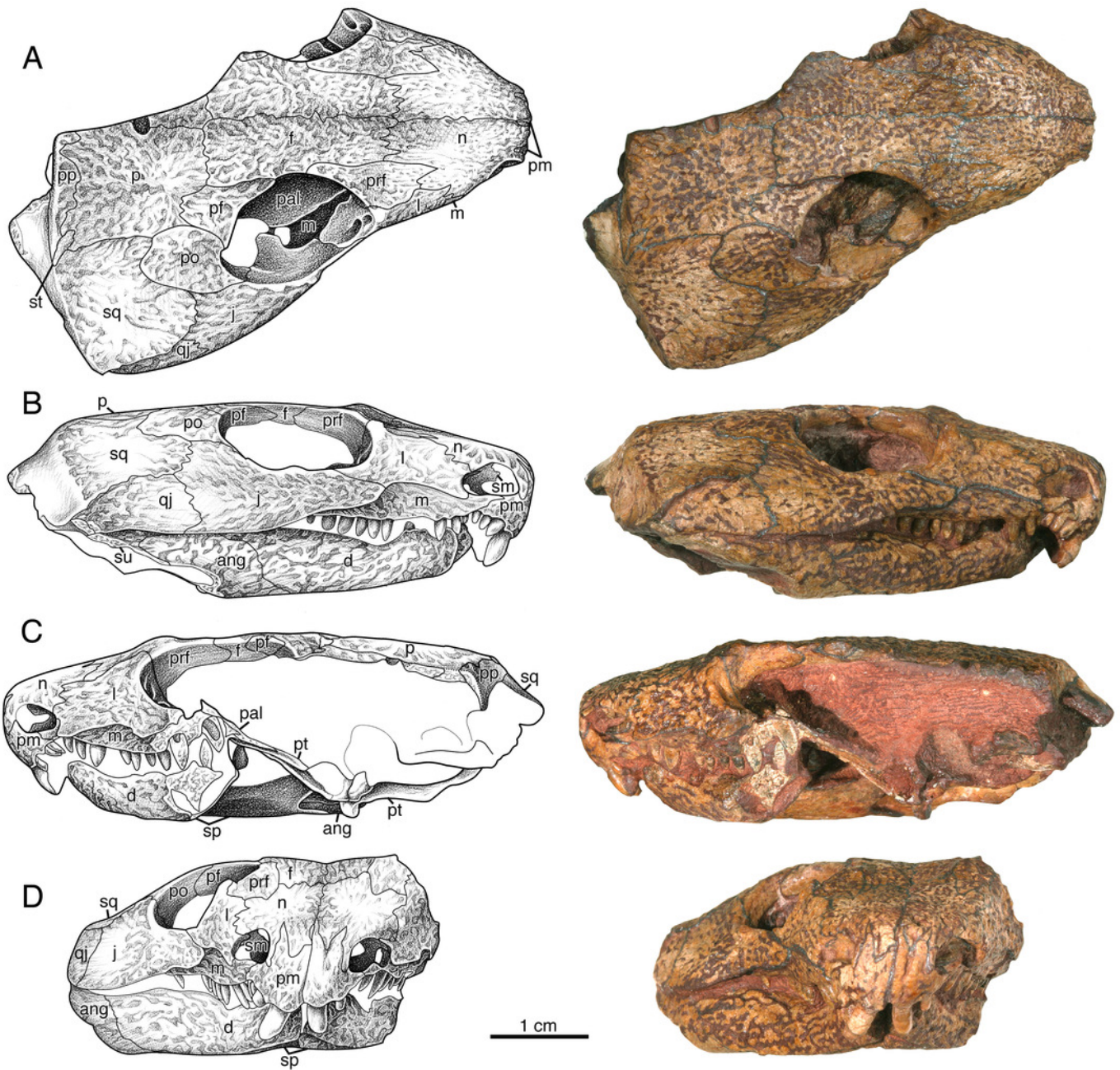
Figure 4

Indosauriscus kuttyi gen. et sp. nov., ISIR 232 and 234, referred specimens

(A) Photograph of ISIR 234, maxillary tooth-plate dentition sections in dorsal view; anterior to the top of image. (B) Photograph of lateral