A new fossil from the early Oligocene of Provence (France) increases the diversity of early Gruoidea and adds constraint on the origin of cranes (Gruidae) and limpkin (Aramidae)

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Abstract

Cranes (Gruidae) have a poor early fossil record, and the oldest ascertained fossils hitherto referred to the family (either as crown or stem-representatives) date back to the early or middle Miocene. Other Gruoidea have an even scarcer fossil record. Psophiidae and Aramidae are virtually unknown as fossils, and other fossil representatives of the Gruoidea are difficult to place. Here we describe a new fossil that sheds new light on the early history of stem Gruidae, a right coracoid in dorsal view preserved on slab in limestone laminites of the early Oligocene « Calcaires de Campagne-Calavon » (Alpes de Haute Provence, France). It is compared with extant and fossil morphologically related taxa, and appears to differ from all extant and fossil relatives in the Gruoidea. The new fossil represents, among the Gruoidea, a new genus and species, *Palaeogeranos tourmenti*, placed within the clade (Aramidae+Gruidae) that is referred to as epifamily Gruoidae. Within Gruoidae, placement is tentative and we give arguments leading to propose a possible position as a stem Gruidae, a hypothesis to be tested with further discoveries. In this hypothesis, aged around 30 million years, the new fossil suggests that the stem of the Gruidae would date back to at least the earliest Oligocene, which is still compatible with current molecular phylogenetic divergence dates estimations, given the confidence intervals. *Palaeogeranos* will potentially help refining future calibrations for molecular phylogenetic studies, at least concerning the earliest Gruoidae (Aramidae+Gruidae).

Keywords: evolution, fossil, France, Gruoidae, Paleogene, phylogeny

Declarations

45

46   Conflicts of interest/Competing interests: the authors declare no conflicts of interests or

47   competing interests.

48

49   Availability of data and material: all the data supporting the study are including in the article.

50   The original fossil is deposited in the public collections of Université Lyon 1.

51

52   Code availability: N/A

53

54   Authors contributions: AD and AL contributed to elaboration of the study, acquisition of data,

55   their analysis and interpretation, and manuscript writing; AD realized illustrations.

56

57   **Introduction**

58   Cranes (Gruidae) are large birds comprising today 15 species in several genera, and are

59   present worldwide except in South America (Winkler et al. 2020a). Their closest extant

60   relative is the South American Limpkin (single representative of the Aramidae). Together, the

61   Gruidae and Aramidae are sister to the South American trumpeters (three species in the

62   Psophiidae). Cranes, Limpkin and trumpeters form together a clade generally referred to as

63   the Gruoidea, which is sister to the Ralloidea (rails and finfoots) in the Gruiformes. Within

64   the Gruoidea, whereas Aramidae and Psophiidae have virtually no confirmed fossil record,

65   the Gruidae comprises a fair number of fossil representatives, essentially in the Neogene of

66   North America and Europe (Segui 2002; Göhlich 2003; Mayr 2017; Mayr et al. 2020). Cranes

67   comprise the Balearicinae (today two species of Crowned cranes, genus *Balearica*), sister to

68   the Gruinae ('true' cranes; the more derived genera and subgenera of cranes relatively to

69   *Balearica*, and comprising principally the genus *Grus*) (Krajewski et al. 2010). Interestingly,

70 several fossils in North America, especially in the Miocene, are referrable to the Balearicinae,

71 whereas the latter live today exclusively in subsaharan Africa (Feduccia and Voorhies 1992).

72 Future investigations might assess whether thes assignments are possibly based on characters

73 that are actually plesiomorphic for the whole Gruidae or not (Mayr 2017). Nevertheless, this

74 probable relictual African distribution is noticeable and mirrors the South American relictual

75 distribution of many taxa (generally represented as fossils earlier, in the Paleogene, in

76 Europe), and which might even concern the Psophiidae (Mayr 2017). The earliest ascertained

77 fossils of Gruidae are known in the early and middle Miocene of France and Germany (Mayr

78 2017). A humerus morphologically similar to that in *Balearica* is known in the early Miocene

79 of Germany (Mourer-Chauviré 2001); it was named *Balearica rummeli*, and is the earliest

80 known crown Gruidae, although Mayr (2017) considered that plesiomorphy might explain the

81 similarity, and that more material would be needed to ascertain the genus. In the early

