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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  $\mu\text{m}$  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 (Hirsch 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

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292

## 293 **References**

- 294 Adaci, M., Tabuce, R., Mebrouk, F., Bensalah, M., Fabre, P.H., Hautier, L., Jaeger,  
295 J.J., Lazzari, V., Mahboubi M., Marivaux, L., Otero, O., Peigné, S., Tong, H., 2007.  
296 Nouveaux sites à vertébrés paléogènes dans la région des Gour Lazib (Sahara  
297 nord-occidental, Algérie). *Comptes Rendus Palevol* 6, 535-544.
- 298 Baumel, J.J., Witmer, L.M., 1993. Osteologia, in : Baumel, J.J., King, A.S., Breazile,  
299 J.E., Evans, H.E., Vanden Berge, J.C., (Eds.), *Handbook of Avian Anatomy*,  
300 Publications of the Nuttall Ornithological Club 23, pp. 45-132.
- 301 Bibi, F., Shabel, A.B., Kraatz, B.P., Stidham, T.A., 2005. New fossil ratite (Aves:  
302 Palaeognathae) eggshell discoveries from the Late Miocene Baynunah Formation  
303 of the United Arab Emirates, Arabian Peninsula. *Palaeontologica Electronica*  
304 9.1.2A.
- 305 Bourdon, E., Bouya, B., Iarochene, M., 2005. Earliest African neornithine bird: a new  
306 species of Prophaethontidae (Aves) from the Paleocene of Morocco. *Journal of*  
307 *Vertebrate Paleontology* 25, 157-170.
- 308 Bourdon, E., Mourer-Chauviré, C., Amaghazaz, M., Bouya, B., 2008. New specimens  
309 of *Lithoptila abdounensis* (Aves, Prophaethontidae) from the lower Paleogene of  
310 Morocco. *Journal of Vertebrate Paleontology* 28, 751-761.

311 Clarke, J.A., Tambussi, C.P., Noriega, J.L., Erickson, G.M., Ketcham, R.A., 2005.  
312 Definitive fossil evidence for the extant avian radiation in the Cretaceous. *Nature*  
313 433, 305-308.

314 Costeur, P., Benammi, M., Mahboubi, M., Tabuce, R., Adaci, M., Marivaux, L.,  
315 Bensalah, M., Mahboubi, S., Mahboubi, A., Mebrouk, F., Maameri, C., Jaeger, J.-  
316 J. 2012. Chronology of the Eocene continental deposits of Africa:  
317 Magnetostratigraphy and biostratigraphy of the El Kohol and Glib Zegdou  
318 Formations, Algeria. *Geological Society of America Bulletin*, doi:  
319 10.1130/B30565.1.

320 De Pietri, V.L., Scofield, R.P., Zelenkov, N., Boles, W.E., Worthy, T.H. 2016. The  
321 unexpected survival of an ancient lineage of anseriform birds into the Neogene of  
322 Australia: the youngest record of Presbyornithidae. *Royal Society open Science* 3,  
323 150635.

324 Dyke, G.J., 2001. The fossil waterfowl (Aves: Anseriformes) from the Eocene of  
325 England. *American Museum Novitates* 3354, 1-15.

326 Eberle, J.J., Greenwood, D.R., 2012. Life at the top of the greenhouse Eocene world.  
327 A review of the Eocene flora and vertebrate fauna from Canada's High Arctic.  
328 *Geologica Society of America Bulletin* 124 (1-2), 3-23.

329 Ecker, M., Botha-Brink, J., Lee-Thorp, J.A., Piuze, A., Kolska Horwitz, L., 2015.  
330 Ostrich eggshell as a source of palaeoenvironmental information in the arid interior  
331 of South Africa, in Runge, J., (Ed.), *Changing climates, ecosystems and*  
332 *environments within arid southern Africa and adjoining Regions, Palaeoecology of*  
333 *Africa* 33, pp. 95-115.

334 Ericson, P.G.P., 2000. Systematic revision, skeletal anatomy, and paleoecology of  
335 the New World early Tertiary Presbyornithidae (Aves: Anseriformes). *PaleoBios* 20  
336 (2), 1-23.

