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. 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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6   **Abstract**

7   After its original description, the Middle Miocene gekkotan *Palaeogekko risgoviensis* remained

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

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

10 Europe during a period when a single gekkotan lineage (i.e. euleptine sphaerodactylids) is

11 confidently reported to have inhabited the continent. However, it is unclear whether *P.*

12 *risgoviensis* may represent a member of this same lineage or a second clade of Gekkota. In

13 order to contribute to shed light on this issue, the type material of *P. risgoviensis* is here

14 redescribed, refigured and extensively compared with extinct and extant geckos from Europe.

15 The new observations confirm the validity of the German species as a distinct taxon, and

16 exclude the previously-suggested chimeric status of the type material of this gecko (with the

17 exception of a single dentary included in the type series, which clearly belong to a different

18 lizard). Phylogenetic relationships of *Palaeogekko* are still unclear, though, with different

19 positions within the gekkotan tree recovered for the taxon. Nevertheless, it is confidently

20 supported as a non-eublepharid gekkonoid, in agreement with hypothesys presented by other

21 scholars.

22 **Keywords:** geckos, Europe, Neogene, taxonomy, phylogeny, Cenozoic

23 **INTRODUCTION**

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

25 European squamate fauna started assembling (Rage 2013; Villa & Delfino 2019b), with fossils

26 related to extant species or species complexes even reported already from the Early Miocene

27 (for lizards, see e.g. Čerňanský 2010; Venczel & Hír 2013). European squamates were negatively

28 affected by changes in the environment around the Oligocene/Miocene transition: significant

29 effects of the climate deterioration, in the form of drier and cooler conditions, were highlighted

30 for snakes (the so-called "Dark period of booid snakes"; Rage & Szyndlar 2005), but similar

31 patterns are also shown by other squamates. This was the prelude to a subsequent faunal

32 turnover facilitated by the establishment of a stable connection between Eurasia and Africa and

33 the return to a warm and humid climate during the Miocene Climatic Optimum, both events

34 occurring in the Early Miocene (Böhme 2003; Rage 2013; Georgalis et al. 2016). The turnover

35 saw the appearance in Europe of several taxa that characterized the European reptilian fauna in

36 the Neogene (e.g. chamaeleons: Georgalis et al. 2016; glass lizards of the genus *Pseudopus*

37 Merrem, 1820: Čerňanský et al. 2015; Vasilyan et al. 2019; Villa et al. 2022a; monitor lizards:

38 Ivanov et al. 2018; Villa et al. 2018; cobras: Szyndlar & Schleich 1993; vipers: Szyndlar & Rage

39 1999, 2002), and in most cases survived in the continent through the Quaternary and up to

40 nowadays.

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

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

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

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

45   & Bauer 2010). Currently represented by the single species *Euleptes europaea* (Gené, 1839),

46   which is endemic to the western Mediterranean (Delaugerre et al. 2011; Sillero et al. 2014;

47   Speybroeck et al. 2016; Uetz et al. 2022), the genus had a continental distribution throughout

48   the Miocene (Müller 2001; Müller & Mödden 2001; Čerňanský & Bauer 2010; Daza et al. 2014;

49   Colombero et al. 2017; Čerňanský et al. 2018; Villa & Delfino 2019b; Villa et al. 2022b). Contrary

50   to other lizards populating Europe during the Neogene, however, it was not a newcomer

51   entering after the Oligocene/Miocene transition. Conversely, it is the last member of an ancient

52   lineage of sphaerodactylid geckos living in Europe at least from the Eocene (Villa et al. 2022b).

53   This lineage includes several genera and species and, based on our current knowledge,

54   represented the dominant clade of gekkotans in Europe for most of the Cenozoic, in contrast

55   with the modern situations that sees phyllodactylids and gekkonids as the most widespread

56   geckos north of the Mediterranean Sea.

57   Members of this lineage in the Miocene included at least two *Euleptes* species, *Euleptes gallica*

58   Müller, 2001 and *Euleptes klembarai* Čerňanský et al., 2018, and two species referred to the

59   genus *Gerandogekko* Hoffstetter, 1946, namely *Gerandogekko arambourgi* Hoffstetter, 1946

60   and *Gerandogekko gaillardi* Hoffstetter, 1946. The phylogenetic relationships of a fifth species,

61   *Palaeogekko risgoviensis* Schleich, 1987 from the Middle Miocene of southern Germany, are

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

63   was used in a wide sense, including all gekkotans exclusive of pygopodids, but Schleich (1987)

64   explicitly mentioned affinities with *Tarentola* Gray, 1825 and *Cyrtodactylus* Gray, 1827 (in fact,

65   *Mediodactylus* Szczerbak & Golubev, 1977, given that he was using *Cyrtodactylus kotschyi*, now

66   part of the other genus, for comparisons). Thus, *P. risgoviensis* would be related to either

67   phyllodactylids or gekkonids (in a modern sense) according to his observations. Later on, Daza

68   et al. (2014) commented on the species, stating that the available information only allowed to

69   exclude belonging to pygopodoids and eublepharids, in agreement with previous conclusions,

70   but preventing further discrimination between other clades within gekkonoids. More recently,

71   a phylogenetic analysis by Villa et al. (2022b) recovered *P. risgoviensis* as an unstable taxon, but

72   resulting topologies possibly placed it either as a crown sphaerodactylid or as a stem

73   pygopodoid. Considering all the possibilities suggested by the different authors, *P. risgoviensis*

74   may either represent another species related to the dominant European sphaerodactylid

75   lineage or the first evidence of a second gekkotan clade in Europe already during the Miocene.

