A redescription of *Palaeogekko risgoviensis* (Squamata, Gekkota) from the Middle Miocene of Germany, with new data on its morphology

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After its original description, the Middle Miocene gekkotan *Palaeogekko risgoviensis* remained an enigma for palaeontologists, due to a rather poor knowledge of its osteology and relationships. Coming from a single locality in southern Germany, this gecko lived in central Europe during a period when a single gekkotan lineage (i.e. euleptine sphaerodactylids) is confidently reported to have inhabited the continent. However, it is unclear whether *P*. *risgoviensis* may represent a member of this same lineage or a second clade of Gekkota. In order to contribute to shed light on this issue, the type material of *P*. *risgoviensis* is here redescribed, refigured and extensively compared with extinct and extant geckos from Europe. A phylogenetic analysis is also conducted in order to investigate its relationships. The new observations confirm the validity of the German species as a distinct taxon, and exclude the previously-suggested chimeric status of the type material of this gecko (with the exception of a single dentary included in the type series, which clearly belong to a different lizard). Phylogenetic relationships of *Palaeogekko* are still unclear, though, with different positions within the gekkotan tree recovered for the taxon. Nevertheless, it is confidently supported as a non-eublepharid gekkonoid, in agreement with hypothesys presented by other scholars.

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11 **Abstract**

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13 an enigma for palaeontologists, due to a rather poor knowledge of its osteology and

14 relationships. Coming from a single locality in southern Germany, this gecko lived in central

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22 previously-suggested chimeric status of the type material of this gecko (with the exception of a

23 single dentary included in the type series, which clearly belong to a different lizard).

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25 within the gekkotan tree recovered for the taxon. Nevertheless, it is confidently supported as a

26 non-eublepharid gekkonoid, in agreement with hypothesys presented by other scholars.

27 **INTRODUCTION**

28 The beginning of the Miocene Epoch is considered to mark the moment when the current

29 European squamate fauna started assembling (Rage 2013; Villa & Delfino 2019b; Georgalis &

30 Scheyer 2021), with fossils related to extant species or species complexes even reported

31 already from the Early Miocene (for lizards, see e.g. Čerňanský 2010; Venczel & Hír 2013).

32 Changes in the environment around the Oligocene/Miocene transition were the prelude to a

33   subsequent faunal turnover facilitated by the establishment of a stable connection between

34   Eurasia and Africa and the return to a warm and humid climate during the Miocene Climatic

35   Optimum, both events occurring in the Early Miocene (Böhme 2003; Rage 2013; Georgalis et al.

36   2016). The turnover saw the appearance in Europe of several taxa that characterized the

37   European reptilian fauna in the Neogene (e.g. chameleons: Georgalis et al. 2016; glass lizards of

38   the genus *Pseudopus* Merrem, 1820: Čerňanský et al. 2015; Vasilyan et al. 2019; Villa et al.

39   2022a; monitor lizards: Ivanov et al. 2018; Villa et al. 2018; cobras: Szyndlar & Schleich 1993;

40   vipers: Szyndlar & Rage 1999, 2002), and in most cases survived in the continent through the

41   Quaternary and up to nowadays.

42   A possible exception to the Miocene roots pattern is modern European geckos, given that

43   fossils of the most widespread extant taxa are not known from fossiliferous deposits older than

44   the Upper Pliocene (Villa & Delfino 2019b). Only the sphaerodactylid *Euleptes* Fitzinger, 1843

45   has its first appearance in the Early Miocene (Müller 2001; Müller & Mödden 2001; Čerňanský

46   & Bauer 2010). Other sphaerodactylids related to the extant western Mediterranean endemic

47   *Euleptes europaea* (Gené, 1839) were present in Europe at least from the Eocene (Villa et al.

48   2022b), including several genera and species that represented the dominant clade of gekkotans

49   in Europe for most of the Cenozoic. This is in contrast to the modern situations that sees

50   phyllodactylids and gekkonids as the most widespread geckos north of the Mediterranean Sea.

51   Members of this sphaerodactylid lineage in the Miocene included at least two other *Euleptes*

52   species and two species referred to the genus *Gerandogekko* Hoffstetter, 1946.

53   The phylogenetic relationships of a fifth Miocene species, *Palaeogekko risgoviensis* Schleich,

54   1987, are unclear. It was described as a gekkonine gekkonid by Schleich (1987). Back then,

55   Gekkonidae was used in a wide sense, including all gekkotans exclusive of pygopodids, but

56   Schleich (1987) explicitly mentioned affinities with *Tarentola* Gray, 1825 and *Cyrtodactylus*

57   Gray, 1827 (in fact, *Mediodactylus* Szczerbak & Golubev, 1977, given that he was using

58   *Cyrtodactylus kotschyi*, now part of the other genus, for comparisons). Thus, *P. risgoviensis*

59   would be related to either phyllodactylids or gekkonids (in a modern sense) according to his

60   observations. Later on, Daza et al. (2014) commented on the species, stating that the available

61   information only allowed to exclude belonging to pygopodoids and eublepharids, in agreement

62   with previous conclusions, but preventing further discrimination between other clades within

63   gekkonoids. More recently, a phylogenetic analysis by Villa et al. (2022b) recovered *P.*

64   *risgoviensis* as an unstable taxon, but resulting topologies possibly placed it either as a crown

65   sphaerodactylid or as a stem pygopodoid. Considering all the possibilities suggested by the

66   different authors, *P. risgoviensis* may either represent another species related to the dominant

67   European sphaerodactylid lineage or the first evidence of a second gekkotan clade in Europe

68   already during the Miocene.

69   Until now, clarification of the taxonomy and phylogenetic affinities of *P. risgoviensis* was

70   hampered by a somehow scarce knowledge of its osteology, which has never been revised after

71   Schleich's (1987) original paper. The original description was rather synthetic and mostly

72   focused on presenting measurements and meristic features, and only part of the material was

73   properly figured. Thus, several aspects of the precise morphology of this gecko remained

74   difficult to assess. Moreover, our understanding of gekkotans osteology significantly increased

75   since the late 80s, in particular as far as the extant and extinct European taxa are concerned

76   (for these, see e.g. Daza et al. 2014, Villa et al. 2018). In light of all of this, a redescription of the

77   type material referred to *P. risgoviensis* under modern knowledge of gekkotan osteology is here

78   presented. Additionally, detailed comparisons particularly focused on other European

79   gekkotans and an attempt at better understanding the possible phylogenetic position of this

80   Middle Miocene gecko are also provided. This will provide new useful data also for future

81   studies further investigating the diversity and evolution of geckos in Europe and nearby

82   continents.

83   **MATERIAL AND METHODS**

84   The type material of *P. risgoviensis* is housed in the Bayerische Staatssammlung für

85   Paläontologie und Geologie (SNSB-BSPG), in Munich (Germany). Schleich (1987) originally

86   referred 118 specimens to his new species, including the holotype lower jaw, 90 dentaries, 23

87   maxillae, and four premaxillae. However, one of the dentaries, SNSB-BSPG 1970 XVIII 7262 (Fig.

88   1), has an open Meckelian fossa and cannot pertain to a gecko. Furthermore, it was not

89   possible to clearly locate two other dentaries, SNSB-BSPG 1970 XVIII 7249 and 7270, in the

90   available material. A single unnumbered specimen stored with the rest of the type series most

91   likely represents the former, even though measurements and tooth count do not exactly agree

92   with those reported by Schleich (1987: tab. 1). Revised measurements and counts of teeth and

93   foramina reported in the descriptions are based on the best-preserved specimens. Detailed

94   data for all specimens are provided in the Supplemental Data S1.

95   The anatomical terminology used in this paper follows Villa et al. (2018) and Villa & Delfino

96   (2019a). Measurements were taken with a digital caliper. Selected specimens were

97   photographed with a Leica M165 FC microscope equipped with a DFC450 camera and the Leica

98   Application Suite (LAS) 4.5. *Mediodactylus kotschyi* (Steindachner, 1870) is here used in a wide

99   sense, without separating it into the several species now recognised (see Speybroeck et al.

100   2020). This is not in opposition to the split, but simply to ease comparisons with the most-

101   widespread European extant geckos as defined by Villa et al. (2018). Comparisons are based on

102   the same specimens of extant gekkotans used by Villa et al. (2018), as well as on available

103   literature and personal observations (for *Gerandogekko arambourgi* Hoffstetter, 1946 and

104   *Geiseleptes delfinoi* Villa et al., 2022b) for extinct taxa.

105   For the phylogenetic analysis, Villa et al.'s (2022b) matrix was used, which is available in

106   MorphoBank (O'Leary & Kaufman 2012) at the following link:

107   http://morphobank.org/permalink/?P4069. *Palaeogekko risgoviensis* was rescored in Mesquite

108   3.70 (Maddison & Maddison 2021) after the new morphological information provided by the

109   updated description herein presented (see the Supplemental Data S2 for the revised scorings).

