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► To cite this version:

Géraldine Garcia, Cecile Mourer-Chauvire, Mohammed Adaci, Mustapha Bensalah, Fateh Mebrouk, et al.. First discovery of avian egg and bone remains (Presbyornithidae) from the Gour Lazib (Eocene, Algeria). *Journal of African Earth Sciences*, 2020, 162, pp.103666. 10.1016/j.jafrearsci.2019.103666 . hal-03046269

HAL Id: hal-03046269

<https://hal.umontpellier.fr/hal-03046269>

Submitted on 8 Dec 2020

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1 First discovery of avian egg and bone remains (Presbyornithidae) from the Gour
2 Lazib (Eocene, Algeria)

3

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20

21 *Keywords:* Aves, eggshell microstructure, Presbyornithidae, Eocene, Algeria.

22

23 **ABSTRACT.**

24 Numerous avian eggshells and one well-preserved small ovoid-shaped egg (32 x 28
25 mm) were collected in the Gour Lazib area, western Algeria from three localities from

26 the Glib Zegdou Formation dated from the late early or early middle Eocene. This
27 material was associated with a rich vertebrate fauna. The scanning electron
28 microscopy (SEM) study of the eggshells led to attribute them to neognathous birds;
29 they are characterized by a thin shell (less than 0.5 mm thick) with a prismatic
30 trilaminate microstructure. The occurrence of an avian carpometacarpus belonging to
31 the Presbyornithidae from HGL50, which is located one meter below the HGL 51
32 level, suggests that the egg remains may be referred to this bird family, which is so
33 far unknown in the Palaeogene of the Afro-Arabian continent.

34

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37

38 1. Introduction

39 Avian fossil eggs and bones from Paleogene formations are rare in the fossil
40 record, due to their fragile nature. In Africa, the fossil record from the Middle Miocene
41 to the Pleistocene is relatively well known (Bourdon et al., 2005, 2008; Rasmussen et
42 al., 1987; Miller et al., 1997, Louchart et al., 2008; Mourer-Chauviré and Geraads,
43 2010; Stidham, 2010; Mayr 2017) but the Paleogene localities with bird remains are
44 very few, particularly those with terrestrial birds (Mourer-Chauviré et al., 2017). The
45 preservation of their eggs is fundamentally different. The majority of the avian eggs
46 described, corresponds to the shell ratite morphotype which is attributed to the
47 palaeognath lineage (Mikhailov, 1997; Grellet-Tinner, 2006). This morphotype is
48 particularly documented from various Miocene and Plio-Pliocene localities from
49 South Africa (Rich, 1980; Kuhn et al., 2015), Namibia (Senut et al., 2009), Tanzania
50 (Harrison and Msuya, 2005), Egypt (Smith, 2013), and Morocco (Sauer and Sauer,
51 1978). These eggshell remains have attracted attention not only for taxonomic
52 studies but also for biogeographical, paleoenvironmental and biostratigraphical
53 implications (Senut et al., 1998; Senut, 2000; Bibi et al., 2005; Ségalen et al., 2006;
54 Ecker et al., 2015).

55 We describe here well preserved avian osteological and oological fossils from
56 four localities from fluvio-lacustrine sediments of the intermediate member of the Glib
57 Zegdou Formation, Gour Lazib area, southwest Algeria. These localities (HGL10, 50,
58 51 and 62, Fig. 1), which are late early or early middle Eocene in age, have yielded a
59 rich vertebrate fauna (e.g., Adaci et al., 2007; Tabuce et al., 2011; Rage et al., in
60 press). Among birds, only the large phororhacoid *Lavocatavis africana* was described
61 so far (Mourer-Chauviré et al., 2011b); this bird was considered closely related to the

62 Phorusrhacidae, an extinct family of giant flightless birds, mainly known from South
63 America.

64 The study of this autochthonous assemblage from the Eocene of Algeria
65 provides new information concerning the diversity and the paleogeography of some
66 modern birds. Furthermore, we describe for the first time the occurrence of
67 unequivocal neognath eggshells (probably Presbyornithids) in the Palaeogene of the
68 Afro-Arabian continent.

69

70 **2. Material and Methods rajouter l'appel aux Fig. + developpement SEM et** 71 **lames minces**

72 The material studied in this paper come from several localities of the Gour
73 Lazib in the province of Tindouf (levels HGL-10, 50, 51 and 62), it corresponds to
74 isolated proximal parts of a right tarsometatarsus (UM-HGL 50-601) and a left
75 carpometacarpus (UM-HGL 50-115), and monospecific amniotic eggshells. The
76 osteological bones are identified in comparison with described fossil and extant bird
77 material, in collection at the University of Lyon. The values are measured with a
78 caliper with a precision of 0.1 mm. The anatomical terminology follows Baumel and
79 Witmer (1993). The eggshells are calcitic and little recrystallized. We have used
80 scanning electron microscope (SEM) and cathodoluminescence method for studying
81 radial sections and outer surfaces. The thin sections were produced using
82 petrographic facilities in both the Universities of Montpellier and Poitiers.