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

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

78   Schleich's (1987) original paper. In order to overcome this issue, a redescription of the type

79   material referred to this species under modern knowledge of gekkotan osteology is here

80   presented. Additionally, detailed comparisons particularly focused on other European extant

81   and extinct gekkotans and an attempt at better understanding the possible phylogenetic

82   position of this Middle Miocene gecko are also provided.

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, has

88   an open Meckelian fossa and cannot pertain to a gecko. Because of this, it is here removed

89   from the paratypes of *P. risgoviensis*. Furthermore, it was not possible to clearly locate two

90   other dentaries, SNSB-BSPG 1970 XVIII 7249 and 7270, in the available material. A single

91   unnumbered specimen stored with the rest of the type series most likely represents the

92   former, even though measurements and tooth count do not exactly agree with those reported

93   by Schleich (1987: tab. 1). Revised measurements and counts of teeth and foramina reported in

94   the descriptions are based on the best-preserved specimens. Detailed data for all specimens

95   are provided in the Supplemental Data S1.

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

97   (2019a). Measurements were taken with a digital caliper. Selected specimens were

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

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

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

101   2020). This is not in opposition to the split, but simply to ease comparisons with the most-

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

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

104   literature and personal observations (for *G. arambourgi* and *Geiseleptes delfinoi* Villa et al.,

105   2022) for extinct taxa.

106   For the phylogenetic analysis, Villa et al.'s (2022b) matrix was used. *Palaeogekko risgoviensis*

107   was rescored in Mesquite 3.70 (Maddison & Maddison 2021) after the new morphological

108   information provided by the updated description herein presented (see the Supplemental Data

109   S2 for the revised scorings). The analysis was run in TNT 1.5 (Goloboff et al. 2008; Goloboff &

110   Catalano 2016). Same as in the second iteration of the analysis by Villa et al. (2022b), *G.*

111 *arambourgi* was removed and the same six constraints were applied (all fossils retained as

112 floating taxa). The matrix was analysed using the New Technology search, with all options

113 selected and the consensus stabilized five times with a factor of 75. The "Collapse trees after

114 search" option was selected, to avoid zero-length branches in the individual resulting trees. A

115 second round of tree bisection and reconnection was run after the first New Technology search.

116 **SYSTEMATIC PALAEONTOLOGY**

117 Squamata Oppel, 1811

118 Gekkota Camp, 1923

119 Gekkonoidea Gray, 1825

120 *Palaeogekko* Schleich, 1987

121 *Palaeogekko risgoviensis* Schleich, 1987

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

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

124 XVIII 7340/7362); 89 dentaries (SNSB-BSPG 1970 XVIII 7249/7261, 7263/7299, 7301/7339).

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

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

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

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

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

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

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

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

133   7) posterior surangular foramen not shifted dorsally.

134   **Description of the holotype**

135   The holotype SNSB-BSPG 1970 XVIII 7300 (Fig. 1) is an almost complete right lower jaw, missing

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

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

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

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

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

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

142   part.

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

144   (Fig. 1C), the Meckelian fossa is almost completely closed in a narrow tubular structure, which

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

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

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

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

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

150   surface is smooth (Fig. 1B), with at least four mental foramina; most probably, the number of

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

152   **Splenial.** The splenial (Fig. 1C) is preserved, even though damaged. It is a small and slender

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

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

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

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

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

158   **Coronoid.** The coronoid is strongly concave in medial direction (Fig. 1A). The anterior part of

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

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

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

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

163   medial side of the bone.

164   **Compound bone.** The compound bone is completely fused. On the medial side (Fig. 1C), the

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

166   the fossa, a very low osseous expansion in visible in dorsal view (Fig. 1A), even though it is not

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

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

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

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

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

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

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

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

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

176   surface of the compound bone is generally smooth (Fig. 1B). Ventral to the contact with the

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

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

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

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

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

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

183   anteroposteriorly elongated. There is no posterior mylohyoid foramen.

184   **Dentition.** Teeth (Fig. 1, 2A) are pleurodont and homodont. They are closely spaced, narrow

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

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

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

188   **Description of the paratypes**

189   All paratypes are moderately small and slenderly built.

190   **Premaxillae (Fig. 3).** The unpaired premaxillae bear well-developed palatal processes, which are

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

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

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

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

195   only in SNSB-BSPG 1970 XVIII 7366; Fig. 3G-H), showing only a variable but always poorly-

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

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

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

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

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

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

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

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

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

205   accessory foramen is absent.