337 Garcia, G., Marivaux, L., Pelissié, J.T., Vianey-Liaud, M., 2006. Earliest Laurasian  
338 sauropod eggshells. *Acta Paleontologica Polonica* 51 1, 99-104.

339 Grellet-Tinner, G., 2000. Phylogenetic interpretation of eggs and eggshells, in: Bravo,  
340 A.M., Reyes, T. (Eds.), *First international symposium on Dinosaur eggs and*  
341 *babies. Isona I Conca Dellà Cataloni, Spain*, pp. 61-75.

342 Grellet-Tinner, G., 2006. Phylogenetic interpretation of eggs and eggshells:  
343 implications for phylogeny of Palaeognathae. *Alcheringa* 30, 141-182.

344 Grellet-Tinner, G., Murelaga, X., Larrasoaña, J.C., Silveira, L.F., Olivares, M., Ortega,  
345 L.A., Trimby, P.W., Pascual, A. 2012. The first occurrence in the fossil record of an  
346 aquatic avian twig-nest with Phoenicopteriformes eggs : Evolutionary Implications.  
347 *Plos one* 7 10, e46972.

348 Harrison, T., Msuya, C.P., 2005. Fossil struthionid eggshells from Laetoli, Tanzania:  
349 Taxonomic and biostratigraphic significance. *Journal of African Earth Sciences* 41,  
350 303-315.

351 Hirsch, K.F., 1994

352 Hirsch, K.F., Quinn, B., 1990. Eggs and eggshells from the upper Cretaceous Two  
353 Medicine Formation of Montana. *Journal of Vertebrate Paleontology* 10, 405-419.

354 Howard, H., 1955. A New Wading Bird from the Eocene of Patagonia. *American*  
355 *Museum Novitates*, 1710, 1-25.

356 Kohring, R., Hirsch, K.F. 1996. Crocodylian and avian eggshells from the middle  
357 Eocene of the Geiseltal, eastern Germany. *Journal of Vertebrate Paleontology* 16  
358 1, 67-80.



359 Kuhn, B.F., Carlson, K.J., Hopley, P.J., Zipfel, B., Berger, L.R. 2015. Identification of  
360 fossilized eggshells from the Taung hominin locality, Taung, Northwest Province,  
361 South Africa. *Palaeontologica Electronica* 18.1.11A.

362 Kurochkin, E.N., Dyke, G.J., Karhu, A.A., 2002. A New *Presbyornithid* Bird (Aves,  
363 Anseriformes) from the Late Cretaceous of Southern Mongolia. *American Museum*  
364 *Novitates*, 3386, 1-11.

365 Kurochkin, E.N., Dyke, G.J., 2010. A large collection of *Presbyornis* (Aves,  
366 Anseriformes, *Presbyornithidae*) from the late Paleocene and early Eocene of  
367 Mongolia. *Geological Journal* 45, 375-387.

368 Lebedinsky 1927

369 Leggitt, V.L., 1998. The stratigraphic setting of three *Presbyornis* nesting sites:  
370 Eocene Fossil Lake, Lincoln County, Wyoming, in Santucci, V.L., McClelland, L.,  
371 (Eds.), *National Park Service Paleontological Research* 3, 61-68.

372 Leggitt, V.L., Buchheim, H.P., 1997. *Presbyornis* (Aves: Anseriformes) eggshell from  
373 three avian mass mortality sites: Eocene Fossil Lake, Lincoln County, Wyoming.  
374 *Journal of Vertebrate Paleontology* 17, 60A.

375 Leggitt, V.L., Buchheim, H.P., 1998. A new *Presbyornis* (Aves: Anseriformes) nesting  
376 site with abundant eggshell: Eocene Fossil Lake, Lincoln County, Wyoming.  
377 *Journal of Vertebrate Paleontology* 18, 58A.

378 Leggitt, V.L., Biaggi, R.E., Buchheim, H.P., 2007. Paleoenvironments associated with  
379 caddisfly-dominated microbial-carbonate mounds from the Tipton Shale member  
380 of the Green River formation: Eocene Lake Gosiute. *Sedimentology* 54, 661-699.

