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)

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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

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Introduction

Cranes (Gruidae) are large birds comprising today 15 species in several genera, and are present worldwide except in South America (Winkler et al. 2020a). Their closest extant relative is the South American Limpkin (single representative of the Aramidae). Together, the Gruidae and Aramidae are sister to the South American trumpeters (three species in the Psophiidae). Cranes, Limpkin and trumpeters form together a clade generally referred to as the Gruoidea, which is sister to the Ralloidea (rails and finfoots) in the Gruiformes. Within the Gruoidea, whereas Aramidae and Psophiidae have virtually no confirmed fossil record, the Gruidae comprises a fair number of fossil representatives, essentially in the Neogene of North America and Europe (Segui 2002; Göhlich 2003; Mayr 2017; Mayr et al. 2020). Cranes comprise the Balearicinae (today two species of Crowned cranes, genus *Balearica*), sister to the Gruinae ('true' cranes; the more derived genera and subgenera of cranes relatively to *Balearica*, and comprising principally the genus *Grus*) (Krajewski et al. 2010). Interestingly,

several fossils in North America, especially in the Miocene, are referable to the Balearicinae, whereas the latter live today exclusively in subsaharan Africa (Feduccia and Voorhies 1992). Future investigations might assess whether these assignments are possibly based on characters that are actually plesiomorphic for the whole Gruidae or not (Mayr 2017). Nevertheless, this probable relictual African distribution is noticeable and mirrors the South American relictual distribution of many taxa (generally represented as fossils earlier, in the Paleogene, in Europe), and which might even concern the Psophiidae (Mayr 2017). The earliest ascertained fossils of Gruidae are known in the early and middle Miocene of France and Germany (Mayr 2017). A humerus morphologically similar to that in *Balearica* is known in the early Miocene of Germany (Mourer-Chauviré 2001); it was named *Balearica rummeli*, and is the earliest known crown Gruidae, although Mayr (2017) considered that plesiomorphy might explain the similarity, and that more material would be needed to ascertain the genus. In the early Miocene of Saint-Gérard-le-Puy (France), remains known as '*Palaeogrus excelsa*' have been renamed *Balearica excelsa*, and thus considered a crown Gruidae, by Mlikovsky (2002), an assignment we follow. These Miocene *Balearica* cranes in Europe, like the American record, attest to subsequent shift or retraction of the distribution of balearicine cranes towards tropical Africa, hence their highly relictual present-day range. Younger localities in the Miocene of France have yielded *B. excelsa*, and an early Middle Miocene crown Gruidae is also known from Germany, named '*Palaeogrus*' *mainburgensis* by Göhlich (2003). As Mayr (2017) noted, such crown Gruidae should belong to a different genus from *Palaeogrus*, which was applied originally to Eocene remains, the affinity of which is now known to be non-gruid, but palaeognathous (Palaeotididae; Mayr 2019). Later in the Neogene and up to the Holocene for insular extinct species, a number of localities have yielded fossil cranes (see e.g., Seguí 2002, Louchart et al. 2008, Mayr et al. 2020).

More basal Gruoidea are known, that were considered until recently to comprise the extinct families Geranoididae, Eogruidae, in addition to the much smaller Parvigruidae. The family Geranoididae was since shown to be non-gruiform, but rather a member of the Palaeognathae (Mayr 2019). The Eogruidae comprised two-toed, cursorial birds (*Ergilornis*, *Amphipelargus*, *Urmiornis*), which were convergent on ostriches, the only other known two-toed birds, and which inhabited central Asian steppes until the late Neogene (Mayr 2017). The Eogruidae might also turn out to be palaeognathous birds (Mayr 2019) but are still tentatively considered gruiform birds. The Parvigruidae (comprising *Parvigrus* and *Rupelrallus*) are known in the Oligocene of Europe, and they were first considered sister to Aramididae+Gruidae (Mayr 2005), then sister to all Gruoidea (Psophiidae+Aramididae+Gruidae; Mayr 2009, 2013, 2017), and recently again as sister to Aramididae+Gruidae (Musser et al. 2019). Here we describe a new fossil, a well-preserved complete coracoid from the early Oligocene of the Konservat Lagerstätte in southeastern France (Luberon) known as the Calcaires de Campagne-Calavon. The morphology of the fossil indicates that it belongs to the Gruoidea, and more closely to the Gruidae than to the two other families. The new coracoid sheds new light on the origin of cranes, and the clade (Aramididae+Gruidae), and the diversity of Gruoidea in the middle of the Cenozoic. It is assignable to a new genus and species, and has implications in terms of timing of diversification, phylogenetic calibration, and paleoenvironment.