206   **Maxillae (Fig. 4).** In medial view, the tooth row runs along the whole length of the maxilla. The

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

208   of a possibly juvenile specimen, SNSB-BSPG 1970 XVIII 7361 (Fig. 4S), is 4.56 mm long.

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

210   the latter displays a shallow, U-shaped anterior concavity (Fig. 4G, P). The anterolateral process

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

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

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

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

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

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

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

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

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

220   is present close to the anterodorsal corner (Fig. 4A, E, Q). The main course of the carina is

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

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

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

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

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

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

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

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

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

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

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

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

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

234   **Dentaries (Fig. 5).** Paratype dentaries generally resemble the homologous bone of the holotype

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

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

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

238   1970 XVIII 7308 and SNSB-BSPG 1970 XVIII 7310, this notch is shorter, about one seventh and

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

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

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

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

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

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

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

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

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

248 specimens goes from 3.92 mm to 7.81 mm.

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

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

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

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

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

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

255 **Dentition.** The dentition of the paratypes (Fig. 2B-D) shares the same morphology as the

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

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

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

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

260 (23 in the juvenile SNSB-BSPG 1970 XVIII 7291 and 27 in the juveniles SNSB-BSPG 1970 XVIII

261 7288 and SNSB-BSPG 1970 XVIII 7290).

262 **PHYLOGENETIC ANALYSIS**

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

264   strict consensus tree (Fig. 6A; consistency index: 0.552; retention index: 0.33) shows a polytomy

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

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

267   maintaining an unresolved Sphaerodactylidae (Fig. 6B). Several alternative positions are

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

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

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

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

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

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

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

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

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

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

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

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

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

281   **DISCUSSION**

282   **The taxonomic identity of *Palaeogekko risgoviensis***

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

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

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

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

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

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

289　(2018). Furthermore, general morphology is comparable within all *Palaeogekko* fossils

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

291　1970 XVIII 7262; see Material and Methods section). Variation is indeed present in a few

292　features: 1) development of the dorsal half of the septonasal crest (premaxillae); 2)

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

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

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

296　(dentary); and 6) lateral exposure of the teeth (dentition). Given the overall similarity in both

297　morphology and size, these are herein considered as intraspecific variation, and all the type

298　material of *P. risgoviensis* as pertaining to a single species. A few smaller remains (e.g. SNSB-

299　BSPG 1970 XVIII 7288, SNSB-BSPG 1970 XVIII 7290, SNSB-BSPG 1970 XVIII 7291, and SNSB-BSPG

300　1970 XVIII 7361) most likely represent juvenile individuals.

301　Schleich mostly based the description and diagnosis of his new species on meristics and

302　morphometry, but more detailed morphological comparisons can be provided to better

303　understand differences and affinities of *P. risgoviensis* with other extinct and extant European

304　gekkotans. *Palaeogekko* cannot be compared with *Rhodanogekko vireti* Hoffstetter, 1946 and

305　the recently-described *Dollogekko dormaalensis* Čerňanský et al., 2022, however, because

306　these two species are only known from a single isolated frontal each. It cannot be compared

307 with *Yantarogekko balticus* Bauer et al., 2005 either, because the latter is preserved in amber.

308 When it comes to other species, for which bones that are also preserved in the material

309 referred to *Palaeogekko* are known, one of the most interesting features to be evaluated is the

310 groove following the last ventrolateral foramen on the maxillae. This is absent in *Laonogekko*

311 (Augé 2003; Daza et al. 2014) and all non-sphaerodactylid extant European gekkotans (Villa et

312 al. 2018) and is one of the main features of euleptine geckos (Villa et al. 2022), being present in

313 all of them but *G. arambourgi* (unknown for *G. gaillardi*). It is absent in *P. risgoviensis*.

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

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

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

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

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

319 (Müller 2001; Villa et al. 2018) compared to *Palaeogekko*. *Cadurcogekko* clearly differs from

320 *Palaeogekko* also in the presence of a postnarial anterodorsal depression (Augé 2005; Daza et

321 al. 2014; Bolet et al. 2015), with *Cadurcogekko piveteaui* Hoffstetter, 1946 further presenting,

322 in contrast with *Palaeogekko*, a marked and wide articulation surface with the nasal on the

323 medial surface of the facial process and a lower count of maxillary teeth, dentary teeth, and

324 ventrolateral foramina. The other undisputed Paleogene euleptine, *Geiseleptes*, is larger than

325 *Palaeogekko* and possesses a longer posterior process of the maxilla and, possibly, a dorsally-

326 shifted posterior surangular foramen (Villa et al. 2022).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

353 the presence of a carina maxillaris (Müller 2001; Čerňanský & Bauer 2010; Daza et al. 2014;

354 Čerňanský et al. 2018), which is however more distinct, straight and more posterodorsally

355 directed in the two extinct *Euleptes*. A peculiar combination of characters is apparently

356 displayed by the material referred to *Euleptes* sp. from the Oppenheim/Niersten quarry, in

357 Germany, which include arrow-shaped premaxillae with eight or 10 teeth and at least one

358 maxilla with a sigmoid carina maxillaris more similar to the one of *Palaeogekko* than to other

359 extinct *Euleptes* (at least based on the drawings provided by Müller & Modden, 2001: fig. 1).