82 Miocene of Saint-Gérand-le-Puy (France), remains known as '*Palaeogrus excelsa*' have been

83 renamed *Balearica excelsa*, and thus considered a crown Gruidae, by Mlikovsky (2002), an

84 assignment we follow. These Miocene *Balearica* cranes in Europe, like the American record,

85 attest to subsequent shift or retractation of the distribution of balearicine cranes towards

86 tropical Africa, hence their highly relictual present-day range. Younger localities in the

87 Miocene of France have yielded *B. excelsa*, and an early Middle Miocene crown Gruidae is

88 also known from Germany, named '*Palaeogrus*' *mainburgensis* by Göhlich (2003). As Mayr

89 (2017) noted, such crown Gruidae should belong to a different genus from *Palaeogrus*, which

90 was applied originally to Eocene remains, the affinity of which is now known to be non-gruid,

91 but palaeognathous (Palaeotididae; Mayr 2019). Later in the Neogene and up to the Holocene

92 for insular extinct species, a number of localities have yielded fossil cranes (see e.g., Segui

93 2002, Louchart et al. 2008, Mayr et al. 2020).

94   More basal Gruoidea are known, that were considered until recently to comprise the

95   extinct families Geranoididae, Eogruidae, in addition to the much smaller Parvigruidae. The

96   family Geranoididae was since shown to be non-gruiform, but rather a member of the

97   Palaeognathae (Mayr 2019). The Eogruidae comprised two-toed, cursorial birds (*Ergilornis,*

98   *Amphipelargus, Urmiornis*), which were convergent on ostriches, the only other known two-

99   toed birds, and which inhabited central Asian steppes until the late Neogene (Mayr 2017). The

100   Eogruidae might also turn out to be palaeognathous birds (Mayr 2019) but are still tentatively

101   considered gruiform birds. The Parvigruidae (comprising *Parvigrus* and *Rupelrallus*) are

102   known in the Oligocene of Europe, and they were first considered sister to Aramidae+Gruidae

103   (Mayr 2005), then sister to all Gruoidea (Psophiidae+Aramidae+Gruidae; Mayr 2009, 2013,

104   2017), and recently again as sister to Aramidae+Gruidae (Musser et al. 2019). Here we

105   describe a new fossil, a well-preserved complete coracoid from the early Oligocene of the

106   Konservat Lagerstätte in southeastern France (Luberon) known as the Calcaires de

107   Campagne-Calavon. The morphology of the fossil indicates that it belongs to the Gruoidea,

108   and more closely to the Gruidae than to the two other families. The new coracoid sheds new

109   light on the origin of cranes, and the clade (Aramidae+Gruidae), and the diversity of Gruoidea

110   in the middle of the Cenozoic. It is assignable to a new genus and species, and has

111   implications in terms of timing of diversification, phylogenetic calibration, and

112   paleoenvironment.

113

114   **Materials and Methods**

115   The new fossil UCBL-FSL-444667 (Fig. 1d,j) is a complete right coracoid visible in dorsal

116   view on a slab, consisting of limestone laminite, originating from a coastal freshwater lagoon

117   (at the time of deposition, the sea was close to the locality). The formation, called "Calcaires

118   de Campagne-Calavon", is Rupelian, 33.9–27.82 Ma (Million years ago), early Oligocene

119   (Cavelier 1984; Ducreux et al. 1985; Escarguel et al. 1997; Sigé and Hugueney 2006). The

120   locality is on the commune of Limans (Alpes-de-Haute-Provence, southeastern France;

121   43.9861°N, 5.7311°E). The fossil is housed in the collections of the Faculté des Sciences de

122   Lyon (Université Claude Bernard Lyon 1, Villeurbanne, France), to which it was donated by

123   Nicolas Tourment.

124   Material of extant Gruoidea was examined as follows: Psophiidae: *Psophia crepitans*,

125   USNM-345626; Aramidae: *Aramus guarauna*, USNM-554339; Gruidae: Balearicinae:

126   *Balearica pavonina*, UCBL-(I-73), UCBL-(XII-72); Gruinae: *Grus* (*Anthropoides*) *virgo*,

127   UCBL (no n°); *Grus* (*Bugeranus*) *carunculata*, UCBL (no n°); *Grus grus*, UCBL-133.1. In

128   addition, UCBL specimens of species in almost all other extant bird families were examined

129   too. USNM: collections of the National Museum of Natural History (Washington, D.C., USA)

130   (the two specimens concerned here were donated to the UCBL). Other comparisons with

131   additional crane species, and with other Gruiformes (extant and extinct) were made using

132   published data.