381 Louchart, A., Haile-Selassie, Y., Vignaud, P., Likius, A., Brunet, M., 2008. Fossil birds  
382 from the Late Miocene of Chad and Ethiopia and zoogeographical implications.  
383 *Oryctos* 7, 147-167.

384 Marivaux, L., Adaci, M., Bensalah, M., Gomes Rodrigues, H., Hautier, L., Mahboubi,  
385 M., Mebrouk, F., Tabuce, R., Vianey-Liaud, M., 2011. Zegdoumyidae (Rodentia,  
386 Mammalia), stem anomaluroid rodents from the early to middle Eocene of Algeria  
387 (Gour Lazib, Western Sahara): New dental evidence. *Journal of Systematic*  
388 *Palaeontology* 9 4, 563-588.

389 Mayr, G., 2005. The Paleogene fossil record of birds in Europe. *Biology Revue* 80,  
390 515-542.

391 Mayr, G., 2007. The renaissance of avian paleontology and its bearing on the higher-  
392 level phylogeny of birds. *Journal of Ornithology* 148 2, S455-S458.

393 Mayr, G., 2008. Phylogenetic affinities and morphology of the late Eocene anseriform  
394 bird *Romainvillia stehlini* Lebedinsky, 1927. *Neues Jahrbuch Geologie*  
395 *Paläontologie Abhandlungen* 248 (3), 365-380.

396 Mayr, G., 2009. *Paleogene Fossil Birds*. Springer-Verlag, Berlin Heidelberg.

397 Mayr, G., 2016. Variation in the hypotarsus morphology of birds and their  
398 evolutionary significance. *Acta zoologica* 97 2, 196-210.

399 Mayr, G., 2017. Avian higher level biogeography: Southern Hemispheric origins or  
400 Southern Hemispheric relicts? *Journal of Biogeography* 44 4, 956-958.

401 Mebrouk, F., 2011. *Les charophytes du Maghreb: systématique, biostratigraphie et*  
402 *environnements crétacés-paléogènes*. PhD Université d'Oran, 192p.

403 Mikhailov, K.E., 1987. The principal structure of the avian eggshell: data of SEM  
404 studies. *Acta Zoologica Cracoviensia* 30 5, 53-70.

405 Mikhailov, K.E., 1995a. The evolutionary implications of eggshell structure in  
406 falconiform and ciconiiform birds. *Courier Forschungsinstitut Senckenberg* 181,  
407 337-355.

408 Mikhailov, K.E., 1995b. Eggshell structure in the Shoebill and pelecaniform birds:  
409 comparison with Hamerkop, herons, ibises and storks. *Canadian Journal of*  
410 *Zoology* 73, 1754-1770.

411 Mikhailov, K.E., 1997. Fossil and recent eggshell in amniotic vertebrates: fine  
412 structure, comparative morphology and classification. *Special Papers in*  
413 *Paleontology* 56, 1-80.

414 Mikhailov, K.E., et al. 1996.

415 Mikhailov, K.E., Bray, E.S., Hirsch, K.F., 1997. Parataxonomy of fossil egg remains  
416 (Veterovata): principles and applications. *Journal of Vertebrate Paleontology*, 16 4,  
417 763-769.

418 Miller, E.R., Rasmussen, D.T., Simons, E.L., 1997. Fossil storks (Ciconiidae) from  
419 the late Eocene and early Miocene of Egypt. *Ostrich* 68, 23-26.

420 Mourer-Chauviré, C., Geraads, D., 2010. The upper Pliocene avifauna of Ahl al  
421 Oughlam, Morocco: systematics and biogeography. *Records of the Australian*  
422 *Museum* 62, 157-184.

423 Mourer-Chauviré, C., Pickford, M., Senut, B., 2015. Stem group galliform and stem  
424 group psittaciform birds (Aves, Galliformes, Paraortygidae, and Psittaciformes,  
425 family incertae sedis) from the Middle Eocene of Namibia. *Journal of Ornithology*  
426 156 (1), 275-286.

427 Mourer-Chauviré, C., Pickford, M., Senut, B., 2017. New data on stem group  
428 Galliformes, Charadriiformes, and Psittaciformes from the middle Eocene of  
429 Namibia. *Contribuciones científicas del Museo Argentino de Ciencias Naturales*  
430 "Bernardino Rivadavia" 7, 99-131.