Materials and Methods

The new fossil UCBL-FSL-444667 (Fig. 1d,j) is a complete right coracoid visible in dorsal view on a slab, consisting of limestone laminite, originating from a coastal freshwater lagoon (at the time of deposition, the sea was close to the locality). The formation, called “Calcaires de Campagne-Calavon”, is Rupelian, 33.9–27.82 Ma (Million years ago), early Oligocene

(Cavelier 1984; Ducreux et al. 1985; Escarguel et al. 1997; Sigé and Hugueney 2006). The locality is on the commune of Limans (Alpes-de-Haute-Provence, southeastern France; 43.9861°N, 5.7311°E). The fossil is housed in the collections of the Faculté des Sciences de Lyon (Université Claude Bernard Lyon 1, Villeurbanne, France), to which it was donated by Nicolas Tourment.

Material of extant Gruoidea was examined as follows: Psophiidae: *Psophia crepitans*, USNM-345626; Aramidae: *Aramus guarauna*, USNM-554339; Gruidae: Balearicinae: *Balearica pavonina*, UCBL-(I-73), UCBL-(XII-72); Gruinae: *Grus (Anthropoides) virgo*, UCBL (no n°); *Grus (Bugeranus) carunculata*, UCBL (no n°); *Grus grus*, UCBL-133.1. In addition, UCBL specimens of species in almost all other extant bird families were examined too. USNM: collections of the National Museum of Natural History (Washington, D.C., USA) (the two specimens concerned here were donated to the UCBL). Other comparisons with additional crane species, and with other Gruiformes (extant and extinct) were made using published data.

Osteological nomenclature follows primarily Baumel and Witmer (1993), and in certain cases Howard (1929), Ballmann (1969) and Gilbert et al. (1981) (see Fig. 1). Taxonomy and bird names follow the International Ornithological Congress (IOC) World Bird List (<http://www.worldbirdnames.org/>).

The present publication is registered in ZooBank under the LSID [to be completed upon acceptance].

Here we wish to precise the contents for the superfamily Gruoidea and what can be considered a suborder Grues, compared with recent usage. For example, Mayr (2005, 2009, 2017) considered that Gruoidea encompassed Psophiidae, Aramidae and Gruidae, and that Grues was a subclade of Gruoidea and encompassed Aramidae and Gruidae. In contrast, Musser et al. (2020) considered that Grues encompassed the Gruoidea, however without

further precisising the contents of these respective clades. Actually, Gruoidea is clearly a superfamily name, and as such it is regulated by the International Code of Zoological Nomenclature (ICZN), even though there is no rule that automatically precisises whether the Gruoidea should encompass Gruidae+Aramidae or Gruidae+Aramidae+Psophiidae. Such flexibility permits adjustments of contents together with new and future advances in the understanding of phylogenetic relationships, which is all the more true of new fossil discoveries, and assignment of fossils to the stem of extant families, for example. In contrast, Grues is not a name that corresponds to the Family-series of zoological nomenclature, nor any other series that is regulated by the ICZN (i.e., up to the superfamily rank); among others it does not bear a family-series suffix. Grues is a Class-series name, and therefore it must automatically be more inclusive than Gruoidea, not the reverse. We do not intend to propose an extension for the Grues here, but we reinstate the normal order from more inclusive to less inclusive: Gruiformes, Grues, Gruoidea, Gruoidae, Gruidae (see Systematic paleontology in the Results section). The clade (Aramidae+Gruidae) is here designated under the epifamily name Gruoidae (see also Discussion), following rules in the family-series (see e.g., Louchart et al. 2013, Dubois et al. 2021).

A drawing of the fossil UCBL-FSL-444667 (Fig. 1d) was realized by A.D. using a camera lucida, which allows to avoid distortion.