110   The analysis was run in TNT 1.5 (Goloboff et al. 2008; Goloboff & Catalano 2016). As in the

111   second iteration of the analysis by Villa et al. (2022b), *G. arambourgi* was removed and the

112   same six constraints were applied (all fossils retained as floating taxa). These constraints follow

113   the topology recovered from molecular data by Gamble et al. (2015). The matrix was analysed

114   using the New Technology search, with all options selected and the consensus stabilized five

115   times with a factor of 75. The "Collapse trees after search" option was selected, to avoid zero-

116   length branches in the individual resulting trees. A second round of tree bisection and

117   reconnection was run after the first New Technology search.

118   **SYSTEMATIC PALAEONTOLOGY**

119   Order Squamata Oppel, 1811

120   Infraorder Gekkota Camp, 1923

121   Superfamily Gekkonoidea Gray, 1825

122   Family incertae sedis

123   Genus *Palaeogekko* Schleich, 1987

124   Species *Palaeogekko risgoviensis* Schleich, 1987

125   **Holotype:** SNSB-BSPG 1970 XVIII 7300, a complete right lower jaw.

126   **Paratypes:** four premaxillae (SNSB-BSPG 1970 XVIII 7363/7366); 23 maxillae (SNSB-BSPG 1970

127   XVIII 7340/7362); 90 dentaries (SNSB-BSPG 1970 XVIII 7249/7299, 7301/7339).

128   **Type locality and age:** Steinberg, Nördlinger Ries, southern Germany; Middle Miocene, MN 6

129   (Heizmann & Fahlbusch 1983; Prieto & Rummel 2016).

130   **Emended diagnosis:** *Palaeogekko risgoviensis* is diagnosed by the following combination of

131   characters: 1) narrow ascending nasal process of the premaxilla, with a shallow expansion at

132   midheight; 2) shallow notch separating the palatal processes of the premaxilla; 3) absence of a

133   groove following the last ventrolateral foramen on the maxilla; 4) short and pointed posterior

134   process of the maxilla; 5) presence of a sigmoid and more-or-less vertically-directed carina

135   maxillaris on the maxilla; 6) anterior mylohyoid foramen present as a notch on the splenial; and

136   7) posterior surangular foramen not shifted dorsally.

137   **Remarks**

138   The dentary SNSB-BSPG 1970 XVIII 7262 (Fig. 1) does not actually pertain to a gecko. The

139   combination of a completely open Meckelian fossa, a narrow subdental shelf, and the

140   pleurodont dentition suggests it belongs to either a lacertoid or scincoid lizard, but the

141   preservation prevents a more precise referral. This specimen is here listed within the paratypes

142   of *P. risgoviensis*, in agreement with Schleich (1987), but it is not considered in the descriptions

143   and the rest of the paper.

144   **Description of the holotype**

145   The holotype SNSB-BSPG 1970 XVIII 7300 (Fig. 2) is an almost complete right lower jaw, missing

146   only the symphyseal region of the dentary. The overall shape of the jaw is rather slender and

147   straight. On the lateral side, a knob-like swelling is visible at the level of the contact between

148   the compound bone and the dentary. The swelling partially obscures the suture between the

149   two skeletal elements. It may have a pathological origin, as already noted by Schleich (1987).

150   The preserved length of the jaw is 13 mm; the length of dentary tooth row is at least 6.38 mm

151   (not considering the missing portion). The dentary carries 30 tooth positions in the preserved

152   part.

153   **Dentary.** The dentary is narrow and elongated, with a straight ventral margin. In medial view

154   (Fig. 2C), the Meckelian fossa is almost completely closed in a narrow tubular structure, which

155   opens posteriorly in a U-shaped notch. The extension of this notch related to the alveolar shelf

156   is not clearly measurable, but it was likely one fifth or smaller. Dorsally, a low subdental ridge is

157   present, as well as a wide and deep sulcus dentalis. The dentary bears a long, narrow and

158   pointed inferior posterior process and a short and forked superior posterior process. In the

159   superior process, the ventral projection seems slightly longer than the dorsal one. The lateral

160   surface is smooth (Fig. 2B), with at least four mental foramina; most probably, the number of

161   foramina was higher in origin, considering the broken anterior end of the bone.

162   **Splenial.** The splenial (Fig. 2C) is preserved, even though damaged. It is a small and slender

163   splint of bone, with pointed anterior and posterior ends. The posterior end of the bone does

164   not bend ventrally to the jaw. Anteriorly, the anterior mylohyoid foramen is clearly represented

165   by a long and shallow notch along the ventral margin of the bone. The smaller anterior inferior

166   foramen is also visible as a notch in the specimen as it is preserved, but this could be the result

167   of a clear breakage of the anterodorsal part of the splenial.

168   **Coronoid.** The coronoid is strongly concave in medial direction (Fig. 2A). The anterior part of

169   the bone is composed by a long and wide anteromedial process and a shorter (roughly half the

170   length of the former) labial process. Both processes are pointed. The coronoid process is

171   straight and dorsally pointed. The posteromedial process is long and slender, with a pointed

172   end. An osseous lamina connects the coronoid process and the posteromedial process on the

173   medial side of the bone.

174   **Compound bone.** The compound bone is completely fused. On the medial side (Fig. 2C), the

175   adductor fossa is rather narrow and anteroposteriorly elongated. Ventral to the anterior end of

176   the fossa, a very low osseous expansion in visible in dorsal view (Fig. 2A), even though it is not

177   clear whether this could be pathological in nature or not. The articular condyle is subcircular in

178   posterodorsal view, with a longitudinal swelling in the middle. The swelling divides the articular

179   surface into two areas, the lateral one slightly larger than the medial one. The base of the

180   retroarticular process is moderately slender, but the process expands posteriorly. The posterior

181   margin of the retroarticular process is broken off, preventing a clear recognition of its complete

182   shape. Nevertheless, the expansion appears rather strong. On the dorsomedial side of the

183   process, the foramen for the chorda tympani is wide and elongated. A second, smaller foramen

184   is also visible by the anterodorsal corner of the medial surface of the retroarticular process. A

185   distinct lateral crest is not visible on the preserved lateral surface of the process. The lateral

186   surface of the compound bone is generally smooth (Fig. 2B). Ventral to the contact with the

187   coronoid, there is a wide anterior surangular foramen, opening in lateral direction. This

188   foramen is completely within the compound bone, with no contribution of neither the coronoid

189   or the dentary to its borders. There is no groove associated to it. The posterior surangular

190   foramen is not shifted dorsally, opening more or less at midheight of the bone. A low ridge

191   running from the posterior surangular foramen to the articular condyle is present. Ventral to

192   the same foramen, a shallow but distinct sunken area is visible, being narrow and

193   anteroposteriorly elongated. There is no posterior mylohyoid foramen.

194   **Dentition.** Teeth (Fig. 2, 3A) are pleurodont and homodont. They are closely spaced, narrow

195   and subcylindrical. They narrow distinctly towards the crown, ending with a pointed tip. They

196   are exposed laterally for about one third of their height. The crown is bicuspid, with a labial and

197   a lingual cusps. There is no striation neither labially nor lingually.

198   **Description of the paratypes**

199   All paratypes are moderately small and slenderly built.

200   **Premaxillae (Fig. 4).** The unpaired premaxillae bear well-developed palatal processes, which are

201   separated posteromedially by a shallow and wide notch. Thus, the processes form a long

202   subtrapezoidal lamina extending posteriorly from the alveolar portion of the bone. The width of

203   the alveolar portion varies between 2.08 mm to 2.21 mm. The ascending nasal process is

204   moderately long and narrow. It has a more or less constant width (slightly narrowing by the tip

205   only in SNSB-BSPG 1970 XVIII 7366; Fig. 4G-H), showing only a variable but always poorly-

206   developed expansion roughly at midheight. The end of the process appears rounded, not

207   pointed, but it is not clear if this could be just an artifact due to breakage. The anterior surface

208 is smooth, whereas the posterior one is characterized by the presence of the septonasal crest.

209 This crest is well distinct and blunt in the ventral half of the process. In the dorsal half, it varies

210 from absent, to very poorly visible, to distinct and sharp. In the same portion of the process, the

211 long and narrow articular surfaces for the anteromedial processes of the nasals are visible by

212 the sides of the crest. The foramina for the longitudinal canals are small. By each side of the

213 ascending nasal process, these foramina are associated to an accessory foramen, which is

214 located dorsal to the former. Only on the right side of SNSB-BSPG 1970 XVIII 7366, this

215 accessory foramen is absent.