83 All the studied material is housed and catalogued in the collections of the
84 University of Montpellier.

85

86 **3. Geological context.**

87 The Gour Lazib area is located in the western part of the Algerian Sahara,
88 approximately between the cities of Béchar and Tindouf (Fig. 1a). The four
89 fossiliferous sites were recovered in the middle member of the Glib Zegdou
90 Formation, a continental sequence dated by magnetostratigraphic and
91 biostratigraphic data close to the Ypresian-Lutetian boundary, either latest Ypresian
92 (~49 Ma) or early Lutetian (~46 Ma) (Adaci et al., 2007; Costeur et al., 2012;
93 Mebrouk 2011). The four fossiliferous levels (Fig. 1 c-f), which consist of clayey-
94 sandstone layers, yielded an abundant charophyte flora (Mebrouk 2011) and a rich
95 vertebrate assemblage (e.g., Adaci et al., 2007, 2016; Tabuce et al., 2009; 2011,
96 Marivaux et al., 2011; Mourer-Chauviré et al., 2011b; Solé et al., 2013; Rage et al., in
97 press). In addition to the bird remains here described, HGL 10 yielded some rodents,
98 primates, hyraxes, crocodiles, squamates, and fishes; HGL 51 yielded the bird
99 *Lavocatavis africana*, some primates, hyraxes, squamates, and fishes; HGL 50 is the
100 most diversified site with abundant aquatic and terrestrial vertebrate remains
101 including several rodents, bats, primates, creodonts, insectivores, hyraxes, a putative
102 condylarth, some crocodiles, squamates, and fishes; finally HGL 62 is an
103 unpublished fossiliferous level, which has yielded only few teeth of hyraxes and
104 fishes.

105

106 **Institutional abbreviations**

107 HGL, Hammada Gour Lazib, Algeria; UM, University of Montpellier, France.

108

109 **4. Results**

110 **4.1. Osteological fossils**

111 Order Galliformes Temminck, 1820

112 Indeterminate family, genus and species

113 UM-HGL 50-601 Right tarsometatarsus, proximal part (Fig. 2 a-c)

114 The morphological characteristics of this tarsometatarsus are: cotyla medialis
115 larger than cotyla lateralis, eminentia intercotylaris blunt, area intercotylaris shallow,
116 wide closed canal for the tendon of musculus flexor digitorum longus, and plantarly to
117 the canal, presence of a crista hypotarsalis medialis and of a sulcus for the tendon of
118 the muscoli flexor perforans et perforatus digiti 2 and flexor perforatus digiti 2. The
119 lateral part of the hypotarsus is not preserved. On the dorsal face the fossa
120 infracotylaris dorsalis is well developed, with two small foramina vascularia
121 proximalia in its bottom. On the plantar face, the fossa parahypotarsalis medialis is
122 deeper than the fossa parahypotarsalis lateralis, these two fossae are separated by a
123 well-developed crista medianoplantaris. The measurements are: proximal width, as
124 preserved, 8.5 mm; proximal depth, as preserved, 8.4 mm.

125 These characteristics correspond to a Galliform, and in particular, the shape of
126 the hypotarsus resembles that of the basal Galliformes, such as Megapodiidae
127 (Mayr, 2016). Some Galliformes have been described in the Eocene of Africa, in
128 Namibia (Mourer-Chauviré et al., 2011a, 2015, 2017), and in Tunisia (Mourer-
129 Chauviré et al., 2013), but in these different localities the proximal part of the
130 tarsometatarsus is unknown. This tarsometatarsus cannot belong to a
131 Presbyornithidae since they do not have a wide closed canal for the tendon of the
132 muscle flexor digitorum longus (Howard, 1955; De Pietri et al., 2016, Fig. 2 a', b', d').