133   Osteological nomenclature follows primarily Baumel and Witmer (1993), and in

134   certain cases Howard (1929), Ballmann (1969) and Gilbert et al. (1981) (see Fig. 1).

135   Taxonomy and bird names follow the International Ornithological Congress (IOC) World

136   Bird List (http://www.worldbirdnames.org/).

137   The present publication is registered in ZooBank under the LSID [to be completed

138   upon acceptance].

139   Here we wish to precise the contents for the superfamily Gruoidea and what can be

140   considered a suborder Grues, compared with recent usage. For example, Mayr (2005, 2009,

141   2017) considered that Gruoidea encompassed Psophiidae, Aramidae and Gruidae, and that

142   Grues was a subclade of Gruoidea and encompassed Aramidae and Gruidae. In contrast,

143   Musser et al. (2020) considered that Grues encompassed the Gruoidea, however without

144 further precising the contents of these respective clades. Actually, Gruoidea is clearly a

145 superfamily name, and as such it is regulated by the International Code of Zoological

146 Nomenclature (ICZN), even though there is no rule that automatically precises whether the

147 Gruoidea should encompass Gruidae+Aramidae or Gruidae+Aramidae+Psophiidae. Such

148 flexibility permits adjustments of contents together with new and future advances in the

149 understanding of phylogenetic relationships, which is all the more true of new fossil

150 discoveries, and assignment of fossils to the stem of extant families, for example. In contrast,

151 Grues is not a name that corresponds to the Family-series of zoological nomenclature, nor any

152 other series that is regulated by the ICZN (i.e., up to the superfamily rank); among others it

153 does not bear a family-series suffix. Grues is a Class-series name, and therefore it must

154 automatically be more inclusive than Gruoidea, not the reverse. We do not intend to propose

155 an extension for the Grues here, but we reinstate the normal order from more inclusive to less

156 inclusive: Gruiformes, Grues, Gruoidea, Gruoidae, Gruidae (see Systematic paleontology in

157 the Results section). The clade (Aramidae+Gruidae) is here designated under the epifamily

158 name Gruoidae (see also Discussion), following rules in the family-series (see e.g., Louchart

159 et al. 2013, Dubois et al. 2021).

160   A drawing of the fossil UCBL-FSL-444667 (Fig. 1d) was realized by A.D. using a

161 camera lucida, which allows to avoid distortion.

162

163 **Results**

164 Systematic Palaeontology

165

166 Class Aves Linnaeus, 1758

167 Order Gruiformes Bonaparte, 1854

168 Suborder Grues Bonaparte, 1854

169   Superfamily Gruoidea Vigors, 1825

170   Epifamily Gruoidae Vigors, 1825

171   ?Family Gruidae Vigors, 1825

172

173   *Palaeogeranos*, gen. nov.

174   <mark>LSID</mark> [to be completed once accepted]

175

176   Type and only included species. *Palaeogeranos tourmenti*, sp. nov.

177

178   Differential diagnosis.

179   *Palaeogeranos* is a crane-like bird, of rather small dimensions, ca 70% of a *Balearica* species

180   in coracoid medial length. *Palaeogeranos* differs more importantly from all other avian taxa

181   than from extant Gruidae. Among extant Gruidae, *Palaeogeranos* differs from the Gruinae as

182   follows: sterno-coracoidal fossa rounder; outline of the sternal border slightly less concave;

183   latero-sternal end less expanded sternad; angulus externus more obtuse and less protruding;

184   processus externus more rounded and much less protruding; an obtuse angle in outline visible

185   between the processus procoracoideus and the medial outline of the coracoideus corpus;

186   portion from cotyla scapularis to omal end relatively shorter; processus acrocoracoideus less

187   twisted. *Palaeogeranos* differs from the Balearicinae (*Balearica*) in: processus lateralis

188   slightly narrower; processus externus rounder and less protruding; an obtuse angle in outline

189   visible between the processus procoracoideus and the medial outline of the coracoideus

190   corpus (angle absent in *Balearica*); portion from cotyla scapularis to omal end relatively

191   slightly shorter than in *Balearica*. *Palaeogeranos* differs, among comparable fossil taxa, from

192   *Geranopsis hastingsiae* (Gruoidea) in: more developed acrocoracoid, cotyla scapularis and

193   facies glenoidalis (the latter enlarged more distally); more enlarged processus procoracoideus;