216 **Maxillae (Fig. 5).** In medial view, the tooth row runs along the whole length of the maxilla. The

217 length of the row in the best-preserved specimens ranges from 5.88 mm to 6.96 mm. The row

218 of a possibly juvenile specimen, SNSB-BSPG 1970 XVIII 7361 (Fig. 5S), is 4.56 mm long.

219 Anteriorly, the maxilla displays a well-developed anterior premaxillary process. In dorsal view,

220 the latter displays a shallow, U-shaped anterior concavity (Fig. 5G, P). The anterolateral process

221 varies from almost absent to short, whereas the anteromedial one is more developed. When

222 developed, the anterolateral process is anteriorly truncated. The anteromedial one, on the

223 other hand, is more pointed, at least based on the only specimen in which it is well preserved,

224 SNSB-BSPG 1970 XVIII 7362; specimens where the process appears truncated are indeed

225 present, but a close inspection suggests that the process is broken in these cases. The

226 moderately wide vomeronasal foramen is located in the middle of the dorsal surface of the

227 anterior premaxillary process. The facial process is roughly half as long as the entire maxilla or

228 slightly less than that. It is laminar and has smooth medial and lateral surfaces. On the medial

229 side, a very low and more-or-less sigmoid carina maxillaris (medial ridge sensu Villa et al. 2018)

230   is present close to the anterodorsal corner (Fig. 5A, E, Q). The main course of the carina is

231   vertically oriented, not inclined. The anterior margin of the process is straight, slightly inclined

232   towards the anterior. This inclination originates a short point extending from the top of the

233   margin. The anterodorsal margin is gently oblique. The posterodorsal part of the process is

234   missing or strongly damaged in all specimens, but the preserved portion of the posterior margin

235   in at least some of them suggests that this was straight and steeply inclined (note that this

236   morphology was figured in the drawings by Schleich, 1987: fig. 6). The superior dental foramen

237   is located dorsally on the palatal shelf, by the end of the facial process. It is wide and opens

238   posteriorly, continuing on a shallow and wide groove on the posterior process. There is no

239   lacrimal groove. The posterior process is pointed and rather short, never exceeding the facial

240   process in length. There is no longitudinal groove following the last ventrolateral foramen

241   laterally. On the lateral surface of the maxilla, the ventrolateral foramina range from five to

242   eight in number. A second row made up by two to seven foramina is also present dorsal to the

243   ventrolateral ones, by the base of the facial process.

244   **Dentaries (Fig. 6).** Paratype dentaries generally resemble the homologous bone of the holotype

245   in morphology. They are slenderly built, with a closed Meckelian fossa. The tubular structure

246   closing the fossa narrows anteriorly and opens posteriorly with a V-shaped (rarely U-shaped)

247   notch that is about as long as one fifth of the tooth row. Only in two specimens, SNSB-BSPG

248   1970 XVIII 7308 and SNSB-BSPG 1970 XVIII 7310, this notch is shorter, about one seventh and

249   one sixth of the tooth row length respectively. Anteriorly, the mandibular symphysis is narrow

250   and slightly inclined in dorsal direction. Ventral to the symphysis, the Meckelian fossa opens on

251   the ventral surface of the dentary in a short longitudinal groove. The dentaries display a distinct

252   subdental ridge (less defined in some cases: e.g. SNSB-BSPG 1970 XVIII 7252), marking a deep

253   and wide sulcus dentalis. The inferior posterior process is long and pointed. The superior

254   posterior process is short and forked, being made up by two triangular projections separated by

255   a notch. When preserved, the ventral projection is longer than the dorsal one. The lateral

256   surface of the dentaries is smooth, with four to seven mental foramina. The ventral margin is

257   straight in medial and lateral views. The length of the tooth row in the best-preserved

258   specimens goes from 3.92 mm to 7.81 mm.

259   **Splenial.** SNSB-BSPG 1970 XVIII 7281 also preserves a fragment of splenial, which is partially

260   fused with the dentary. The preserved portion is only the anterior half of the bone, which

261   appears small and laminar. As in the holotype lower jaw, the anterior mylohyoid foramen is

262   present as a shallow and wide notch on the ventral margin, being completed by the dentary.

263   The smaller and circular anterior inferior foramen pierces the splenial, thus possibly confirming

264   the supposed taphonomical origin of the condition seen in the holotype.

265   **Dentition.** The dentition of the paratypes (Fig. 3B-D) shares the same morphology as the

266   holotype. The only possible difference is that, in some specimens, teeth are exposed laterally

267   for more than one third of their height, even though apparently not reaching half of the height

268   exposed. Tooth-number ranges are as follows: 10 to 11 for premaxillary teeth; 26 to 29 for

269   maxillary teeth (24 in the likely juvenile SNSB-BSPG 1970 XVIII 7361); 30 to 37 in dentary teeth

270   (23 in the juvenile SNSB-BSPG 1970 XVIII 7291 and 27 in the juveniles SNSB-BSPG 1970 XVIII

271   7288 and SNSB-BSPG 1970 XVIII 7290).

272   **PHYLOGENETIC ANALYSIS**

273   The constrained analysis recovered 66 most-parsimonious trees, with a length of 784 steps. The

274   strict consensus tree (Fig. 7A; consistency index: 0.552; retention index: 0.33) shows a polytomy

275   at the base of non-eublepharid gekkonoids, including *Palaeogekko*. Resolution can be improved

276   only by pruning *Palaeogekko* itself and *Laonogekko lefevrei* Augé, 2003, even though still

277   maintaining an unresolved Sphaerodactylidae (Fig. 7B). Several alternative positions are

278   possible for the two pruned taxa. A survey of the resulting most-parsimonious trees revealed

279   that in about 18% of the cases (12 trees out of 66) *Palaeogekko* is recovered in a polytomy with

280   Phyllodactylidae + Gekkonidae and Sphaerodactylidae, either alone or in a clade with

281   *Laonogekko* Augé, 2003. Subsequent most-recovered positions are: 1) sister to the clade of

282   non-eublepharid gekkonoids; 2) sister to *Tarentola mauritanica* (Linnaeus, 1758), the only

283   phyllodactylid present in the analysis; 3) sister to *Laonogekko* + Sphaerodactylidae; and 4)

284   crown sphaerodactylid. Each of these cases is recovered in nine trees (about 14%). Less-

285   recovered positions (three trees each: about 5%) are: 1) sister to the clade including

286   Phyllodactylidae + Gekkonidae and Sphaerodactylidae, but in a clade with *Laonogekko*; 2) Sister

287   to *T. mauritanica*, but in a clade with *Laonogekko*; 3) crown gekkonid, in a clade with

288   *Laonogekko* that is sister to *Hemidactylus turcicus* (Linnaeus, 1758); 4) sister to

289   Sphaerodactylidae, in a clade with *Laonogekko*; 5) sister to Sphaerodactylidae, with *Laonogekko*

290   in a more early-branching position; and 6) sister to Sphaerodactylidae, including *Laonogekko*.

291   **DISCUSSION**

292   **The taxonomic identity of *Palaeogekko risgoviensis***

293   In their review of fossil gekkotans, Daza et al. (2014) raised the matter of multiple species

294   possibly being represented in the type material of *P. risgoviensis*. According to these authors,

295   this was mainly suggested by heterogeneity in the meristic and morphometric data as reported

296   by Schleich (1987). The data presented herein show that the revised measurements and

297   tooth/foramina counts taken on the best-preserved specimens (see Supplemental Data S1)

298   agree with the ranges observed for single species of extant European geckos by Villa et al.

299   (2018). Furthermore, general morphology is comparable within all *Palaeogekko* fossils

300   representing the same skeletal element (except of course for the non-gekkotan SNSB-BSPG

301   1970 XVIII 7262; see Material and Methods section). Variation is indeed present in a few

302   features: 1) development of the dorsal half of the septonasal crest (premaxilla); 2)

303   presence/absence of accessory foramina related to the ones of the longitudinal canals

304   (premaxilla); 3) development of the anterolateral process (maxilla); 4) shape and length of the

305   posterior notch on the Meckelian fossa (dentary); 5) development of the subdental ridge

306   (dentary); and 6) lateral exposure of the teeth (dentition). For at least some of these features,

307   intraspecific variation is known in extant geckos or other lizards. Different development of the

308   dorsal half of the septonasal crest is reported for lacertid lizards, and a trend of increasing

309   development with growth is known for the anguid *Anguis* Linnaeus, 1758 (Villa & Delfino

310   2019a). Lacertids also display variation in the presence of accessory foramina related to the

311   longitudinal canals in the premaxilla (Villa & Delfino 2019a). The anterolateral process is

312   variable in *M. kotschyi*, which has either a little process or no visible process at all (Villa et al.