133

134 Order Anseriformes Wagler, 1831

135 Family Presbyornithidae Wetmore, 1926

136 Indeterminate genus and species

137 UM-HGL 50-115 Left carpometacarpus, proximal part (Fig. 2 d-h)

138 The extinct family Presbyornithidae was mainly known in the Paleocene and
139 early Eocene of the United States (Mayr, 2009). They have also been found in the
140 late Cretaceous of Southern Mongolia (Kurochkin et al., 2002), the late Paleocene
141 and early Eocene of Mongolia (Kurochkin and Dyke, 2010), the early and early
142 middle Eocene of the Canada's High Arctic (Eberle and Greenwood, 2012), and the
143 earliest Eocene of Patagonia (Howard, 1955). In Europe some material from the
144 early Eocene of England had been referred to the Presbyornithidae (Dyke, 2001), but
145 this attribution has not been confirmed (Mayr, 2009). Remains attributed to a
146 Presbyornithidae by Noriega and Tambussi (1995) from the Cretaceous of Vega
147 Island, Antarctica, have been redescribed by Clarke et al. (2005) under the name of
148 *Vegavis iaai*. This genus is placed in the Anseriformes, within a clade which includes
149 the Presbyornithidae and the Anatidae, but is no longer considered as a
150 presbyornithid. The Presbyornithidae were thought to have disappeared by the mid
151 Eocene but they have recently been identified from the late Oligocene and early
152 Miocene of Australia, and it is possible that they were already present in the early
153 Eocene of Australia (De Pietri et al., 2016).

154 Description and comparisons

155 The morphological characteristics of the carpometacarpus of the
156 Presbyornithidae have been given by Howard (1955) for the genus *Telmabates*, and
157 by Ericson (2000) for the genera *Telmabates* and *Presbyornis*. Then two other
158 genera have been described, *Teviornis* from the late Cretaceous of Mongolia
159 (Kurochkin et al. 2002) and *Wilaru* from the Late Oligocene and early Miocene of
160 Australia (De Pietri et al., 2016). One of the main characteristics is that the dorsal
161 crest of the carpal trochlea extends as far or slightly farther caudally as the ventral

162 crest in *Telmabates* and *Teviornis*, and extends well caudally farther in *Presbyornis*.
163 In *Wilaru* both rims of the carpal trochlea extend caudally and distally to about the
164 same level. In the Glib Zegdou specimen, the dorsal crest of the trochlea extends as
165 far caudally as the ventral crest (Fig. 2 e).

166 On the dorsal face there is a conspicuous rim along the caudal border of the
167 dorsal crest of the trochlea. There is a shallow fossa supratrochlearis with a scar for
168 the ligamentum ulnocarpometacarpale dorsale. The processus extensorius is slightly
169 proximally oriented. The processus alularis is well developed with a bilobed articular
170 facet for the phalanx digiti alulae. On the ventral face there is a large fossa
171 infratrochlearis with a scar for the ligamentum radiocarpometacarpale dorsale. In the
172 center of this fossa there is a small vascular foramen (Ericson, 2000) which is called
173 canalis interosseus distalis in Kurochkin et al. (2002) and in De Pietri et al. (2016).
174 The processus pisiformis is situated at the level of the middle of the processus
175 extensorius, as in the other presbyornithids. On the cranial side of the processus
176 pisiformis there is a craniocaudally elongate and deep fossa. At the level of
177 attachment between the major and the minor metacarpals there is shallow and
178 elongate fossa, with the shape of the letter V, bordered by two ridges. The ridge on
179 the cranial side joins the processus pisiformis, and the ridge on the caudal side
180 follows the caudal border of the symphysis of the major and minor metacarpals, then
181 vanishes into the fossa infratrochlearis (Fig. 2 d). This kind of V-shaped shallow
182 fossa also exists in the late Cretaceous presbyornithid *Teviornis gobiensis*
183 (Kurochkin et al., 2002, Figs. 2 D and 3 D; De Pietri et al., 2016, Fig. 2 f). On the
184 caudal face, there is a moderately deep fossa between the distal ends of the dorsal
185 and ventral crests of the carpal trochlea. This fossa also exists in the other
186 presbyornithids (Howard, 1955; Ericson, 2000; De Pietri et al., 2016, see Fig. 2 n-o).

187 The caudal rim of the dorsal portion of the carpal trochlea is not notched.
188 Measurements (in mm) : Length as preserved 21.6; proximal width (dorso-ventral) at
189 the level of processus pisiformis 5.7; proximal depth (cranio-caudal) 9.9; width of
190 carpal trochlea 4.6; width of major metacarpal 3.5; depth of major metacarpal 2.8

191 As a whole, the carpometacarpus also looks like that of *Romainvillia stehlini*
192 Lebedinsky, 1927, from the late Eocene of France, which is a stem group
193 representative of the Anatidae. However it differs because in *Romainvillia* the
194 carpometacarpus shows a “very marked fovea carpalis cranialis on the cranial
195 surface of the trochlea carpalis, immediately proximal to the processus extensorius”
196 (Mayr, 2008, p. 373, and Fig. 2 J) (Fig.3). This fovea is present but shallow in the
197 Glib Zegdou carpometacarpus.