Results

Systematic Palaeontology

Class Aves Linnaeus, 1758

Order Gruiformes Bonaparte, 1854

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 *palaaios* (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

specimen of *Psophia* illustrated here in (Fig. 1g) exhibits no pneumatized sterno-coracoidal fossa, but other individuals do so (Mayr and Mourer-Chauviré 2006; Mayr 2009).

The fossil differs from the Limpkin (Aramidae: *Aramus guarauna*) principally as follows: whole coracoid more incurved medially towards omal and sternal ends (less straight) (Fig. 2); acrocoracoid more incurved medially and with tuberculum brachiale more protruding medially; wider sternal end; more square processus lateralis and less pointed processus externus than in *Aramus*; angulus medialis in more omal position (pointing less sternad); impressio m. sternocoracoidei bearing a round pneumatized fossa (filled with sediment but unambiguously deep) (no pneumatized fossa in *Aramus*) (Fig. 1h). Note that the specimen of *Aramus* illustrated in Mayr (2016 : fig. 5e) is broken and does not show the normally expanded processus lateralis visible in another specimen, illustrated here (Fig. 1h).

Within the extant Gruinae examined, the new coracoid differs from the Gruinae (genera or subgenera *Grus*, *Anthropoides*, *Bugeranus*, *Leucogeranus*) principally as follows: sterno-coracoidal fossa rounder; outline of the sternal border slightly less concave; latero-sternal end less expanded sternad; angulus externus more obtuse and less protruding; processus externus more rounded and much less protruding (pointed in the Gruinae); an obtuse angle in outline visible between the processus procoracoideus and the medial outline of the coracoideus corpus (angle absent in the Gruinae); acrocoracoid (and all portion from cotyla scapularis to omal end) relatively shorter, and acrocoracoid more incurved medially, with a more rounded tuberculum brachiale; processus acrocoracoideus less twisted (in the Gruinae the facies articularis clavicularis appears more in profile) (Fig. 1a-c).

The fossil coracoid differs from the Balearicinae (*Balearica*) principally as follows: outline of the sternal border slightly less concave (albeit with variation visible among individuals of *Balearica pavonina* for example); processus lateralis as expanded latero-sternad, but narrower (although one individual of *B. pavonina* is quite similar; Fig. 1f);

processus externus rounder and less protruding; an obtuse angle in outline visible between the processus procoracoideus and the medial outline of the coracoideus corpus (angle absent in *Balearica*); portion from cotyla scapularis to omal end relatively slightly shorter than in *Balearica* (Fig. 1e,f,i, Fig. 2). All this takes in account the fact that a substantial individual variation within *Balearica*, visible among only three extant specimens, encompasses character states identical to *P. tourmenti*, concerning the shape of the cotyla scapularis, the depth of the sternal facet, and many other features (Fig. 1e,f,i).

The relative length of the acrocoracoid region (percentage ratio measured as the length from acrocoracoid extremity to distal end of cotyla scapularis divided by total length of coracoid to angulus externus) increases from basal Gruoidea to the more derived gruid genera. This ratio is lower in *Psophia* than in *Aramus guarauna* (in the latter 31.0% and 32.9%, respectively specimen in Fig. 1h, and specimen in Mayr 2016), in turn lower than in *Balearica* (33.3%, 34.5%, 37.1%), then in genera of Gruinae (higher ratios; see Fig. 1). In *Palaeozeranus tourmenti*, this ratio is 32.1%, within the variation in *Aramus*.

Compared with known closely related fossil taxa (Parvigruidae), of which the coracoid is known, *P. tourmenti* differs as follows.

In *Rupelrallus saxoniensis*, only the sternal part of the coracoid is known (Fischer 1997; Mayr 2013). Nevertheless, several differences appear in comparison with the Luberon fossil; the new fossil exhibits: an angulus medialis much less expanded sternad; outline of the sternal border less concave; developed processus lateralis (versus much reduced in *R. saxoniensis*, this being visible despite slightly broken processus externus; Fig. 1k).