313   2018) in a similar way to *P. risgoviensis*. In most cases, variable features of the German species

314   are mainly represented in one of the different conditions, with the second one being only rarely

315   observed. This is the case for the accessory foramina on the premaxilla, the different shape and

316   length of the posterior notch in the dentary, and the development of the subdental ridge.

317 Missing variation in features like these in extant European gekkotans may be linked with a

318 lower sampling of skeletons of extant animals in osteological works dealing with these reptiles

319 (such as the one by Villa et al. 2018), compared with the higher number of available fossil

320 specimens for *P. risgoviensis* (in particular as far as the dentaries are concerned). Given the

321 overall similarity in both morphology and size, the six above-mentioned features are herein

322 considered as subject to intraspecific variation, and all the type material of *P. risgoviensis* as

323 pertaining to a single species. A few smaller remains (e.g. SNSB-BSPG 1970 XVIII 7288, SNSB-

324 BSPG 1970 XVIII 7290, SNSB-BSPG 1970 XVIII 7291, and SNSB-BSPG 1970 XVIII 7361) most likely

325 represent juvenile individuals.

326 **Comparison with extinct European taxa.** Schleich (1987) mostly based the description and

327 diagnosis of his new species on meristics and morphometry, but more detailed morphological

328 comparisons can be provided to better understand differences and affinities of *P. risgoviensis*

329 with other extinct and extant European gekkotans (see also Supplementary Data S3).

330 *Palaeogekko* cannot be compared with *Rhodanogekko vireti* Hoffstetter, 1946 and the recently-

331 described *Dollogekko dormaalensis* Čerňanský et al., 2022, however, because these two species

332 are only known from a single isolated frontal each. It cannot be compared with *Yantarogekko*

333 *balticus* Bauer et al., 2005 either, because the latter is preserved in amber. When it comes to

334 other species, for which bones that are also preserved in the material referred to *Palaeogekko*

335 are known, one of the most interesting features to be evaluated is the groove following the last

336 ventrolateral foramen on the maxillae. This is absent in *Laonogekko* (Augé 2003; Daza et al.

337 2014) and all non-sphaerodactylid extant European gekkotans (Villa et al. 2018) and is one of

338 the main features of euleptine geckos (Villa et al. 2022b), being present in all of them but *G.*

339   *arambourgi* (unknown for *Gerandogekko gaillardi* Hoffstetter, 1946). It is absent in *P.*

340   *risgoviensis*.

341   Further differences are present between *Palaeogekko* and euleptines, but there are also shared

342   features. The smooth lateral surface of the maxilla, for example, is shared with *Euleptes* and

343   *Geiseleptes* Villa et al., 2022b, but not *Cadurcogekko* Hoffstetter, 1945. The presence of an

344   anterior point on the facial process is also shared with almost all euleptines (unknown in

345   *Geiseleptes* and *Gerandogekko*), even though the point is longer in *E. europaea* and *Euleptes*

346   *gallica* Müller, 2001 (Müller 2001; Villa et al. 2018) compared to *Palaeogekko*. *Cadurcogekko*

347   clearly differs from *Palaeogekko* also in the presence of a postnarial anterodorsal depression

348   (Augé 2005; Daza et al. 2014; Bolet et al. 2015; Georgalis et al. 2021), with *Cadurcogekko*

349   *piveteaui* Hoffstetter, 1946 further presenting, in contrast to *Palaeogekko*, a marked and wide

350   articulation surface with the nasal on the medial surface of the facial process and a lower count

351   of maxillary teeth, dentary teeth, and ventrolateral foramina. The other undisputed Palaeogene

352   euleptine, *Geiseleptes*, is larger than *Palaeogekko* and possesses a longer posterior process of

353   the maxilla and, possibly, a dorsally-shifted posterior surangular foramen (Villa et al. 2022b).

354   Within Miocene euleptines, comparisons between *Palaeogekko* and the two species of

355   *Gerandogekko* is difficult and insufficient, because of the bad preservation of the maxillae and

356   dentaries known for this French genus (Hoffstetter 1946; Daza et al. 2014). At least *G.*

357   *arambourgi* have a long posterior process of the maxilla with a rounded end (Hoffstetter 1946:

358   fig. 3C; pers. Obs.), but the single topotypic maxilla is missing part of the anterior half of the

359   bone and further material is needed in order to better evaluate this morphology possibly

360   discriminating the species from *P. risgoviensis*. In this sense, it has to be noted that the only

361   known maxilla of *G. gaillardi* seems to have a shorter posterior process, even though its distal

362   end is broken off (Hoffstetter 1946: fig. 4B; Daza et al. 2014: fig. 7C,D). In both the maxillae of

363   *G. arambourgi* and *G. gaillardi*, the facial process is not preserved, further complicating the

364   comparison with *P. risgoviensis*. It is easier, on the other hand, to differentiate *Palaeogekko*

365   from all species of *Euleptes*. The most extensive comparison possible is of course with the

366   extant *E. europaea*, which displays a set of characters that allow to discriminate each skeletal

367   element known for *P. risgoviensis* from the corresponding ones of the European leaf-toed

368   gecko. Apart for the already mentioned presence of the groove following the last ventrolateral

369   foramen in the extant species, these include (Villa et al. 2018): 1) the arrow-shaped ascending

370   nasal process of the premaxilla; 2) the long and posteriorly-rounded posterior process of the

371   maxilla; 3) the absence of a distinct carina maxillaris; 4) the longer extension of the posterior

372   notch of the Meckelian fossa in the dentary; 5) the complete closure of the anterior mylohyoid

373   foramen; 6) the ventral bending of the posterior end of the splenial; 7) the rounded end of the

374   coronoid process; 8) the rounded distal end of the posteromedial process of the coronoid; and

375   9) the dorsally-shifted posterior surangular foramen. Features 1 and 4 in this list apply to *E.*

376   *gallica* as well, when this extinct species is compared with *Palaeogekko*. In addition, tooth

377   count is slightly higher in the premaxilla and slightly lower in the maxilla of *Palaeogekko* as

378   compared to *E. gallica* (Müller 2001; Čerňanský & Bauer 2010; Daza et al. 2014). In contrast to

379   *E. europaea*, *Palaeogekko* shares with both extinct *Euleptes* species, *E. gallica* and *Euleptes*

380   *klembarai* Čerňanský et al., 2018, the presence of a carina maxillaris (Müller 2001; Čerňanský &

381   Bauer 2010; Daza et al. 2014; Čerňanský et al. 2018), which is however more distinct, straight

382   and more posterodorsally directed in the two extinct *Euleptes*. A peculiar combination of

383   characters is apparently displayed by the material referred to *Euleptes* sp. from the

384   Oppenheim/Niersten quarry, in Germany, which include arrow-shaped premaxillae with eight

385   or 10 teeth and at least one maxilla with a sigmoid carina maxillaris more similar to the one of

386   *Palaeogekko* than to other extinct *Euleptes* (at least based on the drawings provided by Müller

387   & Modden, 2001: fig. 1). The rest of the maxilla seems rather comparable with *Palaeogekko* as

388   well (i.e. short and pointed posterior process, smooth lateral surface), but the anterior point of

389   the facial process appears longer and a posterior groove follows the last ventrolateral foramen.

390   The last fossil species that can be compared with *P. risgoviensis* is *L. lefevrei*. Similar to

391   *Palaeogekko*, the maxilla of *Laonogekko* has no groove associated with the last ventrolateral

392   foramen, a short anterior point of the facial process, a smooth lateral surface, and a sigmoid

393   carina maxillaris (Augé 2003, 2005; Daza et al. 2014). However, *Palaeogekko* clearly differs from

394   this Eocene species based on: 1) a steeper posterior margin of the facial process; 2) the absence

395   of a marked articulation surface with the nasal on the medial surface of the facial process

396   ("inner ledge" sensu Daza et al. 2014); and 3) a lower number of maxillary teeth. In the original

397   descriptions made by Augé (2003, 2005), *Laonogekko* also had a higher number of dentary

398   teeth, but Daza et al. (2014) estimated a lower tooth count for the most preserved dentary,

399   which fits the range of *P. risgoviensis*.