198 Among the presbyornithids the Glib Zegdou carpometacarpus is more similar
199 to that of the genera *Presbyornis*, *Telmabates*, and *Teviornis*. It differs from the
200 genus *Wilaru* because the processus extensorius is more craniocaudally and
201 proximodistally developed, and slightly distally oriented in *Wilaru tedfordi*, and ended
202 by an excroissance in *W. prideauxi* (De Pietri et al., 2016, Fig. 2). It also differs from
203 those of the stem group anseriforms *Anatalavis oxfordi*, from the early Eocene of
204 England, and *Conflictio antarcticus* from the early Paleocene of Antarctica. In
205 *Anatalavis* the processus extensorius is situated more distally compared to the top of
206 the trochlea carpalis and slightly distally oriented, and the cranial part of this
207 processus is wide and blunt (Olson, 1999, Fig. 9). In *Conflictio* the processus
208 extensorius is compressed and elongated; the processus alularis is small and the
209 articular facet for the phalanx digiti alulae is not visible (Tambussi et al., 2019, Fig.
210 10).

211

212 **4.2. Oological fossils**

213 Order Neognathes Pycraft, 1900

214 Ornithoid-prismatic morphotype Mikhailov, 1997

215 Indeterminate oofamily, oo-genus and species

216 UM-HGL-10A egg, HGL 62 and 51: 85 analysed fragments (Fig. 4 a-f)

217 Numerous avian eggshells and one well-preserved small ovoid-shaped egg
218 (32 x 28 mm) were recovered from HGL-10, 51 and 62. The eggshells, which are in
219 variable proportions according to the sites, have been collected directly in situ or by
220 screen-washing sediments. Their thickness is less than 0.5 mm, depending and
221 resulting of the recrystallization of the outermost surface by a granular and diagenetic
222 artifact. We used both scanning electron and polarizing light microscopes (SEM and
223 PLM) to study the radial sections and the outer surfaces.

224 The analysed samples are all well preserved, without recrystallization
225 suggesting a lack of fluvial transport, or floating during sedimentological low-flow
226 events. Their microscopic examinations indicate a monotypic avian microstructure,
227 composed of a three-laminated arrangement. The thick internal layer (L1) (200-250
228 μm in average) consists on elongated calcite crystals that radiate outwards from
229 nuclei, forming a semi-circle around a core at the eggshell base (Fig. 4c). This
230 mammillary layer (L1) evolves gradually into interlocking shell columns (L2) overlaid
231 by a thin and not well distinct external layer (L3), which displays long rectangular
232 crystals with a faint spongy appearance (Fig. 4d and f). The outer surface of the
233 eggshell is not ornamented and we can observe the isolated distribution of the pore
234 openings with a sub-circular shape (Fig. 4b).

235 The macro- and microstructures of the egg and eggshells closely match in
236 morphology that of extant and modern neognaths. They are known from different

237 Tertiary deposits throughout the world (Hirsch 1994), but only avian nests from the
238 Eocene of Wyoming have been linked to a taxonomic genus, the anseriform
239 *Presbyornis* (Leggitt and Buchleim, 1997, 1998; Leggitt et al., 2007). The Algerian
240 egg remains are very similar in thickness, ornamentation, and microstructure to
241 *Presbyornis* eggshells and could suggest the same parentage. This is supported also
242 by the shape of the egg (UM-HGL-10A), not as considerably elongated as that of the
243 galliform birds.

244

245 **5. Discussion and conclusion**

246 Descriptions of neognath eggs and nesting sites are rare in the literature, in
247 particular for the Paleogene, due in part to the difficulty to identify precisely the
248 microstructure of the shell. Few studies of the ultrastructure of modern avian eggshell
249 exist (e.g. Mikhailov, 1987, 1995a and b; Grellet-Tinner et al., 2012) and the shell
250 thickness of this morphotype (around 0.3 to 0.7 mm) is easily affected by pre-burial
251 conditions and diagenesis (Khoring and Hirsch, 1996). One of the shell characteristic
252 is the presence of three prismatic structural layers, corresponding to the
253 synapomorphy of the eggs of Neognathae (Grellet-Tinner, 2000). However, it is
254 difficult to make a precise taxonomic assignment except at higher systematic levels
255 (Mikhailov et al., 1996). Indeed, the studies on some recent birds and dinosaurs
256 indicate that several families of egg-layers belonging to a single oofamily (Mikhailov,
257 1997; Zelenitsky and Hirsch, 1997; Garcia et al., 2006).