431 Mourer-Chauviré, C., Pickford, M., Senut, B., 2011a. The first Paleogene galliform  
432 from Africa. *Journal of Ornithology* 152 3, 617-622.

433 Mourer-Chauviré, C., Tabuce, R., Mahboubi, M., Adaci, M., Bensalah, M., 2011b. A  
434 Phororhacoid bird from the Eocene of Africa. *Naturwissenschaften* 98, 815-823.

435 Mourer-Chauviré, C., Tabuce, R., Essid, El M., Marivaux, L., Khayati, H., Vianey-  
436 Liaud, M., Ben Haj Ali, B., 2013. A new taxon of stem group Galliformes and the  
437 earliest record for stem group Cuculidae from the Eocene of Djebel Chambi,  
438 Tunisia, in: Göhlich U.B., Kroh, A., (Eds.), *Proceedings of the 8<sup>th</sup> international  
439 meeting of the Society for Avian Paleontology and Evolution*, pp. 1-15.

444 Noriega, J.L., Tambussi, C.P., 1995. A late Cretaceous Presbyornithidae (Aves:  
445 Anseriformes) from Vega Island, Antarctic Peninsula: palaeobiogeographic  
446 implications. *Ameghiniana* 32, 57-61.

447 Olson, S.L., 1999. The anseriform relationships of *Anatalavis* Olson and Paris  
448 (Anseranatidae), with a new species from the Lower Eocene London Clay, in:  
449 Olson, S.L., (Ed.), *Avian paleontology at the close of the 20<sup>th</sup> century: Proceedings  
450 of the 4<sup>th</sup> international meeting of the Society for Avian Paleontology and  
451 Evolution*. Washington, D.C., 4-7 June 1996. *Smithsonian Contribution to  
452 Paleobiology* 89, pp. 231-243.

453 Pycraft, W.P., 1900. On the morphology and phylogeny of the Paleognathae (Ratitae  
454 and Crypturi) and Neognathae (Carinatae). *Transactions of the Zoological Society  
455 of London* 15: 149-290.

456 Rage, J.-C., Adaci, M., Bensalah, M., Mahboubi, M., Marivaux, L., Mebrouk, F.,  
457 Tabuce, R., (in press) Latest early-early middle Eocene deposits of Algeria (Glib  
458 Zegdou, HGL50), yield the richest and most diverse fauna of amphibians and  
459 squamate reptiles from the Palaeogene of Africa. *Palaeovertebrata*.

460 Rasmussen, D.T., Olson, S.L., Simons, E.L., 1987. Fossil birds from the Oligocene  
461 Jebel Qatrani Formation, Fayum Province, Egypt. *Smithsonian Contributions to*  
462 *Paleobiology* 62, 1-20.

463 Rich, P.V., 1980. Preliminary report on the fossil avian remains from Late Tertiary  
464 sediments at Langebaanweg (Cape Province), South Africa. *South African Journal*  
465 *of Science* 76, 166-170.

466 Sauer, E.G.F., Sauer, E.M., 1978. Ratite eggshell fragments from Mio-Pliocene-  
467 continental sediments in the district of Ouarzazate, Morocco. *Palaeontographica.*  
468 *Abteilung A: Palaeozoologie-Stratigraphie*, 161 1-3, 1-54.

469 Schweitzer, M.H., Jackson, F.D., Chiappe, L.M., Schmitt, J.G., Calvo, J.O., Rubilar,  
470 D.E., 2002. Late cretaceous avian eggs with embryos from Argentina. *Journal of*  
471 *Vertebrate Paleontology* 22 1, 191-195.

472 Ségalen, L., Renard, M., Lee-Thorp, J.A., Emmanuel, L., Le Callonnec, L., Rafelis,  
473 de M., Senut, B., Pickford, M., Melice, J.L., 2006. Neogene climate change and  
474 emergence of C4 grasses in the Namib, southwestern Africa, as reflected in ratite  
475  $^{13}\text{C}$  and  $^{18}\text{O}$ . *Earth Planetary Science Letters* 244, 725-734.