194 wider sternal end with angulus medialis much more protruding medially as an acute angle;

195 more developed processus lateralis; sterno-coracoidal fossa smaller and more central; from

196 *Parvigrus pohli* (Parvigruidae) in: angulus medialis more pointed; outline of the sternal

197 border more concave; medial edge from base of processus procoracoideus to angulus medialis

198 much more concave; whole latero-sternal end much more expanded sternally; processus

199 lateralis almost square-shaped; coracoid corpus narrower (at mid-length); processus

200 procoracoideus wider (omalo-sternally); tuberculum brachiale more prominent; from

201 *Rupelrallus saxoniensis* (Parvigruidae) at least in: angulus medialis much less expanded

202 sternad; outline of the sternal border less concave; more developed processus lateralis; and

203 from *Camusia quintanai* (Gruidae) in: portion from cotyla scapularis to omal end relatively

204 shorter; coracoid corpus narrower (at mid-length); sterno-coracoidal fossa larger; absence of

205 an angle between the medial border of corpus and the omalo-medial border of the angulus

206 medialis.

207

208 Etymology. From the greek *palaios* (ancient) and *geranos* (crane), to reflect the

209 morphological similarity of the fossil with cranes, and its relatively old age.

210

211 *Palaeogeranos tourmenti*, sp. nov.

212 LSID [to be completed upon acceptance]

213

214 Holotype. Complete right coracoid on slab, showing dorsal aspect, n° UCBL-FSL-444667, in

215 the Collections of the Faculté des Sciences de Lyon, Université Lyon 1, Villeurbanne, France.

216

217 Type locality and horizon. The locality is Limans (Alpes de Haute Provence, southeastern

218 France; 43.9861°N, 5.7311°E). The formation, called "Calcaires de Campagne-Calavon", is

219   Rupelian, 33.9–27.82 Ma, early Oligocene (Cavelier 1984; Escarguel et al. 1997; Sigé and

220   Hugueney 2006).

221

222   Diagnosis. As for genus.

223

224   Measurements (mm). Greatest length (from omal end to end of processus lateralis), 53.0;

225   medial length (from omal end to angulus medialis), 44.0; minimal corpus width, 8.2; sternal

226   maximal width (from angulus medialis to end of processus lateralis), 27.0.

227

228   Etymology. Named after Nicolas Tourment, for his long scientific cooperation, and precious

229   contribution to palaeornithology, and who donated the present specimen to the collections of

230   Université Lyon 1.

231

232   Description and comparisons

233   The new fossil coracoid UCBL-FSL-444667 (Fig. 1d,j) was compared with at least one

234   member of almost every of the non-passerine extant bird families (passerine coracoids being

235   readily separated, among others being much more elongated). The new fossil appears much

236   closer in shape to members of the Gruoidea, and especially Gruidae, than to any other bird

237   clade. Hereafter, comparisons are detailed with extant and extinct (fossil) Gruoidea.

238   Among extant Gruoidea, the new fossil coracoid differs from trumpeters (Psophiidae:

239   *Psophia*) principally as follows: much more triangular shape (elongated with a relatively

240   narrow sternal end in *Psophia*); absence of the thin crest, or blade, which connects in the

241   Psophiidae the processus procoracoideus straight to near the angulus medialis, and which

242   leads to an evenly very wide outline of the coracoid corpus in *Psophia*. Note that the

243   specimen of *Psophia* illustrated here in (Fig. 1g) exhibits no pneumatized sterno-coracoidal

244   fossa, but other individuals do so (Mayr and Mourer-Chauviré 2006; Mayr 2009).

245   The fossil differs from the Limpkin (Aramidae: *Aramus guarauna*) principally as

246   follows: whole coracoid more incurved medially towards omal and sternal ends (less straight)

247   (Fig. 2); acrocoracoid more incurved medially and with tuberculum brachiale more protruding

248   medially; wider sternal end; more square processus lateralis and less pointed processus

249   externus than in *Aramus*; angulus medialis in more omal position (pointing less sternad);

250   impressio m. sternocoracoidei bearing a round pneumatized fossa (filled with sediment but

251   unambiguously deep) (no pneumatized fossa in *Aramus*) (Fig. 1h). Note that the specimen of

252   *Aramus* illustrated in Mayr (2016 : fig. 5e) is broken and does not show the normally

253   expanded processus lateralis visible in another specimen, illustrated here (Fig. 1h).