258 Fossil eggs can be attributed unequivocally to a taxon only by identifiable
259 embryonic bones or hatchlings found inside or in association of the eggs (Hirsh and
260 Quin, 1990). Very few examples have been reported for neognaths (Schweitzer et
261 al., 2002) but the co-occurrence of eggs with monospecific adult bones in an

262 autochthonous fossil assemblage allows indirect correlations. It is on this point that
263 Leggitt and Buchheim (1997) have assigned the avian eggshells coming from nesting
264 sites (Eocene, Wyoming) rich in *Presbyornis* remains, to this bird taxon. This report
265 suggests that the egg remains with the same features, found on the Gour Lazib area
266 may thus be referred to the Presbyornithidae, which were so far unknown in the
267 Paleogene deposits of the Afro-Arabian continent. In fact, this extinct waterfowl
268 family, found in very large numbers in lacustrine environments (bones sometimes
269 associated with eggshell fragments (Leggitt and Buchheim, 1998) was particularly
270 recovered in Upper Cretaceous to Paleogene deposits from both North America and
271 Asia (Ericson, 2000; Kurochkin et al., 2002; Kurochkin and Dyke, 2010; Eberle and
272 Greenwood 2012; Mayr, 2009).

273 The Presbyornithidae were mainly known in the Northern Hemisphere. The
274 discovery of Presbyornithidae in Australia, coupled with the fact that they were also
275 present in South America, led De Pietri et al (2016) to propose a gondwanian
276 radiation within this family. The presence of a member of this family in the South of
277 Algeria confirms the existence of this gondwanian radiation. It is possible to make a
278 connection between the occurrence of a Presbyornithidae and that of *Lavocatavis*
279 *africana*, found in the same locality, and which is related to the South American
280 family Phorusrhacidae (Mourer-Chauviré et al. 2011b).

281

282 **Acknowledgements**

283 We would thank the Vice-Chancellor of the University of Tlemcen (Algeria) and
284 the authorities of the Bechar and Tindouf districts which facilitated our field
285 expeditions to the Gour Lazib area from 2004 to 2011; we are very grateful to P.-H.
286 Fabre, E. Fara, H. Gomes Rodrigues, L. Hautier, J.-J. Jaeger, A. Mahboubi, L.

287 Marivaux, S. Peigné†, and A. Ravel for their help during these fieldtrips. We
288 acknowledge also J. Sudre who discovered UM-HGL-10A during a field expedition in
289 1974, A. L. Charruault (Montpellier) for her efficient technical assistance (acid etching
290 of the fossiliferous clayey sandstone), and S. Petit and E. Berre for SEM analysis
291 (IC2MP Poitiers).

292

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524

525 **Figure legends**

526 Figure 1. Gour Lazib location map and outcrops showing localities yielding avian egg
527 and bone remains. (a-b) geographic location of the Gour Lazib in western Algeria and
528 satellite image the four fossiliferous localities; (c) panoramic view of the Gour Lazib
529 showing HLG 10 and HGL 50-51 localities; view is to the northeast, the Glib Zegdou
530 outlier (HGL50-51 localities) is on the background; (d) photograph of the “gara
531 *Azibius*” outcrops showing HGL 10 locality; (e) photograph of the Glib Zegdou outlier
532 showing HGL 50 and 51 localities; (f) photograph of the HGL 61 locality,
533 southwestern of the Gour Lazib.

534

535 Figure 2. (a-c) Indeterminate galliform, UM-HGL 50-601, right tarsometatarsus,
536 proximal part. (a) dorsal view; (b) proximal view; (c) plantar view. (d-h)
537 Presbyornithidae, genus and species indeterminate, UM-HGL 50-115, left
538 carpometacarpus, proximal part. (d) ventral view; (e) caudal view; (f) dorsal view; (g)
539 cranial view; (h) proximal view. Scale equals 1 cm. Abbreviations: dtc – dorsal rim of
540 trochlea carpalis, fcc – fossa carpalis cranialis, fdl – canal for the tendon of muscle
541 flexor digitorum longus, fit – fossa infratrochlearis, fpp2 – sulcus for the tendon of
542 muscle flexor perforans et perforatus digiti 2, pal – processus alularis, ppi –
543 processus pisiformis, vtc – ventral rim of trochlea carpalis.