400   **Comparison with extant European taxa.** In a similar way to *E. europaea*, other extant, non-

401   sphaerodactylid European geckos also allow more detailed comparisons with *Palaeogekko* than

402   the mentioned extinct species. Both differences and similarities can be highlighted, based on

403   the morphological data reported by Villa et al. (2018). *Palaeogekko* differs from all *H. turcicus*,

404   *M. kotschyi*, and *T. mauritanica* in having: 1) a shallow notch separating the palatal processes of

405   the premaxilla (this feature is shared with *E. europaea*); and 2) a shallow expansion at

406   midheight of the ascending nasal process. The ascending nasal process is also not expanded at

407   the distal end as it is in *M. kotschyi*. The maxilla of the German species has a well-developed

408   and pointed anteromedial process like *T. mauritanica* (and *E. europaea*), but not *H. turcicus* and

409   *M. kotschyi*. The anterior margin of the facial process is inclined anteriorly in *P. risgoviensis*, *E.*

410   *europaea*, and *H. turcicus*, and vertical in *M. kotschyi*. In *T. mauritanica*, it presents a small

411   notch, unlike *P. risgoviensis*. The smooth lateral surface is shared with all species (including *E.*

412   *europaea*), but *H. turcicus*. The maxilla of the latter species also differs from the one of

413   *Palaeogekko* in the presence of the lacrimal groove and the absence of a strong anterior point

414   on the facial process, but they similarly display a distinct carina maxillaris. Nevertheless, the

415   latter is more vertically oriented in *P. risgoviensis* than in *H. turcicus*, whose carina is

416   posterodorsally directed. As far as the dentary is concerned, the extension of the posterior

417   notch of the Meckelian fossa is longer in *H. turcicus*, but similar to *Palaeogekko* in *M. kotschyi*

418   and *T. mauritanica*. The dentary of *T. mauritanica* differs from that of *P. risgoviensis*, however,

419   because the anterior opening of the Meckelian fossa is not continued into a groove in the

420   phyllodactylid. The splenial of *P. risgoviensis* is comparable with the one of *M. kotschyi* in both

421   the anterior mylohyoid foramen present as a notch on the ventral margin of the bone and the

422   posterior end of the bone not bending ventrally. Both these features are different in *H. turcicus*,

423   whereas *T. mauritanica* has a splenial with a bending posterior end but can present both a

424   notch-like or, more rarely, completely-closed anterior mylohyoid foramen. In the end, *P.*

425   *risgoviensis* shares with both *H. turcicus* and *M. kotschyi* a pointed posteromedial process of the

426   coronoid and a posterior surangular foramen not shifted dorsally. Both these features are

427   different in *T. mauritanica*, which shows a rounded process and a shifted foramen.

428   In terms of measurements and meristic characters, *Palaeogekko* compares with *H. turcicus* and

429   *M. kotschyi* in premaxillary width and tooth-row length of both maxillae and dentaries, whereas

430   it is larger than *E. europaea* and smaller than *T. mauritanica*. It has more teeth than *E. europaea*

431   in the premaxilla, but a similar number to other European extant geckos. Total counts for

432   maxillary and dentary teeth are comparable with all four extant species. Tooth density indexes

433   (Tab. 1) for premaxillae, maxillae, and dentaries are lower in *Palaeogekko* than in *E. europaea*,

434   higher than in *T. mauritanica*, and comparable with *H. turcicus* and *M. kotschyi*, thus following

435   an inverted pattern then the one shown by measurements.

436   ***Palaeogekko risgoviensis* as a distinct species.** Putting together all the information presented

437   above, *Palaeogekko* clearly stands out as different from almost all European geckos with which

438   it can be compared, both extinct and extant. Uncertainties remains only on the characters

439   possibly discriminating this Middle Miocene German species with the French *Gerandogekko*,

440   remains of which come from Lower and Upper Miocene deposits (Hoffstetter 1946; Daza et al.

441   2014). This is mainly due to the facts that the most significant fossils of both *Gerandogekko*

442   species are frontals, an element that is unknown for *Palaeogekko*, and that maxillae and

443   dentaries of the French species are insufficiently preserved. The different morphologies shown

444   by the posterior processes of the maxillae of *G. arambourgi* and *G. gaillardi* further complicates

445   this situation, given that only the long and rounded process of the former undisputedly differs

446   from the condition observed in maxillae of *Palaeogekko*. Whether this means that *P.*

447   *risgoviensis* is somehow related with at least *G. gaillardi* or even with *Gerandogekko* as a whole

448   cannot be stated pending the recovery of further fossils (i.e. a frontal referrable to *P.*

449   *risgoviensis* or better-preserved maxillae of the two *Gerandogekko* species). For the time being,

450   *P. risgoviensis* can be maintained as a distinct species, living in central Europe in a moment (MN

451   6) when only one other gecko is currently known to have been present: the Slovakian euleptine

452   *E. klembarai*.

453   **Phylogenetic relationships of *Palaeogekko risgoviensis***

454   Available data and phylogenetic data matrixes still fail to confidently clarify the phylogenetic

455   relationships of *P. risgoviensis*. The German species is recovered in several possible positions

456   within the gekkotan tree by the phylogenetic analysis herein presented, including as a stem

457   non-eublepharid gekkonoid, a possible phyllodactylid (or at least related to the only

458   phyllodactylid in the analysis, *T. mauritanica*), a crown gekkonid, and either a stem or crown

459   sphaerodactylid. Thus, the new analysis concurs with Daza et al. (2014) in the non-eublepharid

460   gekkonoid nature of *Palaeogekko*, without being able to further disentangle its relationships

461   within this clade in a confident way. The potential stem-pygopodoid topology recovered by Villa

462   et al. (2022b) is not emerging here, most likely as a result of the revised scorings. These new

463   results agree with the current south-Pacific distribution of pygopodoids and the absence of any

464   other convincing evidence of either stem- or crown-pygopodoid presence outside from their

465   modern range (pygopodoid affinities recovered for *R. vireti* here and by Villa et al., 2022b, are

466   most likely due to convergence and overall poor knowledge of this taxon; see also Daza et al.

467   2014). Similar to Villa et al.'s (2022b) analysis, on the other hand, a certain link between

468   *Palaeogekko* and *Laonogekko* is revealed. Considering the striking time span separating the two

469   taxa (Middle Miocene vs early Eocene, respectively) and the clear morphological differences,

470   this possible relation is worth of further investigations in future works.

471   Partly in contrast to the results of the phylogenetic analysis, comparisons with other European

472   fossil geckos seem to exclude affinities of *Palaeogekko* with euleptine sphaerodactylids.

473   Significant differences can be highlighted, and most similarities are represented by features

474   shared with taxa belonging to other clades (e.g. the smooth lateral surface shared with *Euleptes*

475   and *Geiseleptes*, but also *Mediodactylus* and *Tarentola*; the presence of a carina maxillaris

476   shared with extinct *Euleptes* and *Hemidactylus*). The same can be told for the comparison with

477   the extant *E. europaea*. A significant exception is *Gerandogekko*, for which available

478   information are insufficient for a detailed comparison. This is unfortunate, because

479   *Gerandogekko* is currently the only undisputed euleptine devoid of a groove following the last

480   ventrolateral foramen of the maxilla, the same condition seen in *Palaeogekko*. *Gerandogekko*

481   could, thus, represent an important taxon to verify possible euleptine affinities of *Palaeogekko*,

482   and whether members of the clade with ungrooved maxillae where more widespread during

483   the Miocene.

484   Evaluating affinities with other clades is hampered by the lack of extinct species that can be

485   directly compared with *Palaeogekko*. Some information can be retrieved from comparisons

486   with extant species, but these face a limit in the fact that at least some modern European

487   populations of non-sphaerodactylid geckos are interpreted as recent colonizers (*H. turcicus*:

488   Carranza & Arnold 2006; Rato et al. 2011; *T. mauritanica*: Harris et al. 2004; Rato et al. 2010)

489   and may thus not be related with a Miocene species. Fossil evidence of a previous occupation

490   of Europe by at least some of these is also available, however (Villa & Delfino 2019a). Schleich

491 (1987) already pointed out affinities of his new species with *Tarentola* and *Mediodactylus*, even

492 though without discussing them in detail. *Palaeogekko risgoviensis* indeed presents similarities

493 with these taxa, as well as with European *Hemidactylus*. Significant differences are also present,

494 though (see comparisons above). Simply based on the number of shared characters and

495 differences observed, the most comparable among non-sphaerodactylid extant European

496 species seems to be *M. kotschyi*, but again, there is no character uniquely shared with this

497 species and differences are also evident. It is, therefore, clear that phylogeny of *P. risgoviensis*

498 is still far from being resolved, and new data and analyses are greatly anticipated.