254   Within the extant Gruidae examined, the new coracoid differs from the Gruinae

255   (genera or subgenera *Grus, Anthropoides, Bugeranus, Leucogeranus*) principally as follows:

256   sterno-coracoidal fossa rounder; outline of the sternal border slightly less concave; latero-

257   sternal end less expanded sternad; angulus externus more obtuse and less protruding;

258   processus externus more rounded and much less protruding (pointed in the Gruinae); an

259   obtuse angle in outline visible between the processus procoracoideus and the medial outline

260   of the coracoideus corpus (angle absent in the Gruinae); acrocoracoid (and all portion from

261   cotyla scapularis to omal end) relatively shorter, and acrocoracoid more incurved medially,

262   with a more rounded tuberculum brachiale; processus acrocoracoideus less twisted (in the

263   Gruinae the facies articularis clavicularis appears more in profile) (Fig. 1a-c).

264   The fossil coracoid differs from the Balearicinae (*Balearica*) principally as follows:

265   outline of the sternal border slightly less concave (albeit with variation visible among

266   individuals of *Balearica pavonina* for example); processus lateralis as expanded latero-

267   sternad, but narrower (although one individual of *B. pavonina* is quite similar; Fig. 1f);

268   processus externus rounder and less protruding; an obtuse angle in outline visible between the

269   processus procoracoideus and the medial outline of the coracoideus corpus (angle absent in

270   *Balearica*); portion from cotyla scapularis to omal end relatively slightly shorter than in

271   *Balearica* (Fig. 1e,f,i, Fig. 2). All this takes in account the fact that a substantial individual

272   variation within *Balearica*, visible among only three extant specimens, encompasses character

273   states identical to *P. tourmenti*, concerning the shape of the cotyla scapularis, the depth of the

274   sternal facet, and many other features (Fig. 1e,f,i).

275   The relative length of the acrocoracoid region (percentage ratio measured as the length

276   from acrocoracoid extremity to distal end of cotyla scapularis divided by total length of

277   coracoid to angulus externus) increases from basal Gruoidea to the more derived gruid genera.

278   This ratio is lower in *Psophia* than in *Aramus guarauna* (in the latter 31.0% and 32.9%,

279   respectively specimen in Fig. 1h, and specimen in Mayr 2016), in turn lower than in

280   *Balearica* (33.3%, 34.5%, 37.1%), then in genera of Gruinae (higher ratios; see Fig. 1). In

281   *Palaeogeranos tourmenti*, this ratio is 32.1%, within the variation in *Aramus*.

282

283   Compared with known closely related fossil taxa (Parvigruidae), of which the coracoid

284   is known, *P. tourmenti* differs as follows.

285   In *Rupelrallus saxoniensis*, only the sternal part of the coracoid is known (Fischer

286   1997; Mayr 2013). Nevertheless, several differences appear in comparison with the Luberon

287   fossil; the new fossil exhibits: an angulus medialis much less expanded sternad; outline of the

288   sternal border less concave; developed processus lateralis (versus much reduced in *R.*

289   *saxoniensis*, this being visible despite slightly broken processus externus; Fig. 1k).

290   The new fossil coracoid differs from that in *Parvigrus pohli*, at least in several features

291   of the outline (the coracoid of *P. pohli* being visible in ventral view only; Mayr 2005),

292   principally as follows: medial edge from base of processus procoracoideus to angulus

293 medialis much more concave; angulus medialis more pointed (moderately acute angle, versus

294 square-shaped in *P. pohli*); outline of the sternal border concave (straight in *P. pohli*); whole

295 latero-sternal end much more expanded sternally; processus lateralis almost square-shaped

296 (versus making only an acute corner to the processus externus in *P. pohli*); coracoid corpus

297 narrower (at mid-length); processus procoracoideus wider (omalo-sternally) than in *P. pohli*;

298 tuberculum brachiale more prominent; (Fig. 1l, Fig. 2).

299   The coracoid of *P. tourmenti* differs from that of the probable gruoid *Geranopsis*

300 *hastingsiae* (Lydekker 1891) principally as follows: proportionately more developed

301 acrocoracoid, cotyla scapularis and facies glenoidalis (the latter enlarged more distally); more

302 enlarged processus procoracoideus; wider sternal end with angulus medialis much more

303 protruding medially as an acute angle (much less protruding, more obtuse and more distad in

304 *G. hastingsiae*); more developed processus lateralis; sterno-coracoidal fossa smaller and more

305 central.