360 The rest of the maxilla seems rather comparable with *Palaeogekko* as well (i.e. short and

361 pointed posterior process, smooth lateral surface), but the anterior point of the facial process

362 appears longer.

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

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

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

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

367 this Eocene species based on: 1) a less inclined posterior margin of the facial process; 2) the

368 absence of a marked articulation surface with the nasal on the medial surface of the facial

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

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

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

372 dentary, which fits the range of *P. risgoviensis*.

373   In a similar way to *E. europaea*, other extant, non-sphaerodactylid European geckos also allow

374   more detailed comparisons with *Palaeogekko* than the mentioned extinct species. Both

375   differences and similarities can be highlighted, based on the morphological data reported by

376   Villa et al. (2018). *Palaeogekko* differs from all *H. turcicus*, *M. kotschyi*, and *T. mauritanica* in

377   having: 1) a shallow notch separating the palatal processes of the premaxilla (this feature is

378   shared with *E. europaea*); and 2) a shallow expansion at midheight of the ascending nasal

379   process. The ascending nasal process is also not expanded at the distal end as it is in *M.*

380   *kotschyi*. The maxilla of the German species has a well-developed and pointed anteromedial

381   process like *T. mauritanica* (and *E. europaea*), but not *H. turcicus* and *M. kotschyi*. The anterior

382   margin of the facial process is inclined anteriorly in *P. risgoviensis*, *E. europaea*, and *H. turcicus*,

383   and vertical in *M. kotschyi*. In *T. mauritanica*, it presents a small notch, unlike *P. risgoviensis*.

384   The smooth lateral surface is shared with all species (including *E. europaea*), but *H. turcicus*. The

385   maxilla of the latter species also differs from the one of *Palaeogekko* in the presence of the

386   lacrimal groove and the absence of a strong anterior point on the facial process, but they

387   similarly display a distinct carina maxillaris. Nevertheless, the latter is more vertically oriented

388   in *P. risgoviensis* than in *H. turcicus*, whose carina is posterodorsally directed. As far as the

389   dentary is concerned, the extension of the posterior notch of the Meckelian fossa is longer in *H.*

390   *turcicus*, but similar to *Palaeogekko* in *M. kotschyi* and *T. mauritanica*. The dentary of *T.*

391   *mauritanica* differs from that of *P. risgoviensis*, however, because the anterior opening of the

392   Meckelian fossa is not continued into a groove in the phyllodactylid. The splenial of *P.*

393   *risgoviensis* is comparable with the one of *M. kotschyi* in both the anterior mylohyoid foramen

394   present as a notch on the ventral margin of the bone and the posterior end of the bone not

395   bending ventrally. Both these features are different in *H. turcicus*, whereas *T. mauritanica* has a

396   splenial with a bending posterior end but can present both a notch-like or, more rarely,

397   completely-closed anterior mylohyoid foramen. In the end, *P. risgoviensis* shares with both *H.*

398   *turcicus* and *M. kotschyi* a pointed posteromedial process of the coronoid and a posterior

399   surangular foramen not shifted dorsally. Both these features are different in *T. mauritanica*,

400   which shows a rounded process and a shifted foramen.

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

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

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

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

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

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

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

408   an inverted pattern then the one shown by measurements.

409   Putting together all the information presented above, *Palaeogekko* clearly stands out as

410   different from almost all European geckos with which it can be compared, both extinct and

411   extant. Uncertainties remains only on the characters possibly discriminating this Middle

412   Miocene German species with the French *Gerandogekko*, remains of which come from Lower

413   and Upper Miocene deposits (Hoffstetter 1946; Daza et al. 2014). This is mainly due to the facts

414   that the most significant fossils of both *Gerandogekko* species are frontals, an element that is

415   unknown for *Palaeogekko*, and that maxillae and dentaries of the French species are

416   insufficiently preserved. The different morphologies shown by the posterior processes of the

417　maxillae of *G. arambourgi* and *G. gaillardi* further complicates this situation, given that only the

418　long and rounded process of the former undisputedly differs from the condition observed in

419　maxillae of *Palaeogekko*. Whether this means that *P. risgoviensis* is somehow related with at

420　least *G. gaillardi* or even with *Gerandogekko* as a whole cannot be stated pending the recovery

421　of further fossils (i.e. a frontal referrable to *P. risgoviensis* or better-preserved maxillae of the

422　two *Gerandogekko* species). For the time being, *P. risgoviensis* can be maintained as a distinct

423　species, living in central Europe in a moment (MN 6) when only another gecko is currently

424　known to have been present: the Slovakian euleptine *E. klembarai*.