499 **CONCLUSIONS**

500 The redescription and reevaluation of the type material of *P. risgoviensis* supports the status of

501 the Middle Miocene German gecko as a valid species, which can be differentiated from almost

502 all other known extant and extinct geckos in Europe. With the single exception of a dentary

503 pertaining to another lizard group, there is also no evidence of multiple species being

504 represented in the type material, suggesting a particular abundance of this gecko at the

505 Steinberg locality. Available data are not sufficient to make confident inferences on the

506 phylogenetic relationships of this taxon, however, in particularly due to the absence of

507 preserved frontals. The question still remains open, therefore, on whether or not *P. risgoviensis*

508 could be evidence of the presence of non-euleptine geckos in Europe already during the

509 Miocene. Possible relationships with the Eocene *Laonogekko* suggested by the phylogenetic

510 analysis are interesting and worth of further scrutiny. European geckos were already

511 demonstrated as one of the few clades including inhabitants of the continent that persisted

512 with the same lineage from the Palaeogene to the Neogene (with euleptines; Villa et al. 2022b),

513   and a link between *Laonogekko* and *Palaeogekko* may further add on this pattern. However,

514   this is still covered with uncertainty, given the combination of strongly unstable phylogenetic

515   results and amount of missing data regarding the two taxa. Morphological affinities with

516   *Mediodactylus*, on the other hand, also deserve further investigation, because this is the only

517   extant non-euleptine gekkotan genus whose European population (currently referred to several

518   different species) started to differentiate and possibly to colonize the continent already during

519   the Miocene (Kotsakiozi et al. 2018). Additional work on the phylogeny and evolutionary history

520   of European gekkotans, combining data on both extant animals and fossils, are greatly

521   anticipated. The present contribution will allow to better include the enigmatic *P. risgoviensis* in

522   these new studies as well.

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674   **FIGURE CAPTIONS**

675   **Figure 1. SNSB-BSPG 1970 XVIII 7262, left dentary of Lacertoidea vel Scincoidea indet.**

676   A) Medial view. B) Lateral view. Scale bar equals 1 mm. Pictures of the specimen were taken by

677   Victor Beccari.

678   **Figure 2. Holotype right lower jaw (SNSB-BSPG 1970 XVIII 7300) of *Palaeogekko risgoviensis*.**

679   A) Dorsal view. B) Lateral view. C) Medial view. Scale bar equals 1 mm. Abbreviations: af,

680   adductor fossa; amf, anterior mylohyoid foramen; asf, anterior surangular foramen; cp,

681   coronoid process; psf, posterior surangular foramen; rp, retroarticular process.

682   **Figure 3. Dentition of *Palaeogekko risgoviensis*.**

683   A) SNSB-BSPG 1970 XVIII 7300 (Holotype). B) SNSB-BSPG 1970 XVIII 7252. C) SNSB-BSPG 1970

684   XVIII 7299. D) SNSB-BSPG 1970 XVIII 7301. All in lingual view. Scale bars equal 0.2 mm (A) and

685   0.5 mm (B-D).

686   **Figure 4. Paratype premaxillae of *Palaeogekko risgoviensis*.**

687   A, B) SNSB-BSPG 1970 XVIII 7363. C, D) SNSB-BSPG 1970 XVIII 7364. E, F) SNSB-BSPG 1970 XVIII

688   7365. G, H) SNSB-BSPG 1970 XVIII 7366. A, C, E, G) Anterior views. B, D, F, H) Posterior views.

689   Scale bars equal 1 mm. Abbreviations: asn, ascending nasal process; sc, septonasal crest.

690   **Figure 5. Paratype maxillae of *Palaeogekko risgoviensis*.**

691   A) SNSB-BSPG 1970 XVIII 7344. B) SNSB-BSPG 1970 XVIII 7348. C) SNSB-BSPG 1970 XVIII 7350.

692   D) SNSB-BSPG 1970 XVIII 7351. E) SNSB-BSPG 1970 XVIII 7352. F) SNSB-BSPG 1970 XVIII 7353. G-

693   I) SNSB-BSPG 1970 XVIII 7354. J) SNSB-BSPG 1970 XVIII 7355. K, L) SNSB-BSPG 1970 XVIII 7356.

694   M) SNSB-BSPG 1970 XVIII 7357. N-P) SNSB-BSPG 1970 XVIII 7359. Q, R) SNSB-BSPG 1970 XVIII

695   7360. S) SNSB-BSPG 1970 XVIII 7361. A-F, H, J, K, M, N, Q, S) Medial views. G, P) Dorsal views. I,

696   L, O, R) Lateral views. Scale bars equal 1 mm. Abbreviations: app, anterior premaxillary process;

697   cm, carina maxillaris; fp, facial process; pp, posterior process.

698   **Figure 6. Paratype dentaries of *Palaeogekko risgoviensis*.**

699   A, B) SNSB-BSPG 1970 XVIII 7250. C, D) SNSB-BSPG 1970 XVIII 7251. E, F) SNSB-BSPG 1970 XVIII

700   7252. G) SNSB-BSPG 1970 XVIII 7253. H) SNSB-BSPG 1970 XVIII 7254. I) SNSB-BSPG 1970 XVIII

701   7257. J) SNSB-BSPG 1970 XVIII 7259. K) SNSB-BSPG 1970 XVIII 7263. L) SNSB-BSPG 1970 XVIII

702   7274. M) SNSB-BSPG 1970 XVIII 7290. N) SNSB-BSPG 1970 XVIII 7291. O) SNSB-BSPG 1970 XVIII

703   7299. P) SNSB-BSPG 1970 XVIII 7301. Q) SNSB-BSPG 1970 XVIII 7302. R) SNSB-BSPG 1970 XVIII

704   7307. A, C, E) Lateral views. B, D, F-R) Medial views. Scale bars equal 1 mm. Abbreviations: ipp,

705   inferior posterior process; spp, superior posterior process.

706   **Figure 7. Results of the phylogenetic analysis with the revised scorings for *Palaeogekko***

707   ***risgoviensis*.**

708   A) Strict consensus of 66 most-parsimonious trees, with a length of 784 steps. B) Pruned strict

709   consensus tree, excluding *P. risgoviensis* (a) and *L. lefevrei* (b); arrows mark the possible

710   positions of the pruned taxa. White circles mark the constraints implemented in the analysis

711   (not all constraints are mapped in A, because some clades are collapsed in a polytomy due to

712   unstable wild-card taxa).

Table 1(on next page)

Tooth density indexes (number of tooth position per mm) for *P. risgoviensis* and European extant gekkotans.

Values for the extinct German species are based on the most complete specimens. This, together with differences in the revised measurements and tooth counts, explains the differences between ranges presented here and those reported by Schleich (1987). Values for the single fossils are available in the Supplemental Data S1. Data for extant species come from personal observations on specimens listed by Villa et al. (2018).

1 **Table 1:**

2 **Tooth density indexes (number of tooth position per mm) for *P. risgoviensis* and European**

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5 together with differences in the revised measurements and tooth counts, explains the

6 differences between ranges presented here and those reported by Schleich (1987). Values for

7 the single fossils are available in the Supplemental Data S1. Data for extant species come from

8 personal observations on specimens listed by Villa et al. (2018).

	Premaxilla		Maxilla		Dentary	
	min	max	min	max	min	max
P. risgoviensis	4.5	5.3	4.2	5.3	4.3	5.9
E. europaea	5.3	6.4	5.3	6.6	5.8	7.4
H. turcicus	5.3	5.5	4.4	5	4.1	4.8
M. kotschyi	4.7	5.8	4.2	4.9	4.9	5.5
T. mauritanica	3	4.1	2.8	3.8	3	3.4

9

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Figure 1

SNSB-BSPG 1970 XVIII 7262, left dentary of Lacertoidea vel Scincoidea indet.

A) Medial view. B) Lateral view. Scale bar equals 1 mm. Pictures of the specimen were taken by Victor Beccari.

Figure 2

Holotype right lower jaw (SNSB-BSPG 1970 XVIII 7300) of *Palaeogekko risgoviensis*.