306   Among the fossil Gruidae in extinct genera, of which the coracoid is known, is

307 *Camusia quintanai*, from the late Miocene or Pliocene of Menorca (Balearic Islands) (Segui

308 2002). *Palaeogeranos tourmenti* differs from *Camusia* principally in: portion from cotyla

309 scapularis to omal end relatively shorter; coracoid corpus narrower (at mid-length); sterno-

310 coracoidal fossa larger; absence of an angle between the medial border of corpus and the

311 omalo-medial border of the angulus medialis. Another extinct gruid, *'Palaeogrus'*

312 *mainburgensis* (which should now be designated under another genus name), from the early

313 Middle Miocene of Germany, comprises a tentatively referred proximal coracoid, albeit

314 fragmentary (only an incomplete omal end) (Göhlich 2003). This fossil exhibits few

315 diagnostic features useful in the present case; at least *Palaeogeranos tourmenti* differs with a

316 facies articularis humeralis having a lateral border less convex and less protruding laterally.

317

Discussion

Phylogenetic position

The coracoid UCBL-FSL-444667 is morphologically closer to the Gruoidea than to any other bird clade, and among extant Gruoidea (the coracoids of which differ importantly), it appears closer to the Gruidae than to the Aramidae, and even more so than to the Psophiidae. UCBL-FSL-444667 appears sufficiently different from the coracoids of extant genera and species of Gruidae, fossil Gruidae (such as *Camusia*), and more basal fossil Gruoidea (such as *Rupelrallus* and *Parvigrus* in the Parvigruidae), to be assigned to a new genus and species, *Palaeogeranos tourmenti*. Compared with gruoid taxa more basal than the clade (Aramidae+Gruidae), *P. tourmenti* exhibits characters that are found in Gruidae and not in *Parvigrus*, the most obvious being: angulus medialis more pointed; outline of the medial edge concave; outline of the sternal border concave; whole latero-sternal end much more expanded sternally; processus lateralis almost square-shaped (versus making only an acute corner to the processus externus in *P. pohli*); tuberculum brachiale more prominent medially.

Palaeogeranos tourmenti also exhibits characters found in extant Gruidae and not in the parvigruid *Rupelrallus saxoniensis* (of which only the sternal half of the coracoid is known): angulus medialis much less expanded sternad; outline of the sternal border less concave; more developed processus lateralis. More precisely within the clade (Aramidae+Gruidae), *Palaeogeranos tourmenti* exhibits characters that are found in extant Gruidae and not in the Aramidae, and can be proposed as gruid synapomorphies prominently as follows (compared with *Aramus*): whole coracoid more incurved medially towards omal and sternal ends (less straight), acrocoracoid more incurved medially and tuberculum brachiale round and more protruding medially (found in *Balearica*), wider sternal end (also more obvious in *Balearica*); as for the impressio m. sternocoracoidei bearing a round pneumatized fossa (similar deep pneumatized fossa found in all gruids, and round in *Balearica*, with variable diameter), absent

14

343 in Aramidae, it might be a plesiomorphy (found in *Psophia*, in *Rupelrallus*) and lost only in

344 Aramidae. Comparisons of the outline of *P. tourmenti* coracoid with those of *Parvigrus*,

345 *Aramus* and *Balearica*, scaled at the same dimensions (Fig. 2), show greater overall proximity

346 with *Balearica* as well. A few features of *Palaeogeranos* might be plesiomorphic for stem

347 Gruidae, such as the relatively short omal (acrocoracoidal) part of the bone (from omal

348 extremity to sternal end of cotyla scapularis), reminiscent of the condition in *Aramus*. We

349 interpret all the preceding as a consequence of probable position as a stem-Gruidae (Fig. 3),

350 which we propose here only tentatively, although this is based only on a coracoid, and more

351 material will help precise its systematic position and test this hypothesis. At the very least, *P.*

352 *tourmenti* is assignable to the epifamily Gruoidae, i.e., the clade (Aramidae+Gruidae;

353 including possibly a short stem portion). The position, in all cases more basal than crown

354 cranes, seems reinforced by the general greater resemblance of *P. tourmenti* with Balearicinae

355 than with the Gruinae, the former being the most basal genus (*Balearica*) within the Gruidae

356 (Krajewski et al. 2010).