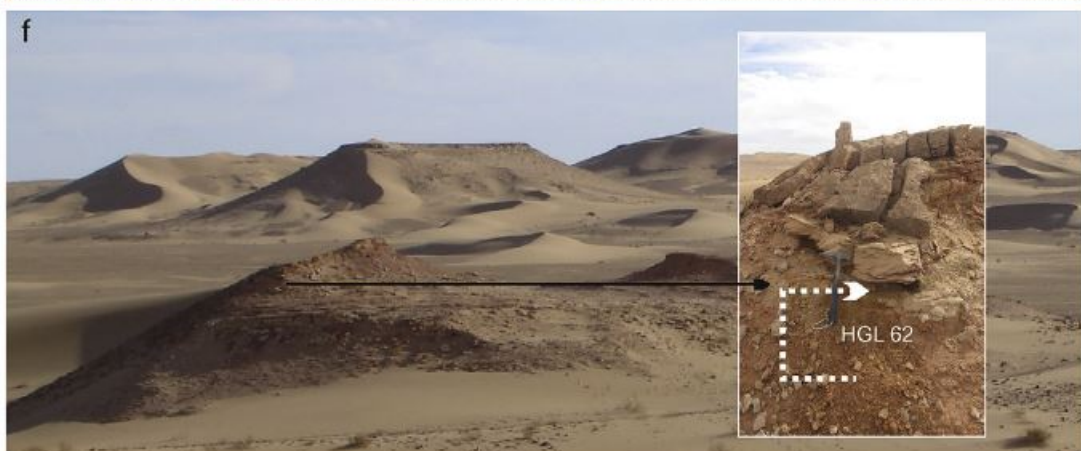
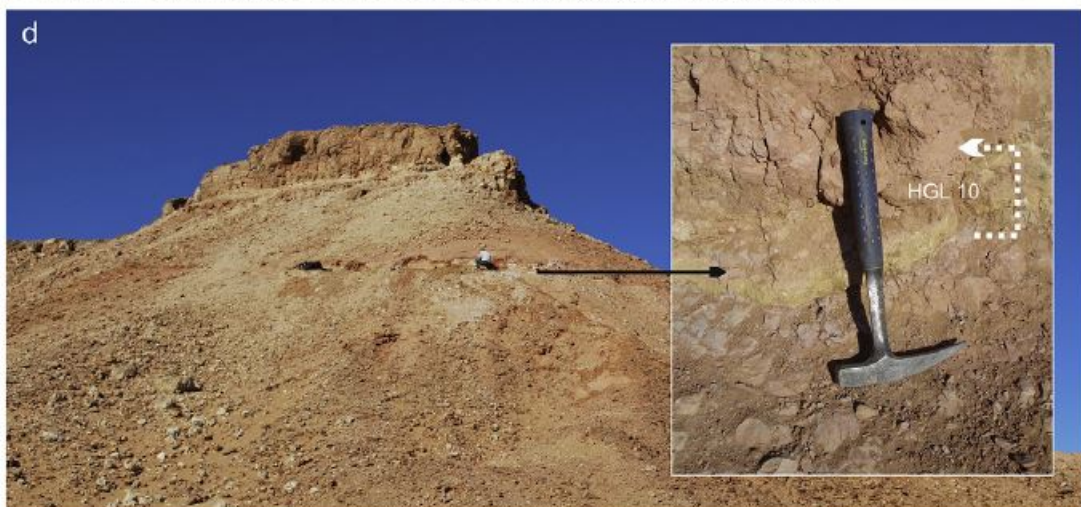
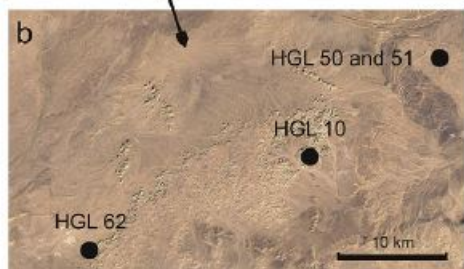
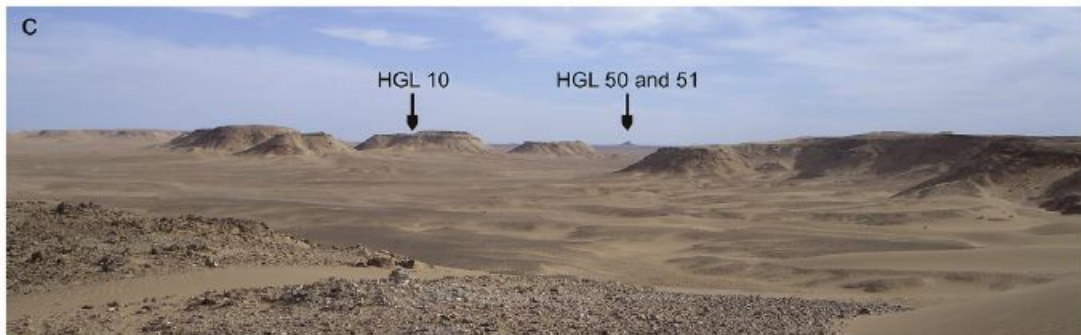
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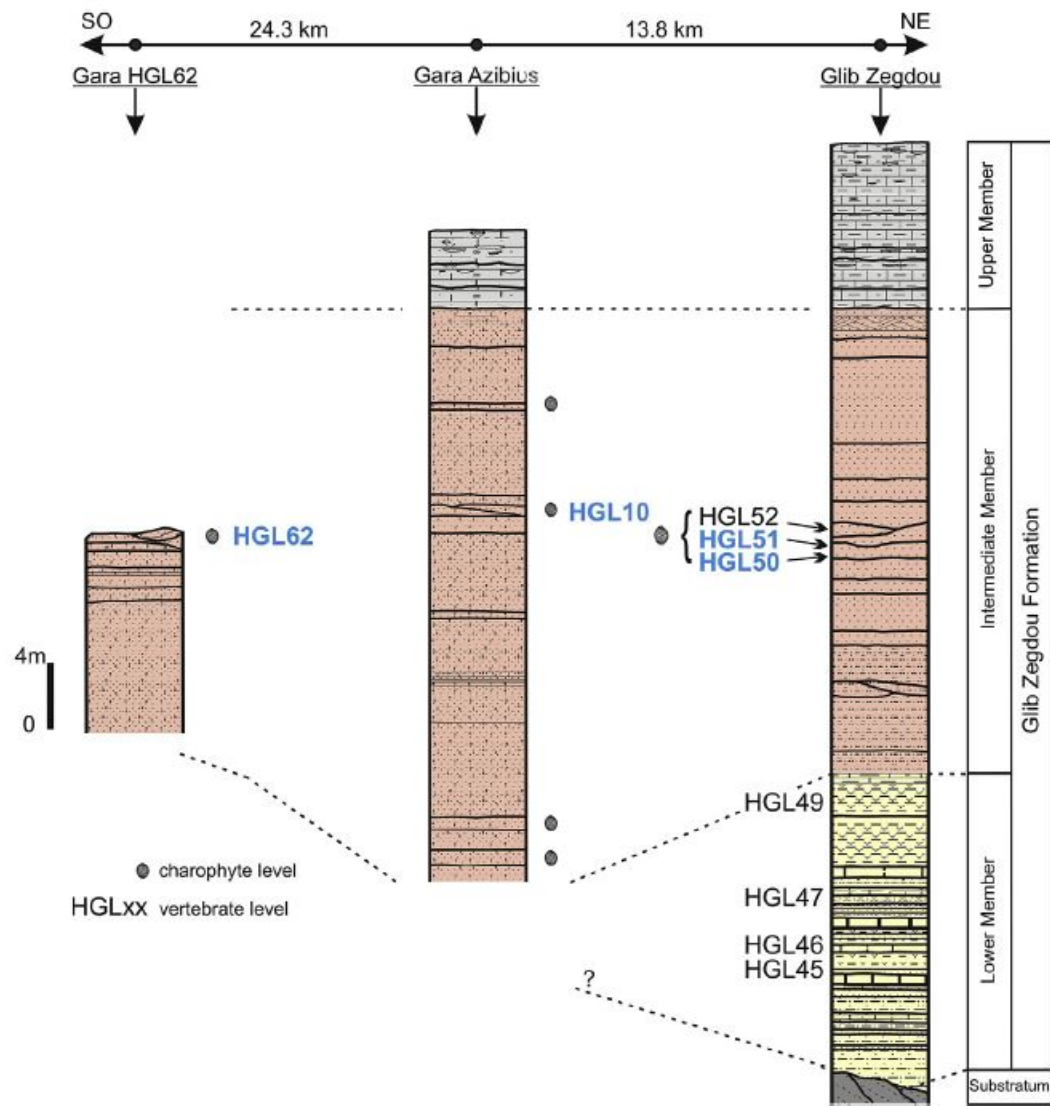
545 Figure 3. *Romainvillia stehlini* Lebedinsky, 1927, from the late Eocene of France. Left
546 carpometacarpus (NMB P.G. 53), (a) ventral view; (b) cranial view; (c) dorsal view.
547 Scale bars equal 5 mm. Abbreviation: fcc – fossa carpalis cranialis. After Mayr (2008,
548 fig. 2, I-K).