425　**Phylogenetic relationships of *Palaeogekko risgoviensis***

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

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

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

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

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

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

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

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

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

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

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

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

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

439   2014). Similar to Villa et al.'s (2022) analysis, on the other hand, a certain link between

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

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

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

443   Partly in contrast with the results of the phylogenetic analysis, comparisons with other

444   European fossil geckos seem to exclude affinities of *Palaeogekko* with euleptine

445   sphaerodactylids. Significant differences can be highlighted, and most similarities are

446   represented by features shared with taxa belonging to other clades (e.g. the smooth lateral

447   surface shared with *Euleptes* and *Geiseleptes*, but also *Mediodactylus* and *Tarentola*; the

448   presence of a carina maxillaris shared with extinct *Euleptes* and *Hemidactylus*). The same can be

449   told for the comparison with the extant *E. europaea*. A significant exception is *Gerandogekko*,

450   for which available information are insufficient for a detailed comparison. This is unfortunate,

451   because *Gerandogekko* is currently the only undisputed euleptine devoid of a groove following

452   the last ventrolateral foramen of the maxilla, the same condition seen in *Palaeogekko*.

453   *Gerandogekko* could, thus, represent an important taxon to verify possible euleptine affinities

454   of *Palaeogekko*, and whether members of the clade with ungrooved maxillae where more

455   widespread during the Miocene.

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

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

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

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

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

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

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

463   (1987) already pointed out affinities of his new species with *Tarentola* and *Mediodactylus*, even

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

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

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

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

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

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

470   is still far from been resolved, and new data and analyses are greatly anticipated.

471   **CONCLUSIONS**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

494   these new studies as well.

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650   **FIGURE CAPTIONS**

651   **Figure 1. Holotype right lower jaw (SNSB-BSPG 1970 XVIII 7300) of *Palaeogekko risgoviensis*.**

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

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

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

655   **Figure 2. Dentition of *Palaeogekko risgoviensis*.**

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

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

658   0.5 mm (B-D).

659   **Figure 3. Paratype premaxillae of *Palaeogekko risgoviensis*.**

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

661   7365. G, H) SNSB-BSPG 1970 XVIII 7366. A, C, E, G) Anterior views. B, D, F, H) Posterior views.

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

663   **Figure 4. Paratype maxillae of *Palaeogekko risgoviensis*.**

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

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

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

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

668   7360. S) SNSB-BSPG 1970 XVIII 7361. A-F, H, J, K, M, N, Q, S) Medial views. G, P) Dorsal views. I,

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

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

671   **Figure 5. Paratype dentaries of *Palaeogekko risgoviensis*.**

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

673   7252. G) SNSB-BSPG 1970 XVIII 7253. H) SNSB-BSPG 1970 XVIII 7254. I) SNSB-BSPG 1970 XVIII

674   7257. J) SNSB-BSPG 1970 XVIII 7259. K) SNSB-BSPG 1970 XVIII 7263. L) SNSB-BSPG 1970 XVIII

675   7274. M) SNSB-BSPG 1970 XVIII 7290. N) SNSB-BSPG 1970 XVIII 7291. O) SNSB-BSPG 1970 XVIII

676   7299. P) SNSB-BSPG 1970 XVIII 7301. Q) SNSB-BSPG 1970 XVIII 7302. R) SNSB-BSPG 1970 XVIII

677 7307. A, C, E) Lateral views. B, D, F-R) Medial views. Scale bars equal 1 mm. Abbreviations: ipp,

678 inferior posterior process; spp, superior posterior process.

679 **Figure 6. Results of the phylogenetic analysis with the revised scorings for *Palaeogekko***

680 ***risgoviensis*.**

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

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

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

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

685 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

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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