357

358 Palaeoenvironment

359 *Palaeogeranos tourmenti* adds to the known diversity of Gruoidea in the early Oligocene of

360 southeastern France, which comprises also *Parvigrus* (Parvigruidae) in the same formation in

361 the nearby locality of Pichovet (Mayr 2005). Compared with Parvigruidae, *Palaeogeranos*

362 *tourmenti* is 59% larger than *Parvigrus pohli* (based on greatest length of coracoid without the

363 proc. lat.), and 33% larger than *Rupelrallus saxoniensis* (based on coracoid distal width

364 without the proc. lat.). It can be inferred that *P. tourmenti* is also ca 19% larger than

365 *Rupelrallus belgicus*, (based indirectly on carpometacarpus length, the coracoid of the latter

366 species being unknown). In contrast, *P. tourmenti* is 30% smaller than *Balearica pavonina*

367 and *B. regulorum*, and 23% smaller than a specimen of *Anthropoides virgo*, the smallest

368 living crane. Among the Gruoidea, the preferred habitats of extant cranes are open, humid

369 habitats, such as marshes or grasslands (Winkler et al. 2020a). The Limpkin *Aramus*

370 *guarauna*, sister species of cranes, lives in open freshwater marshes, hence also open habitats

371 but more humid/aquatic (Winkler et al. 2020b). In contrast, the next sister clade, the

372 trumpeters (Psophiidae), live in lowland tropical forest (Winkler et al. 2020c). *Palaeogeranos*

373 *tourmenti*, assigned here tentatively to ?stem Gruidae and being at the very least a member of

374 the clade (Aramidae+Gruidae), therefore tends to indicate the presence of rather

375 humid/aquatic, open habitats around the locality in the early Oligocene. This adds to known

376 palaeoenvironmental evidence for the formation and nearby localities, including from other

377 vertebrates, insects and plants (Louchart et al. 2008). Other birds comprise at least 15 other

378 species, including some taxa indicative of tropical or subtropical climate, and diverse habitats

379 (aquatic, humid, open or semi-open, and woodland or forest) (Mayr 1999, 2000; Louchart et

380 al. 2008, 2011; Duhamel et al. 2020; Riamon et al. 2020; Duhamel and Louchart in prep.).

381

382 Diversification of Gruoidea

383 In a recent molecular phylogeny that resolved the position of difficult taxa (such as the

384 Hoatzin), the age of the divergence between Aramidae and Gruidae is centered near 26 Ma,

385 but the 95% confidence interval is very large, and encompasses ages from 46 to 12 Ma (Kuhl

386 et al. 2020) (Fig. 3). In the proposed hypothesis of *P. tourmenti* being a ?stem Gruidae, it is

387 therefore plausible that, at ca 30 Ma, *P. tourmenti* derives from the earliest stem of Gruidae,

388 which would have diverged slightly earlier from the stem of Aramidae (case illustrated in Fig.

389 3). In the hypothesis of *P. tourmenti* being slightly more basal, on the stem of the clade

390 (Aramidae+Gruidae), there is also congruence with these recent molecular extimates.

391 Calibration using fossils incidentally serves as minimizing such large confidence intervals and

392 precising the age of nodes. In addition, there are other, non-exclusive possible explanations

393   for incomplete coincidence between morphology and molecules in phylogeny. These include

394   too much load of homoplasy in morphology to reflect phylogeny, which is frequent when

395   morphology is confronted to recent molecular phylogenies that did considerable progress in

396   the last decade, with morphologically unexpected clades such as the Mirandornithes

397   (Podicipedidae+Phoenicopteridae), the Australaves (including Psittaciformes+Passeriformes),

398   and Otididae+Musophagidae (e.g., Hackett et al. 2008; Jarvis et al. 2014; Prum et al. 2015;

399   Kuhl et al. 2020). Other possible explanations include the possibility of discordant

400   topologogies between the real phylogenetic (species tree) and gene trees due to hemiplasy

401   (Avise and Robinson 2008). Obtaining more skeletal elements of *P. tourmenti* in the future

402   will also help better approaching the morphological aspect of the phylogenetic history of the

403   Gruoidea, since mosaicism between the different elements is also a recurrent aspect of avian

404   evolution (Olson 1985; Mayr 2017).

405

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519

520 **Figure legends**

521

522 **Fig. 1** The new fossil coracoid UCBL-FSL-444667, of *Palaeogeranos tourmenti* n. gen. n. sp.