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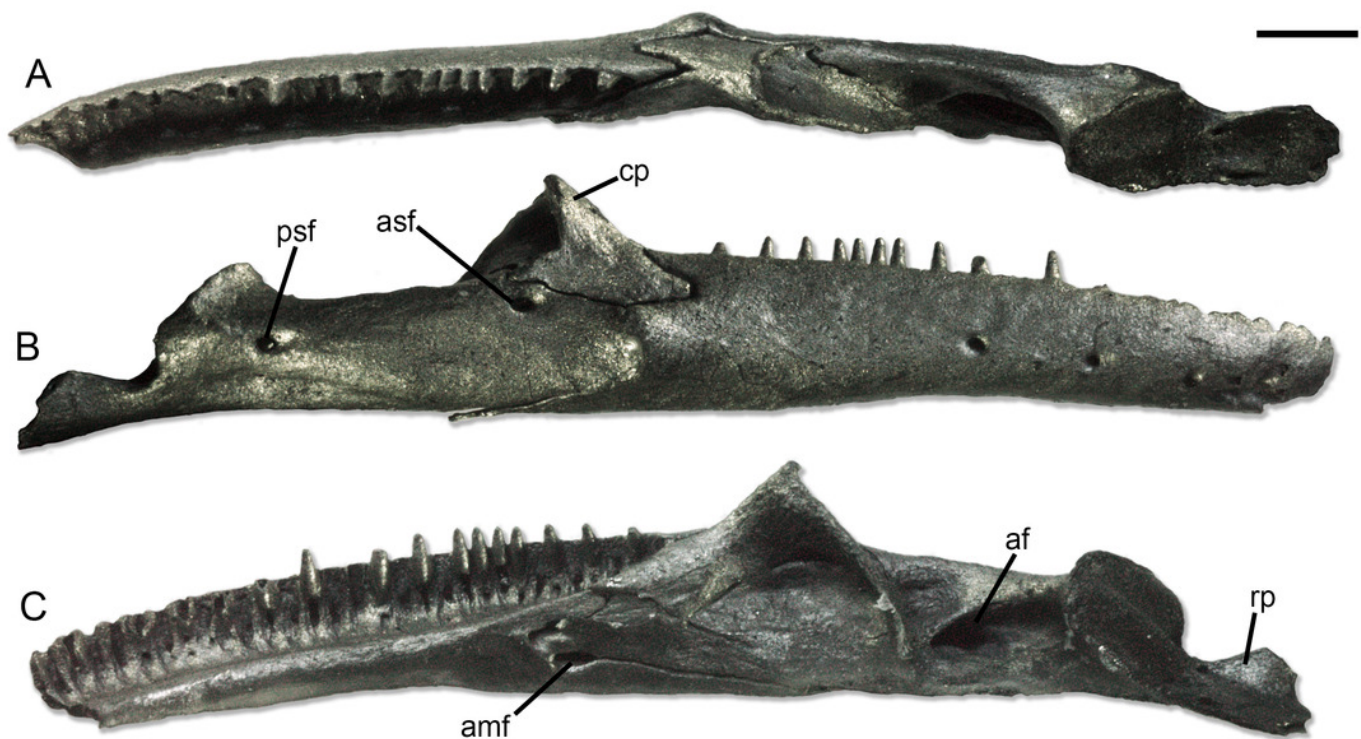
Figure 3

Dentition of *Palaeogekko risgoviensis*.

A) SNSB-BSPG 1970 XVIII 7300 (Holotype). B) SNSB-BSPG 1970 XVIII 7252. C) SNSB-BSPG
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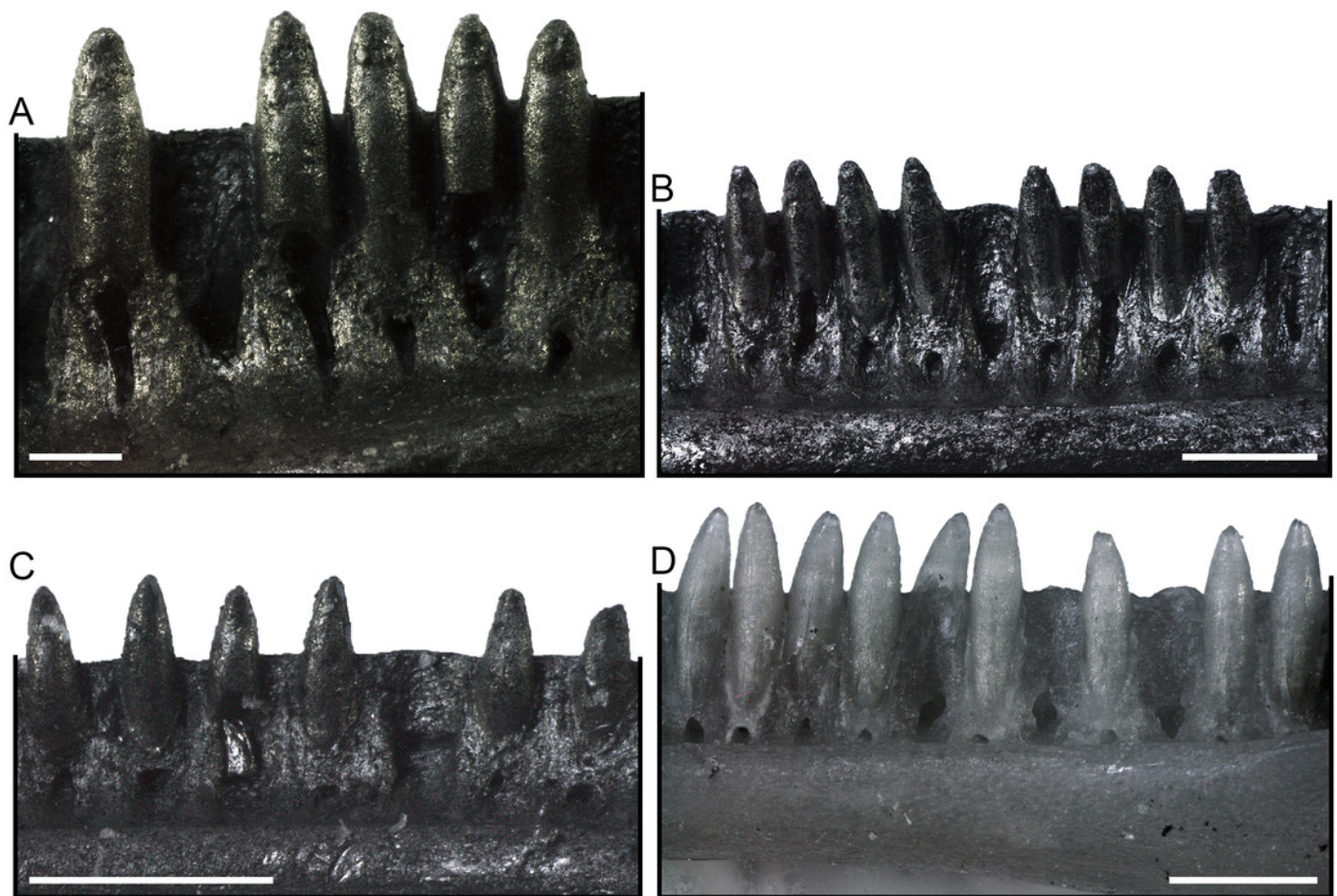(A) and 0.5 mm (B-D).

Figure 4

Paratype premaxillae of *Palaeogekko risgoviensis*.

A, B) SNSB-BSPG 1970 XVIII 7363. C, D) SNSB-BSPG 1970 XVIII 7364. E, F) SNSB-BSPG 1970 XVIII 7365. G, H) SNSB-BSPG 1970 XVIII 7366. A, C, E, G) Anterior views. B, D, F, H) Posterior views. Scale bars equal 1 mm. Abbreviations: asn, ascending nasal process; sc, septonasal crest.
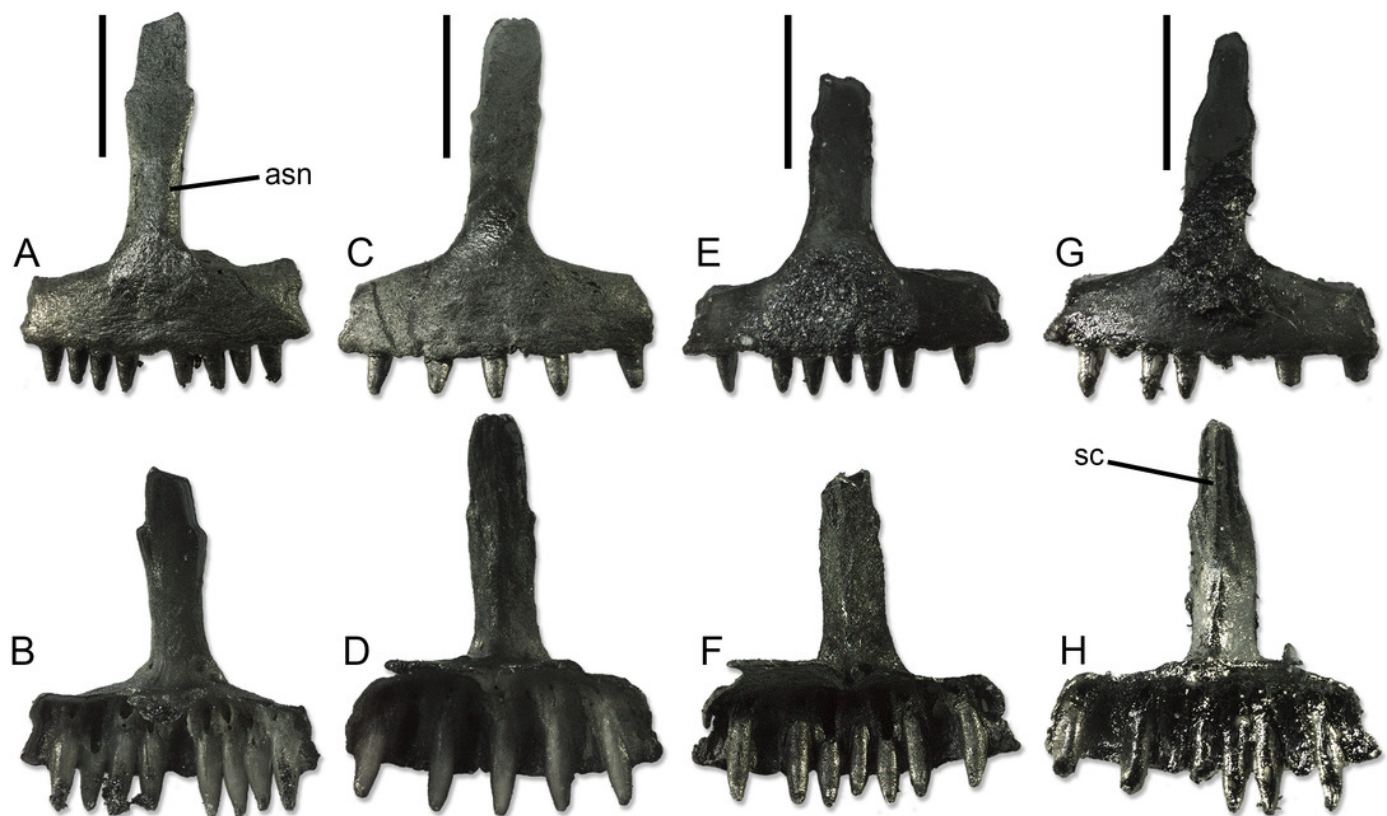
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Paratype maxillae of *Palaeogekko risgoviensis*.