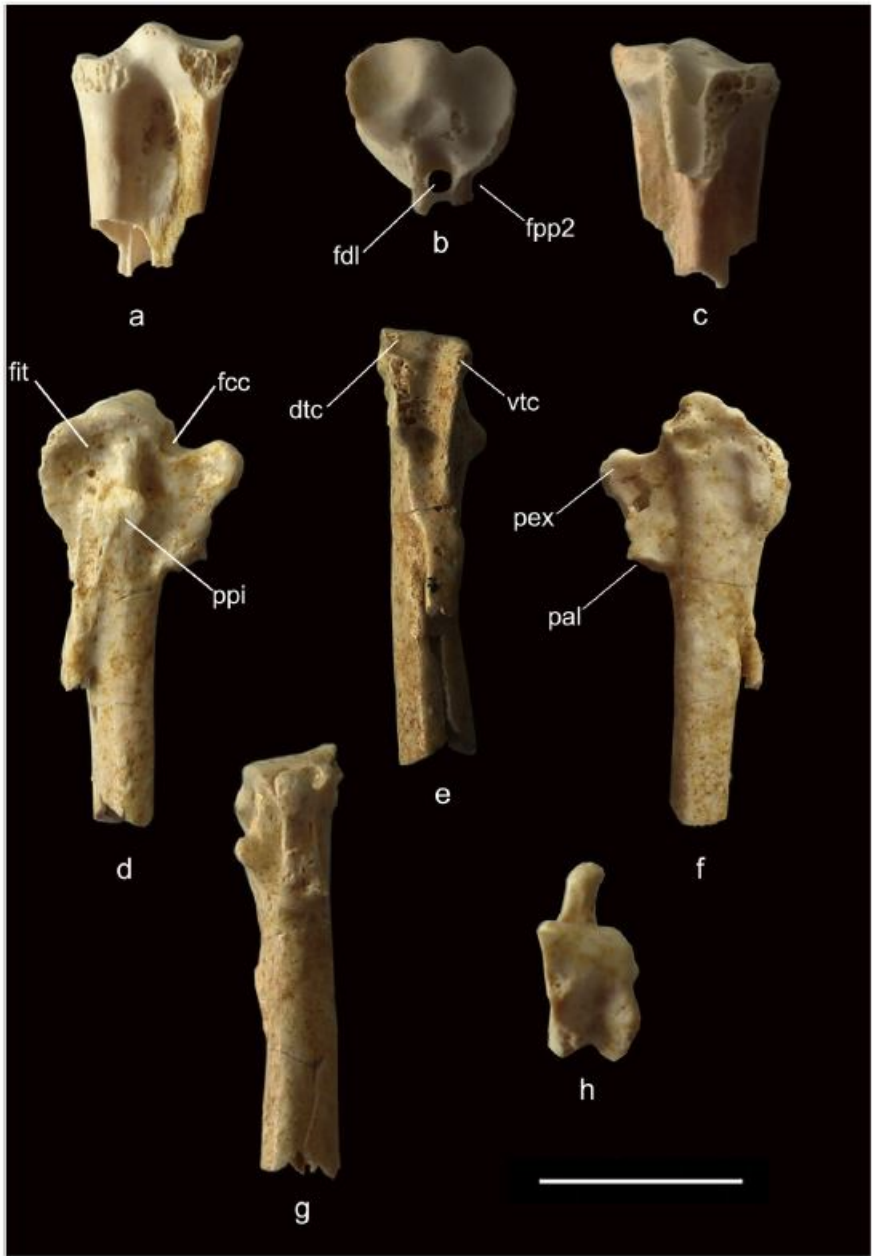
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550 Figure 4. (a) UM-HGL10A, a nearly complete egg with an ovoid shape, discovered
551 isolated in the HGL10 locality. (b-d) SEM micrograph images of eggshells; (b) UM-
552 HGL10-4a Circular pore orifices on the outer surface (arrows) x 180; (c) UM-HGL10B
553 eggshell exhibits a typical neognathous microstructure with three prismatic structural
554 layers (L1-L3), radial view SEM x 150. Wedges of the mammillary layer (L1) grade
555 into prisms. The boundary between the mammillary layer and continuous layer (L2) is
556 gradational; (d) UM-HGL62A Detail of the smallest external layer (L3) which is a
557 synapomorphic feature of the crown clade Aves, SEM x 550; (e and f) Polarizing light
558 micrographs of thin sections; (e) UM-HGL10A-1 Eggshell fragment from the
559 specimen HGL10A. Note the prismatic structure with well distinct columns x 40; (f)