523 (**d**, drawing after the actual fossil; **j**, photograph of fossil on slab), compared with extant and

524 fossil representatives of the Gruoidea. **a**, *Grus* (*Bugeranus*) *carunculata*; **b**, *Grus grus*; **c**,

525 *Grus* (*Anthropoides*) *virgo*; **e**,**f**, *Balearica pavonina*; **g**, *Psophia crepitans*; **h**, *Aramus*

526 *guarauna*; **i**, *Balearica regulorum*; **k**, *Rupelrallus saxoniensis*; **l**, *Parvigrus pohli*. All right

527 coracoids in dorsal view except (**l**), which is a left coracoid in ventral view, useful in outline

528 comparison, and except (**b**,**h**,**i**), which are left coracoids (in dorsal view) that were mirrored

529 for convenience. (**i**), modified after photograph in Mayr (2016). (**k**,**l**), modified after

530 photographs in Mayr (2013). *ae*, angulus externus; am, angulus medialis; chs*, coraco-

531 humeral surface (after Howard 1929); cs, cotyla scapularis; fac, facies articularis clavicularis;

532 fah, facies articularis humeralis; fas, facies articularis sternalis; *fsc*, foramen

533 supracoracoideum; *fg*, facies glenoidalis; ims, impressio m. sternocoracoidei; pa, processus

534 acrocoracoideus; *pe*, processus externus; pl, processus lateralis; pp, processus procoracoideus;

535 scf**, sterno-coracoidal fossa (after Gilbert et al. 1981), which is deep in *P. tourmenti* (and

536 filled with sediment); *tb*, tuber brachialis (all terms after Baumel and Witmer 1993, except for

537 the ones marked with asterisks, and the ones in italics that derive from Ballmann 1969). Small

538 arrows indicate the principal differences from *P. tourmenti*, observed in extant Gruidae, and

539 on the other hand in the fossil taxa *Rupelrallus* and *Parvigrus*. Scale bars, 10 mm.

540

541　**Fig. 2** Three comparisons of the outlines, drawn at same scale, between *Palaeogeranos*

542　*tourmenti* n. gen. n. sp., coracoid UCBL-FSL-444667, with coracoids of *Aramus guarauna*

543　(a), *Parvigrus pohli* (b), and *Balearica pavonina* (c).

544

545　**Fig. 3** Phylogenetic position hypothesized for *Palaeogeranos tourmenti* n. gen. n. sp. This

546　proposed possible position derives from comparisons with other Gruoidea. Other fossil

547　Gruoidea are also placed, based on literature (see text). The phylogenetic frame of extant taxa

548　derives from Kuhl et al. (2020). The 95% confidence interval is shown (bar and limits on

549　either side of average date marked by X, the latter being the age of maximal probability) for

550　the node (Gruidae+Aramidae) based on Kuhl et al. (2020). The approximate position of *P.*

551　*tourmenti* proposed here (*) takes into account this wide interval. We placed here the node

552　(Gruidae+Aramidae) at an earlier date than the average (maximum probability age), but still

553　within the 95% confidence interval, at ca. 35 Ma (circle). Consequently, *P. tourmenti* can

554　possibly be considered posterior to this node (Gruidae+Aramidae) and as a ?stem Gruidae

555　(see text). Alternatively, it might be slightly more basal, slightly stemward from this node, on

556　the stem of Gruoidea (Aramidae+Gruidae). Squares indicate the age of crown Balearicinae

557　and crown Gruinae, based on OneZoom Tree of Life Explorer (Jetz et al. 2012; Rosindell and

558　Harmon 2012). The timescale is logarithmic to avoid compression of branchings of interest

559　here. Crosses indicate fossil taxa.

Figure labels: pa, chs*, fac =tb, fah =fg, pp, cs, fsc, ims, scf**, am, fas, ae, pe, pl, ae (broken), ae

a *Aramus*

Palaeogeranos

b *Parvigrus*

Palaeogeranos

c *Balearica*

Palaeogeranos

Charadriiformes			
«*Palaeogrus*» *mainburgensis* †			
Balearicinae 3.24 Ma			
Balearica rummeli †			
Balearica excelsa †			
Gruinae 8.35 Ma			
Camusia quintanai †			
Palaeogeranos tourmenti †			
Aramidae			
Parvigrus †			
Rupelrallus †			
Psophiidae			
Eogruidae †			
Rallidae + Heliornithidae			

?

Gruidae | Gruoidea | Gruoidea | Gruiformes

AGE (Ma)

70 60 50 40 30 20 10 5 3 0