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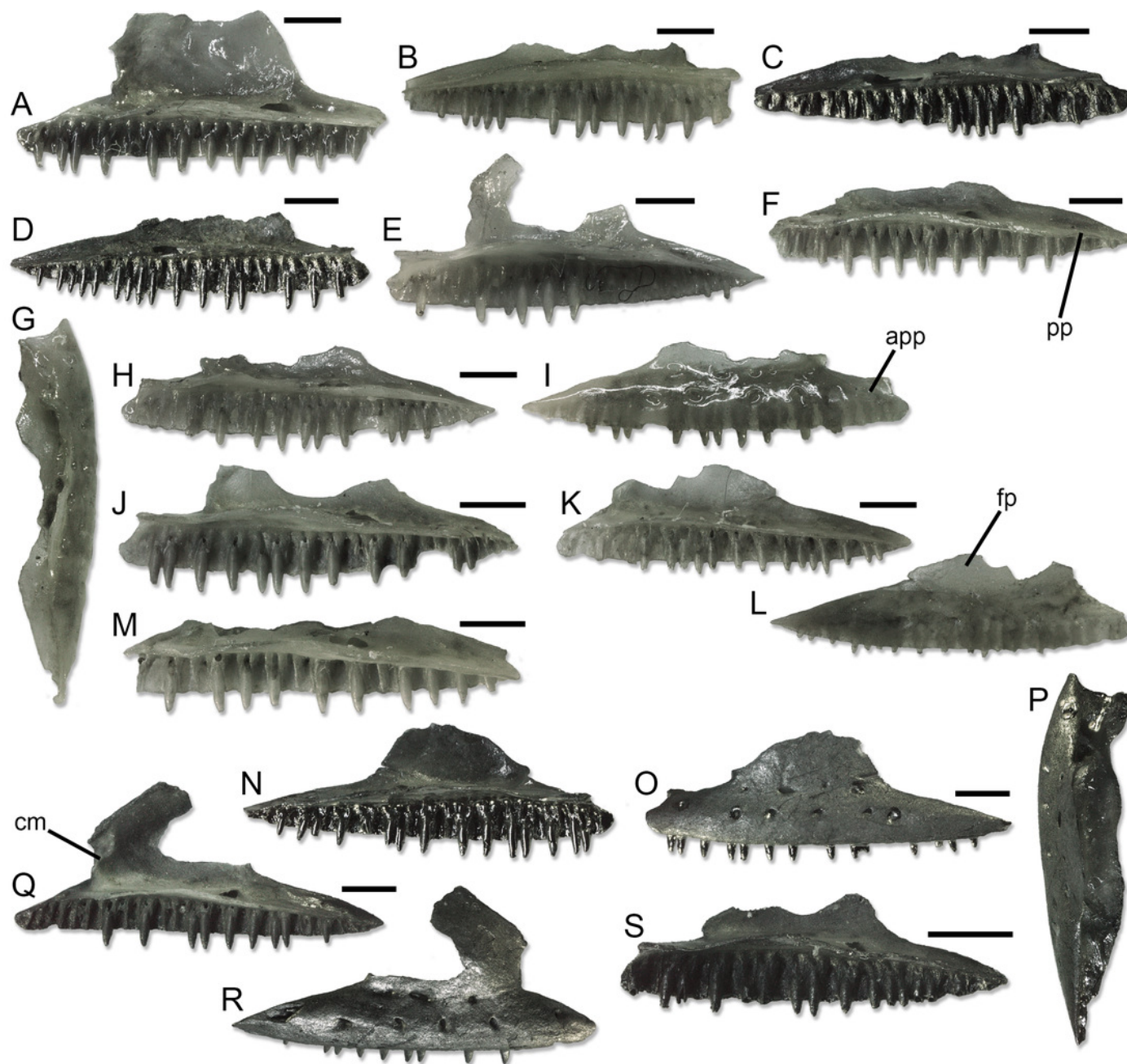
Figure 6

Paratype dentaries of *Palaeogekko risgoviensis*.

A, B) SNSB-BSPG 1970 XVIII 7250. C, D) SNSB-BSPG 1970 XVIII 7251. E, F) SNSB-BSPG 1970 XVIII 7252. G) SNSB-BSPG 1970 XVIII 7253. H) SNSB-BSPG 1970 XVIII 7254. I) SNSB-BSPG 1970 XVIII 7257. J) SNSB-BSPG 1970 XVIII 7259. K) SNSB-BSPG 1970 XVIII 7263. L) SNSB-BSPG 1970 XVIII 7274. M) SNSB-BSPG 1970 XVIII 7290. N) SNSB-BSPG 1970 XVIII 7291. O) SNSB-BSPG 1970 XVIII 7299. P) SNSB-BSPG 1970 XVIII 7301. Q) SNSB-BSPG 1970 XVIII 7302. R) SNSB-BSPG 1970 XVIII 7307. A, C, E) Lateral views. B, D, F-R) Medial views. Scale bars equal 1 mm. Abbreviations: ipp, inferior posterior process; spp, superior posterior process.

spp

ipp

Figure 7

Results of the phylogenetic analysis with the revised scorings for *Palaeogekko risgoviensis*.

A) Strict consensus of 66 most-parsimonious trees, with a length of 784 steps. B) Pruned strict consensus tree, excluding *P. risgoviensis* (a) and *L. lefevrei* (b); arrows mark the possible positions of the pruned taxa. White circles mark the constraints implemented in the analysis (not all constraints are mapped in A, because some clades are collapsed in a polytomy due to unstable wild-card taxa).

A

Pamelina
Sphenodon
Dibamus
Gobekko
Norellius
Hoburogekko
Aeluroscalabotes
Eublepharis
Sphaerodactylus
Geiseleptes delfinoi
Cadurcogekko piveteaui
Cadurcogekko verus
Gerandogekko gaillardi
Laonogekko lefevrei
Palaeogekko risgoviensis
Euleptes gallica
Euleptes klembarai
Euleptes europaea
Tarentola mauritanica
Hemidactylus turcicus
Mediodactylus kotschyi
Gekko
Phelsuma
Yantarogekko balticus
Oedura
Pygopus
Nephrurus
Saltuarius
Rhodanogekko vireti

B

Pamelina
Sphenodon
Dibamus
Gobekko
Norellius
Hoburogekko
Aeluroscalabotes
Eublepharis
Tarentola mauritanica
ab
Mediodactylus kotschyi
Hemidactylus turcicus
ab
Gekko
Phelsuma
Yantarogekko balticus
ab>ab
Sphaerodactylus
Geiseleptes delfinoi
Cadurcogekko piveteaui
Cadurcogekko verus
Gerandogekko gaillardi
ab>ab
Euleptes gallica
Euleptes klembarai
Euleptes europaea
Oedura
Pygopus
Nephrurus
Saltuarius
Rhodanogekko vireti