476 Senut, B., 2000. Fossil ratite eggshells: a useful tool for Cenozoic biostratigraphy in  
477 Namibia. Special Issue: Henno Martin Commemorative volume, *Communications*  
478 *of the Geological Survey of Namibia* 12, 367-373.

479 Senut, B., Dauphin, Y., Pickford, M., 1998. Nouveaux restes aviens du Néogène de  
480 la Sperrgebiet (Namibie): complément à la biostratigraphie des éolianites du  
481 désert de Namib, *Comptes Rendus de l'Académie des Sciences de Paris Série*  
482 327, 639-644.

483 Senut, B., Pickford, M., Ségalen, L., 2009. Neogene desertification of Africa.  
484 *Comptes Rendus Géosciences* 341, 591-602.

485 Smith, N.A., 2013. Avian fossils from the Early Miocene Moghra Formation of Egypt.  
486 OSTRICH - Journal of African Ornithology 84 3, 181-189.

487 Solé, F., Lhuillier, J., Adaci, M., Bensalah, M., Mahboubi, M., Tabuce, R. 2013. The  
488hyaenodontidans from the Gour Lazib area (? Early Eocene, Algeria): implications  
489concerning the systematics and the origin of the Hyainailourinae and  
490Teratodontinae. Journal of Systematic Palaeontology doi:  
49110.1080/14772019.2013.795196.

492 Stevens, N.J., Gottfried, M.D., Roberts, E.M., Kapilima, S., Ngasala, S., O'Connor,  
493P.M., 2008. Paleontological Exploration in Africa. A View from the Rukwa Rift  
494Basin of Tanzania, in: Fleagle, J.G., Gilbert, C.C., (Eds.), Elwyn Simons: A Search  
495for Origins, pp. 159-180.

496 Stidham, T.A., 2010. A small Pleistocene lovebird (Psittacidae: *Agapornis*) from  
497Plovers Lake, South Africa. Neues Jahrbuch für Geologie und Paläeontologie 256,  
498123-128.

499 Tabuce, R., Marivaux, L., Lebrun, R., Adaci, M., Bensalah, M., Fabre, P.-H., Fara, E.,  
500Gomes-Rodrigues, H., Hautier, L., Jaeger, J.J., Lazzari, V., Mebrouk, F., Peigné,  
501S., Sudre, J., Tafforeau, P., Valentin, X., Mahboubi, M. 2009. Anthropoid vs.  
502strepsirhine status of the African Eocene primates *Algeripithecus* and *Azibius*:  
503craniodental evidence. Proceedings of the Royal Society B, Biological Science  
504276, 4087-4094.

505 Tabuce, R., Charruault, A.-L., Adaci, M., Bensalah, M., Ben Haj Ali, M., Essid E.M.,  
506Marivaux L., Vianey-Liaud M., Mahboubi, M., 2011. The early Eocene radiation of  
507Hyracoidea (Mammalia, Afrotheria): new fieldwork evidence from northwestern  
508Africa, in: The World at the Time of Messel. Senckenberg Research Institute and  
509Natural History Museum Frankfurt, pp. 161-162.

510 Tambussi, C.P., Degrange, F.J., De Mendoza, R.S., Sferco, E., Santilliana, S., 2019.  
511 A stem anseriform from the early Palaeocene of Antarctica provides key evidence  
512 in the early evolution of waterfowl. *Zoological Journal of the Linnean Society*, 1-28.

513 Temminck, C.J. 1820. *Manuel d'ornithologie ou Tableau systématique des oiseaux*  
514 *qui se trouvent en Europe: précédé d'une analyse du système général*  
515 *d'ornithologie, et suivi d'un tableau alphabétique des espèces.*

516 Wagler, J.G., 1831. *Einige Mittheilungen über Thiere Mexicos.* *Isis von Oken* 24,  
517 510-535.

518 Wetmore, A., 1926. *Fossil birds from the Green River deposits of eastern Utah.*  
519 *Annals of the Carnegie Museum* 16: 391-497.