Figure 1

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

A) Dorsal view. B) Lateral view. C) Medial view. Scale bar equals 1 mm. Abbreviations: af, adductor fossa; amf, anterior mylohyoid foramen; asf, anterior surangular foramen; cp, coronoid process; psf, posterior surangular foramen; rp, retroarticular process.
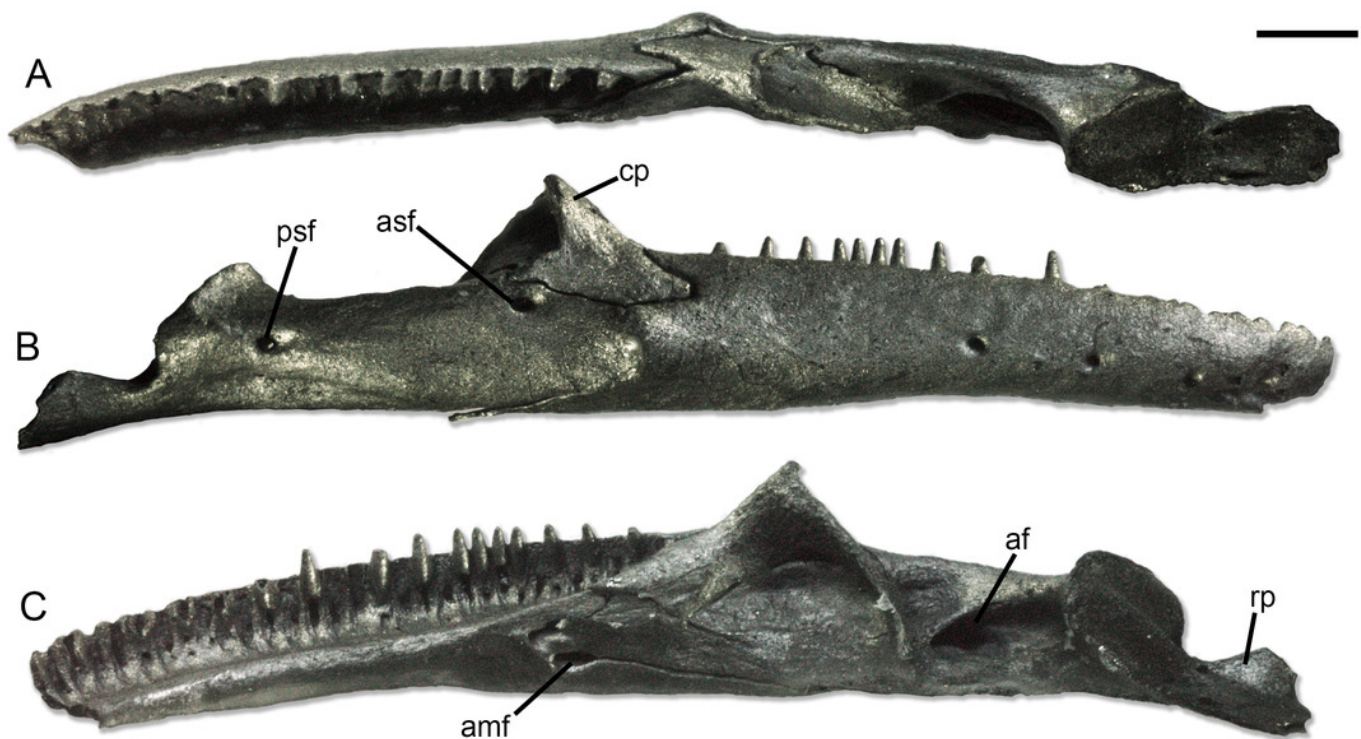
Figure 2

Dentition of *Palaeogekko risgoviensis*.

A) SNSB-BSPG 1970 XVIII 7300 (Holotype). B) SNSB-BSPG 1970 XVIII 7252. C) SNSB-BSPG 1970 XVIII 7299. D) SNSB-BSPG 1970 XVIII 7301. All in lingual view. Scale bars equal 0.2 mm (A) and 0.5 mm (B-D).

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Paratype premaxillae of *Palaeogekko risgoviensis*.