The new fossil coracoid differs from that in *Parvigrus pohli*, at least in several features of the outline (the coracoid of *P. pohli* being visible in ventral view only; Mayr 2005), 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 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

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 *Palaeoegeranos 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 *Palaeoegeranos 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 *Palaeoegeranos 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

in Aramididae, it might be a plesiomorphy (found in *Psophia*, in *Rupelrallus*) and lost only in Aramididae. Comparisons of the outline of *P. tourmenti* coracoid with those of *Parvigrus*, *Aramus* and *Balearica*, scaled at the same dimensions (Fig. 2), show greater overall proximity with *Balearica* as well. A few features of *Palaeogeros* might be plesiomorphic for stem Gruidae, such as the relatively short omal (acrocoracoidal) part of the bone (from omal extremity to sternal end of cotyla scapularis), reminiscent of the condition in *Aramus*. We interpret all the preceding as a consequence of probable position as a stem-Gruidae (Fig. 3), which we propose here only tentatively, although this is based only on a coracoid, and more material will help precise its systematic position and test this hypothesis. At the very least, *P. tourmenti* is assignable to the epifamily Gruoidea, i.e., the clade (Aramididae+Gruidae; including possibly a short stem portion). The position, in all cases more basal than crown cranes, seems reinforced by the general greater resemblance of *P. tourmenti* with Balearicinae than with the Gruinae, the former being the most basal genus (*Balearica*) within the Gruidae (Krajewski et al. 2010).

Palaeoenvironment

Palaeogeros tourmenti adds to the known diversity of Gruoidea in the early Oligocene of southeastern France, which comprises also *Parvigrus* (Parvigruidae) in the same formation in the nearby locality of Pichovet (Mayr 2005). Compared with Parvigruidae, *Palaeogeros tourmenti* is 59% larger than *Parvigrus pohli* (based on greatest length of coracoid without the proc. lat.), and 33% larger than *Rupelrallus saxoniensis* (based on coracoid distal width without the proc. lat.). It can be inferred that *P. tourmenti* is also ca 19% larger than *Rupelrallus belgicus*, (based indirectly on carpometacarpus length, the coracoid of the latter species being unknown). In contrast, *P. tourmenti* is 30% smaller than *Balearica pavonina* and *B. regulorum*, and 23% smaller than a specimen of *Anthropoides virgo*, the smallest

living crane. Among the Gruoidea, the preferred habitats of extant cranes are open, humid habitats, such as marshes or grasslands (Winkler et al. 2020a). The Limpkin *Aramus guarauna*, sister species of cranes, lives in open freshwater marshes, hence also open habitats but more humid/aquatic (Winkler et al. 2020b). In contrast, the next sister clade, the trumpeters (Psophiidae), live in lowland tropical forest (Winkler et al. 2020c). *Palaeogeros tourmenti*, assigned here tentatively to ?stem Gruidae and being at the very least a member of the clade (Aramidae+Gruidae), therefore tends to indicate the presence of rather humid/aquatic, open habitats around the locality in the early Oligocene. This adds to known palaeoenvironmental evidence for the formation and nearby localities, including from other vertebrates, insects and plants (Louchart et al. 2008). Other birds comprise at least 15 other species, including some taxa indicative of tropical or subtropical climate, and diverse habitats (aquatic, humid, open or semi-open, and woodland or forest) (Mayr 1999, 2000; Louchart et al. 2008, 2011; Duhamel et al. 2020; Riamon et al. 2020; Duhamel and Louchart in prep.).

Diversification of Gruoidea

In a recent molecular phylogeny that resolved the position of difficult taxa (such as the Hoatzin), the age of the divergence between Aramidae and Gruidae is centered near 26 Ma, but the 95% confidence interval is very large, and encompasses ages from 46 to 12 Ma (Kuhl et al. 2020) (Fig. 3). In the proposed hypothesis of *P. tourmenti* being a ?stem Gruidae, it is therefore plausible that, at ca 30 Ma, *P. tourmenti* derives from the earliest stem of Gruidae, which would have diverged slightly earlier from the stem of Aramidae (case illustrated in Fig. 3). In the hypothesis of *P. tourmenti* being slightly more basal, on the stem of the clade (Aramidae+Gruidae), there is also congruence with these recent molecular estimates. Calibration using fossils incidentally serves as minimizing such large confidence intervals and precisising the age of nodes. In addition, there are other, non-exclusive possible explanations

