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

4

5

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13

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18

19

20 **Abstract**

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

39

40 Keywords: evolution, fossil, France, Gruoidea, Paleogene, phylogeny

41

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43

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48

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51

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53

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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 (Seguí 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 referable to the Balearicinae,  
71 whereas the latter live today exclusively in subsaharan Africa (Feduccia and Voorhies 1992).  
72 Future investigations might assess whether these 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-Gérard-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 retraction 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 *Amhipelargus*, *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 Aramididae+Gruidae  
103 (Mayr 2005), then sister to all Gruoidea (Psophiidae+Aramididae+Gruidae; Mayr 2009, 2013,  
104 2017), and recently again as sister to Aramididae+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 (Aramididae+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 Huguéney 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 precisising 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 precisises 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 **LSID [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 guaranauna* (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 *Palaeogerranus 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. 11, 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) (Seguí  
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 gruoid, '*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

318 **Discussion**

319 Phylogenetic position

320 The coracoid UCBL-FSL-444667 is morphologically closer to the Gruoidea than to any other  
321 bird clade, and among extant Gruoidea (the coracoids of which differ importantly), it appears  
322 closer to the Gruidae than to the Aramidae, and even more so than to the Psophiidae. UCBL-  
323 FSL-444667 appears sufficiently different from the coracoids of extant genera and species of  
324 Gruidae, fossil Gruidae (such as *Camusia*), and more basal fossil Gruoidea (such as  
325 *Rupelrallus* and *Parvigrus* in the Parvigruidae), to be assigned to a new genus and species,  
326 *Palaeogermanos tourmenti*. Compared with gruoid taxa more basal than the clade  
327 (Aramidae+Gruidae), *P. tourmenti* exhibits characters that are found in Gruidae and not in  
328 *Parvigrus*, the most obvious being: angulus medialis more pointed; outline of the medial edge  
329 concave; outline of the sternal border concave; whole latero-sternal end much more expanded  
330 sternally; processus lateralis almost square-shaped (versus making only an acute corner to the  
331 processus externus in *P. pohli*); tuberculum brachiale more prominent medially.  
332 *Palaeogermanos tourmenti* also exhibits characters found in extant Gruidae and not in the  
333 parvigruid *Rupelrallus saxoniensis* (of which only the sternal half of the coracoid is known):  
334 angulus medialis much less expanded sternad; outline of the sternal border less concave; more  
335 developed processus lateralis. More precisely within the clade (Aramidae+Gruidae),  
336 *Palaeogermanos tourmenti* exhibits characters that are found in extant Gruidae and not in the  
337 Aramidae, and can be proposed as gruid synapomorphies prominently as follows (compared  
338 with *Aramus*): whole coracoid more incurved medially towards omal and sternal ends (less  
339 straight), acrocoracoid more incurved medially and tuberculum brachiale round and more  
340 protruding medially (found in *Balearica*), wider sternal end (also more obvious in *Balearica*);  
341 as for the impressio m. sternocoracoidei bearing a round pneumatized fossa (similar deep  
342 pneumatized fossa found in all gruids, and round in *Balearica*, with variable diameter), absent

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 *Palaeogeros* 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 Gruoidea, 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 *Palaeogeros 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, *Palaeogeros*  
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. regulatorum*, 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 estimates.  
391 Calibration using fossils incidentally serves as minimizing such large confidence intervals and  
392 precisising 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 topologies between the real phylogenetic (species tree) and gene trees due to hemiplasy  
401 (Avice 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 *Palaeogeros*  
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 *Palaeogeros 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.