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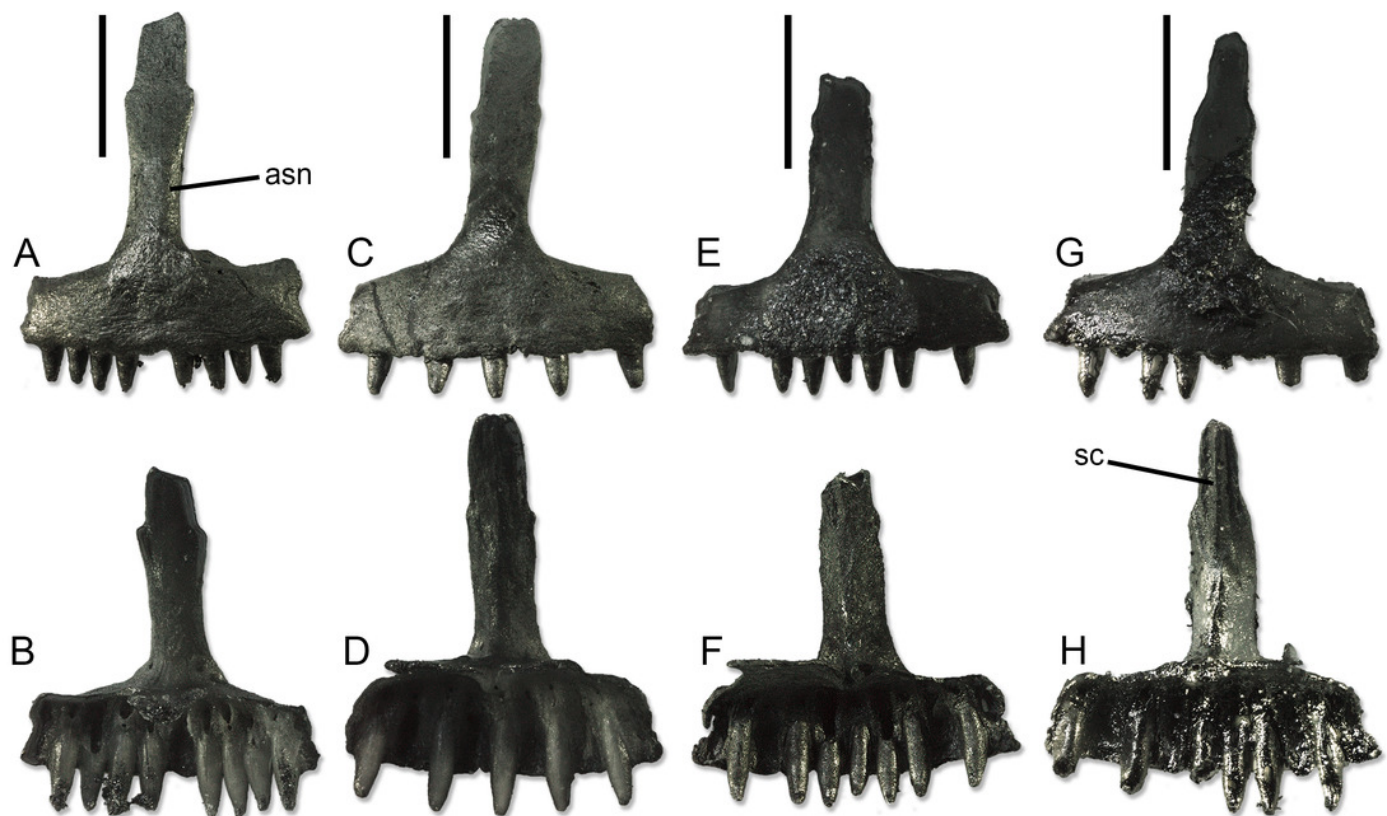
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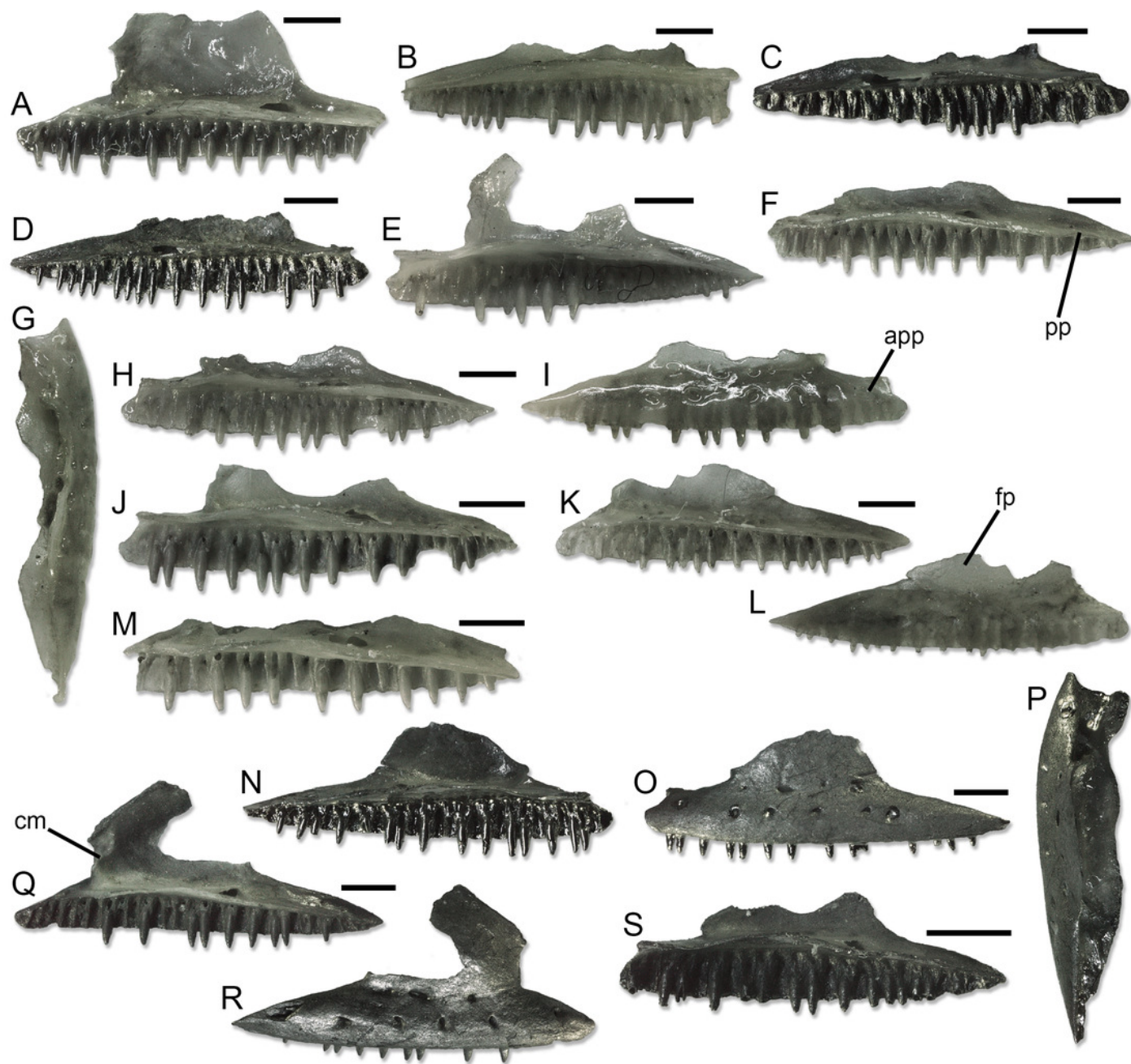
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Paratype dentaries of *Palaeogekko risgoviensis*.