aspect of ISIR 232, skull showing left epipterygoid in lateral view and Meckelian foramen of right mandibular ramus. Abbreviations: ep, epipterygoid; mf, Meckelian foramen
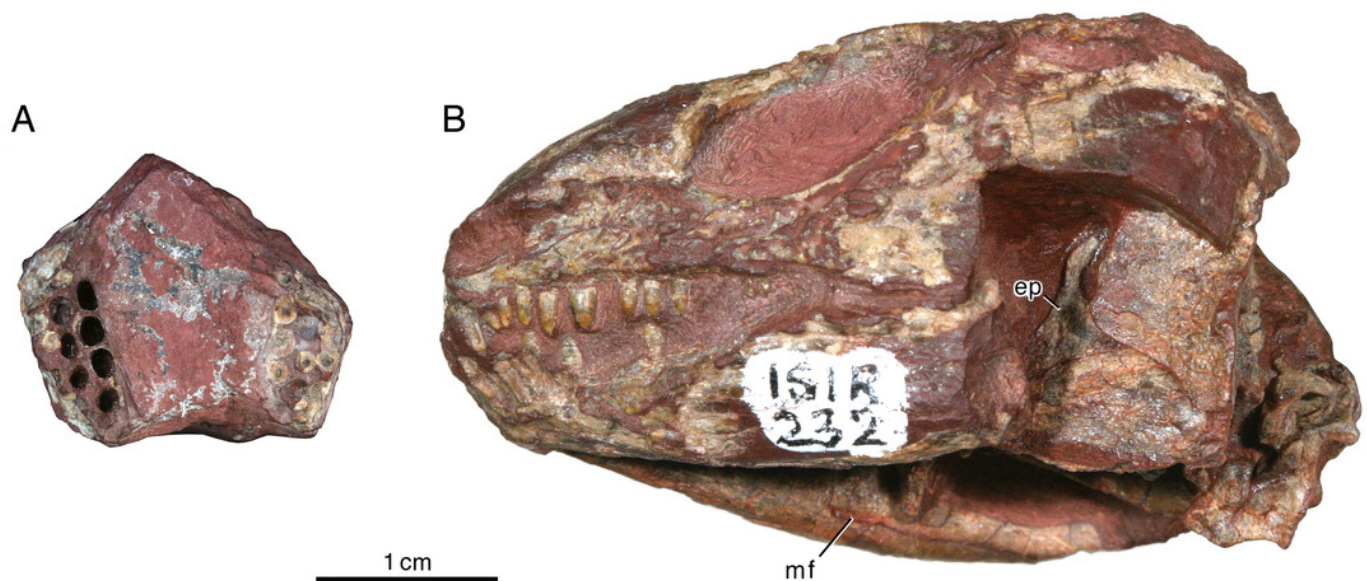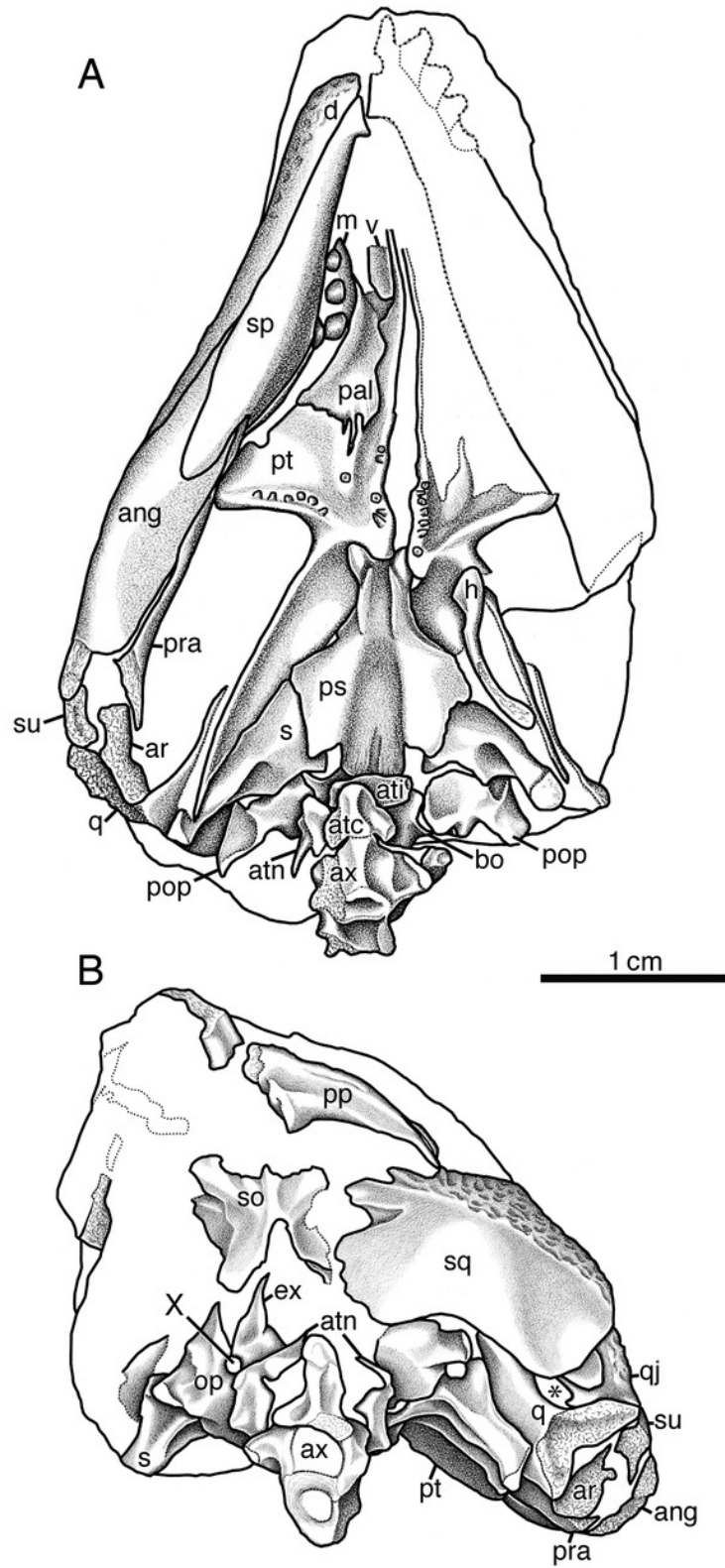
Figure 5