for incomplete coincidence between morphology and molecules in phylogeny. These include too much load of homoplasy in morphology to reflect phylogeny, which is frequent when morphology is confronted to recent molecular phylogenies that did considerable progress in the last decade, with morphologically unexpected clades such as the Mirandornithes (Podicipedidae+Phoenicopteridae), the Australaves (including Psittaciformes+Passeriformes), and Otididae+Musophagidae (e.g., Hackett et al. 2008; Jarvis et al. 2014; Prum et al. 2015; Kuhl et al. 2020). Other possible explanations include the possibility of discordant topologies between the real phylogenetic (species tree) and gene trees due to hemiplasy (Avice and Robinson 2008). Obtaining more skeletal elements of *P. tourmenti* in the future will also help better approaching the morphological aspect of the phylogenetic history of the Gruoidea, since mosaicism between the different elements is also a recurrent aspect of avian evolution (Olson 1985; Mayr 2017).

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Figure legends

Fig. 1 The new fossil coracoid UCBL-FSL-444667, of *Palaeoegeranos tourmenti* n. gen. n. sp. (d, drawing after the actual fossil; j, photograph of fossil on slab), compared with extant and fossil representatives of the Gruoidea. a, *Grus (Bugeranus) carunculata*; b, *Grus grus*; c, *Grus (Anthropoides) virgo*; e,f, *Balearica pavonina*; g, *Psophia crepitans*; h, *Aramus guarauna*; i, *Balearica regulorum*; k, *Rupelrallus saxoniensis*; l, *Parvigrus pohli*. All right coracoids in dorsal view except (l), which is a left coracoid in ventral view, useful in outline comparison, and except (b,h,i), which are left coracoids (in dorsal view) that were mirrored for convenience. (i), modified after photograph in Mayr (2016). (k,l), modified after photographs in Mayr (2013). ae, angulus externus; am, angulus medialis; chs*, coraco-humeral surface (after Howard 1929); cs, cotyla scapularis; fac, facies articularis clavicularis; fah, facies articularis humeralis; fas, facies articularis sternalis; fsc, foramen supracoracoideum; fg, facies glenoidalis; ims, impressio m. sternocoracoidei; pa, processus acrocoracoideus; pe, processus externus; pl, processus lateralis; pp, processus procoracoideus; scf**, sterno-coracoidal fossa (after Gilbert et al. 1981), which is deep in *P. tourmenti* (and filled with sediment); tb, tuber brachialis (all terms after Baumel and Witmer 1993, except for the ones marked with asterisks, and the ones in italics that derive from Ballmann 1969). Small arrows indicate the principal differences from *P. tourmenti*, observed in extant Gruidae, and on the other hand in the fossil taxa *Rupelrallus* and *Parvigrus*. Scale bars, 10 mm.

Fig. 2 Three comparisons of the outlines, drawn at same scale, between *Palaeogeros* *tourmenti* n. gen. n. sp., coracoid UCBL-FSL-444667, with coracoids of *Aramus guarauna* (a), *Parvigrus pohli* (b), and *Balearica pavonina* (c).

Fig. 3 Phylogenetic position hypothesized for *Palaeogeros tourmenti* n. gen. n. sp. This proposed possible position derives from comparisons with other Gruoidea. Other fossil Gruoidea are also placed, based on literature (see text). The phylogenetic frame of extant taxa derives from Kuhl et al. (2020). The 95% confidence interval is shown (bar and limits on either side of average date marked by X, the latter being the age of maximal probability) for the node (Gruidae+Aramidae) based on Kuhl et al. (2020). The approximate position of *P. tourmenti* proposed here (*) takes into account this wide interval. We placed here the node (Gruidae+Aramidae) at an earlier date than the average (maximum probability age), but still within the 95% confidence interval, at ca. 35 Ma (circle). Consequently, *P. tourmenti* can possibly be considered posterior to this node (Gruidae+Aramidae) and as a ?stem Gruidae (see text). Alternatively, it might be slightly more basal, slightly stemward from this node, on the stem of Gruoidea (Aramidae+Gruidae). Squares indicate the age of crown Balearicinae and crown Gruinae, based on OneZoom Tree of Life Explorer (Jetz et al. 2012; Rosindell and Harmon 2012). The timescale is logarithmic to avoid compression of branchings of interest here. Crosses indicate fossil taxa.