560 UM-HGL10B The mammillae are underlined by alterations and a possible canal pore
561 is observable (black arrows) x 100. Scale bar 1 cm.









a



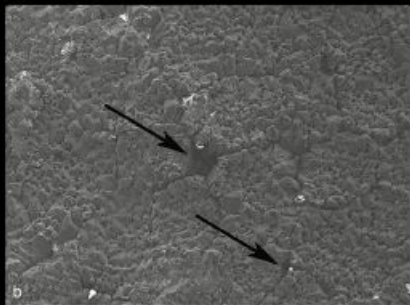
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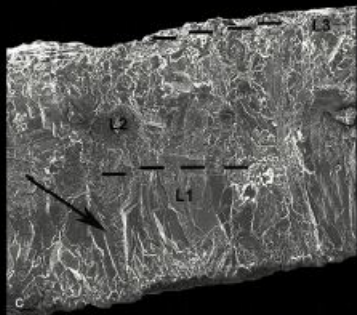
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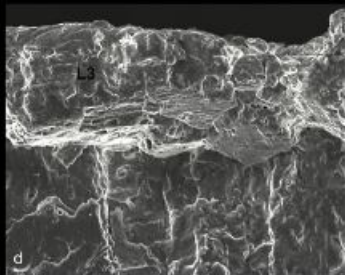
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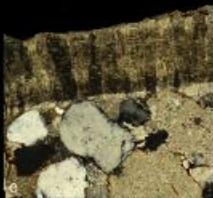
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