Indosauriscus kuttyi gen. et sp. nov., referred specimen

Illustrations and photographs of ISIR 232, partial skull with braincase, mandible, and atlas-axis complex in (A) palatal and (B) occipital views; an asterisk (*) indicates the quadrate foramen. Abbreviations: ang, angular; ar, articular; atc, atlantal centrum; ati, atlantal intercentrum; atn, atlantal neural arch; ax, axis vertebra; bo, basioccipital; d, dentary; ex, exoccipital; h, hyoid element; m, maxilla; op, opisthotic; pal, palatine; pop, paroccipital process; pp, postparietal; pra, prearticular; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; so, supraoccipital; sp, splenial; sq, squamosal; su, surangular; v, vomer; X, vagus foramen.
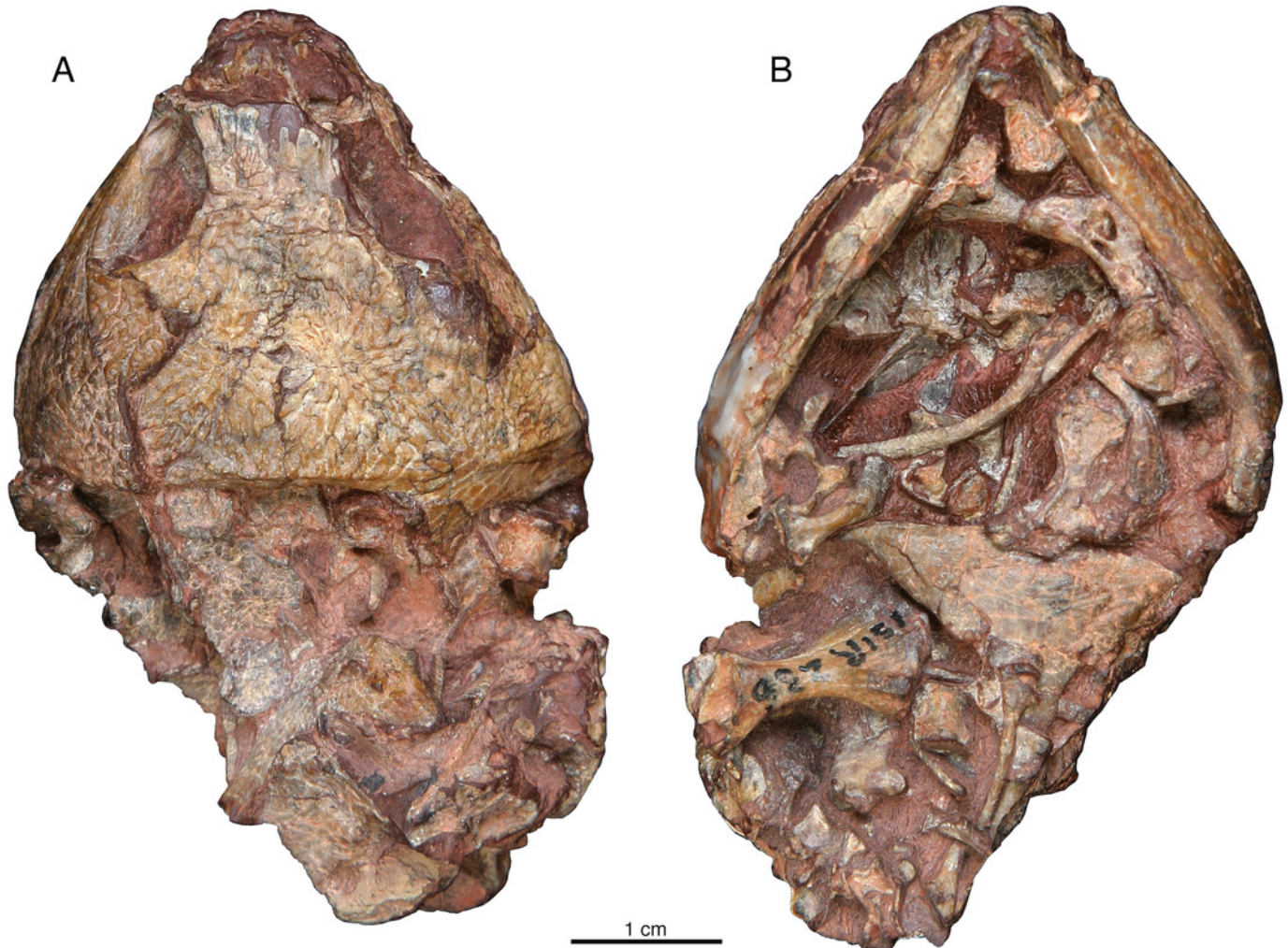
Figure 6

Indosauriscus kuttyi gen. et sp. nov., ISIR 236, referred specimen.

Skull and postcrania in (A) dorsal and (B) ventral views.

Figure 7

Moradisaurine captorhinid interrelationships.

(A) Strict consensus of 4 trees following phylogenetic analysis of a data matrix of 24 taxa and 79 characters; moradisaurine branches in green; basal captorhinid branches in blue; outgroup branches in black. (B) Single most parsimonious tree following phylogenetic analysis of reduced number of taxa, with *Rhiodenticulatus heatoni* as the outgroup; basal captorhinid branches in blue; branches of North American moradisaurines in solid green; moradisaurine branches in green. Bremer support (Roman font, above branch) and bootstrap support (italicized font, below branch) values are shown for clades. (C) Resolved moradisaurine topology from tree in C illustrating one biogeographic scenario of two independent dispersals out of tropical western Euramerica; branches of North American moradisaurines in open green; branches of extra-North American moradisaurines in solid green. Arrow 1: dispersal of ancestor of *Labidosaurikos meachami* and *Rothianiscus multidontus* into tropical western Euramerica (i.e. North America [NA]) from extra-NA Pangea. Arrow 2: dispersal of ancestor of *Captorhinikos valensis* and *Sumidadectes chozaensis* into NA from extra-NA Pangea. (D) Resolved moradisaurine topology from tree in C illustrating alternate biogeographic scenario; branch colors as in C. Arrow 3: dispersal of ancestor of clade containing *Gansurhinus naobaogouensis*, *L. meachami*, *R. multidontus*, *C. valensis* and *S. chozaensis* into NA from extra-NA Pangea. Arrow 4: dispersal of *G. naobaogouensis* into extra-NA Pangea from NA