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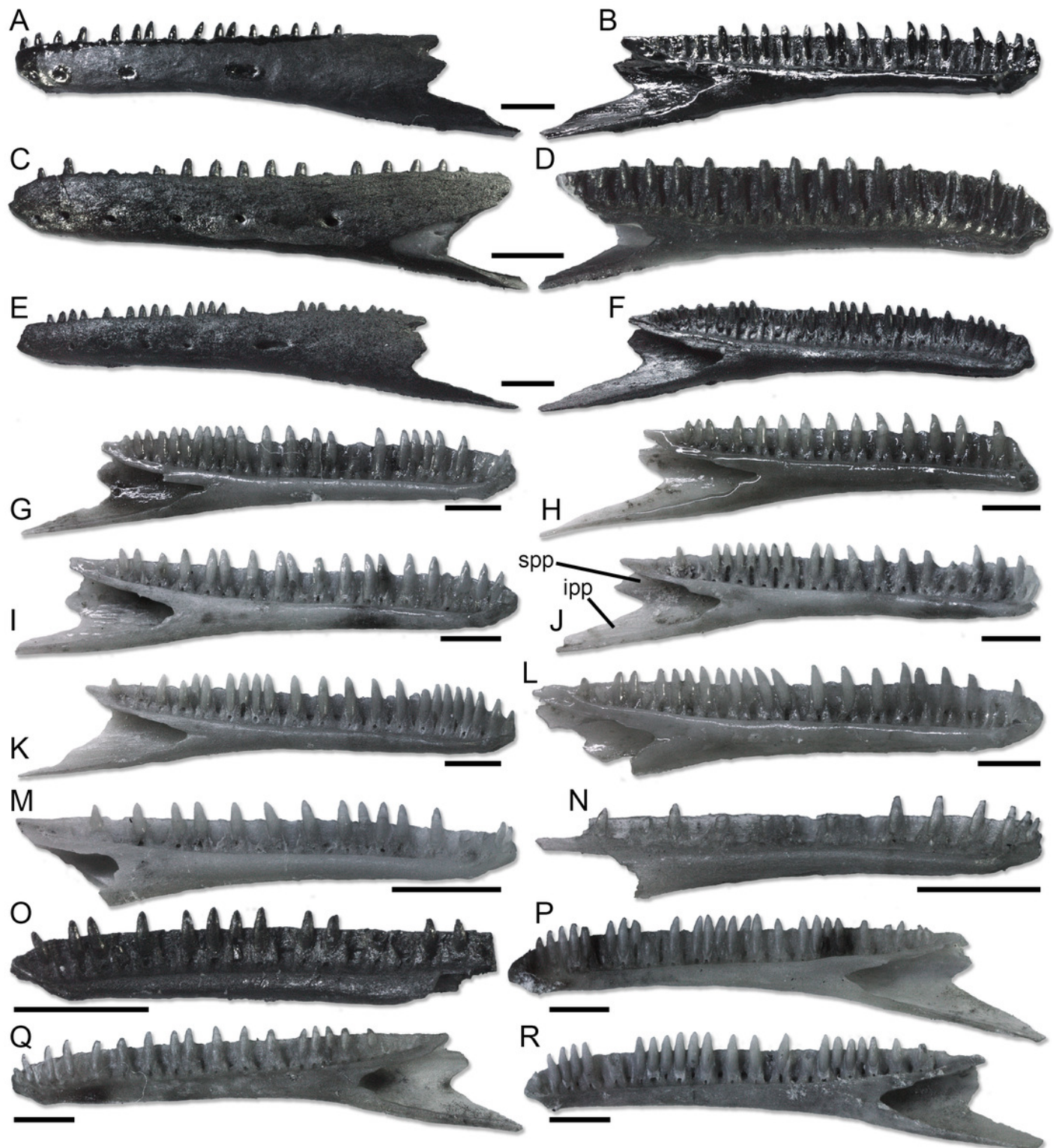
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Figure 6

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).