520 Zelenitsky, D.K., Hirsch, K.F. 1997. *Fossil eggs: identification and classification*, in:  
521 *Wolberg, D.L., Stump, E., Rosenberg, G., (Eds.), Dinofest International: A*  
522 *symposium held at Arizona State University, Academy of Natural Sciences,*  
523 *Philadelphia, pp. 279-286.*

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.

544

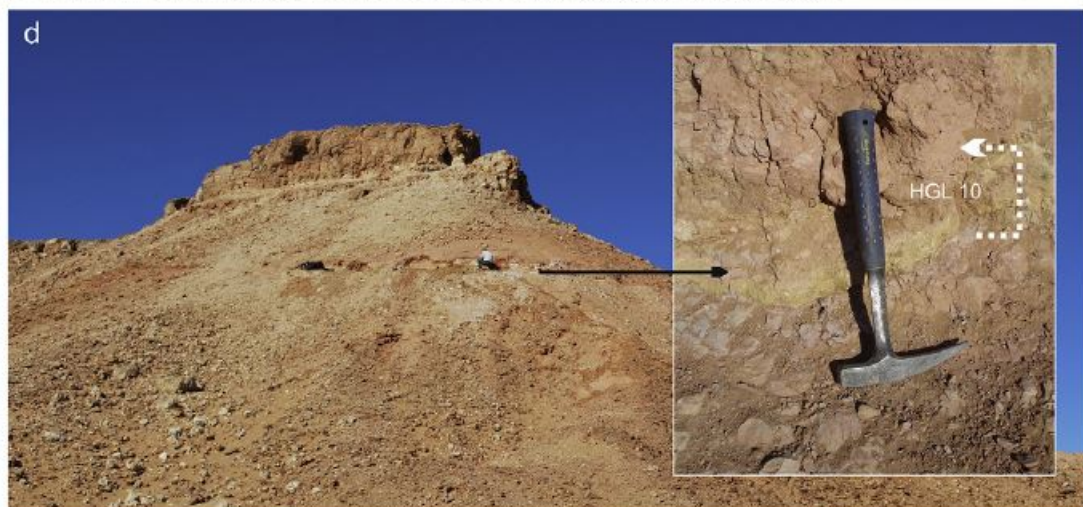
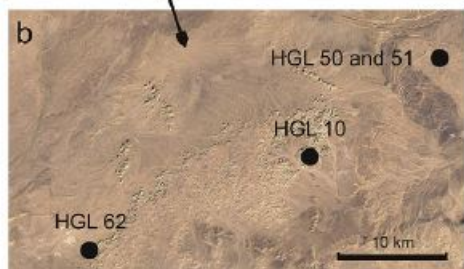
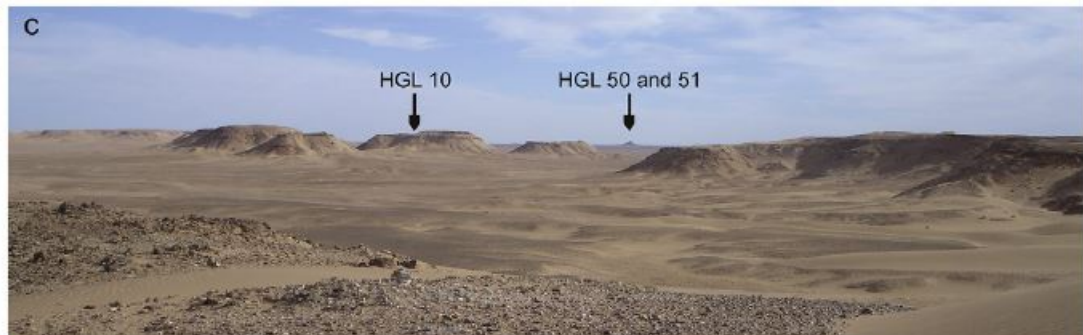
545 Figure 3. *Romainvillia stehlini* Lebedinsky, 1927, from the late Eocene of France. Left  
546 carpometacarpus (NMB P.G. 53), (a) ventral view; (b) cranial view; (c) dorsal view.  
547 Scale bars equal 5 mm. Abbreviation: fcc – fossa carpalis cranialis. After Mayr (2008,  
548 fig. 2, I-K).

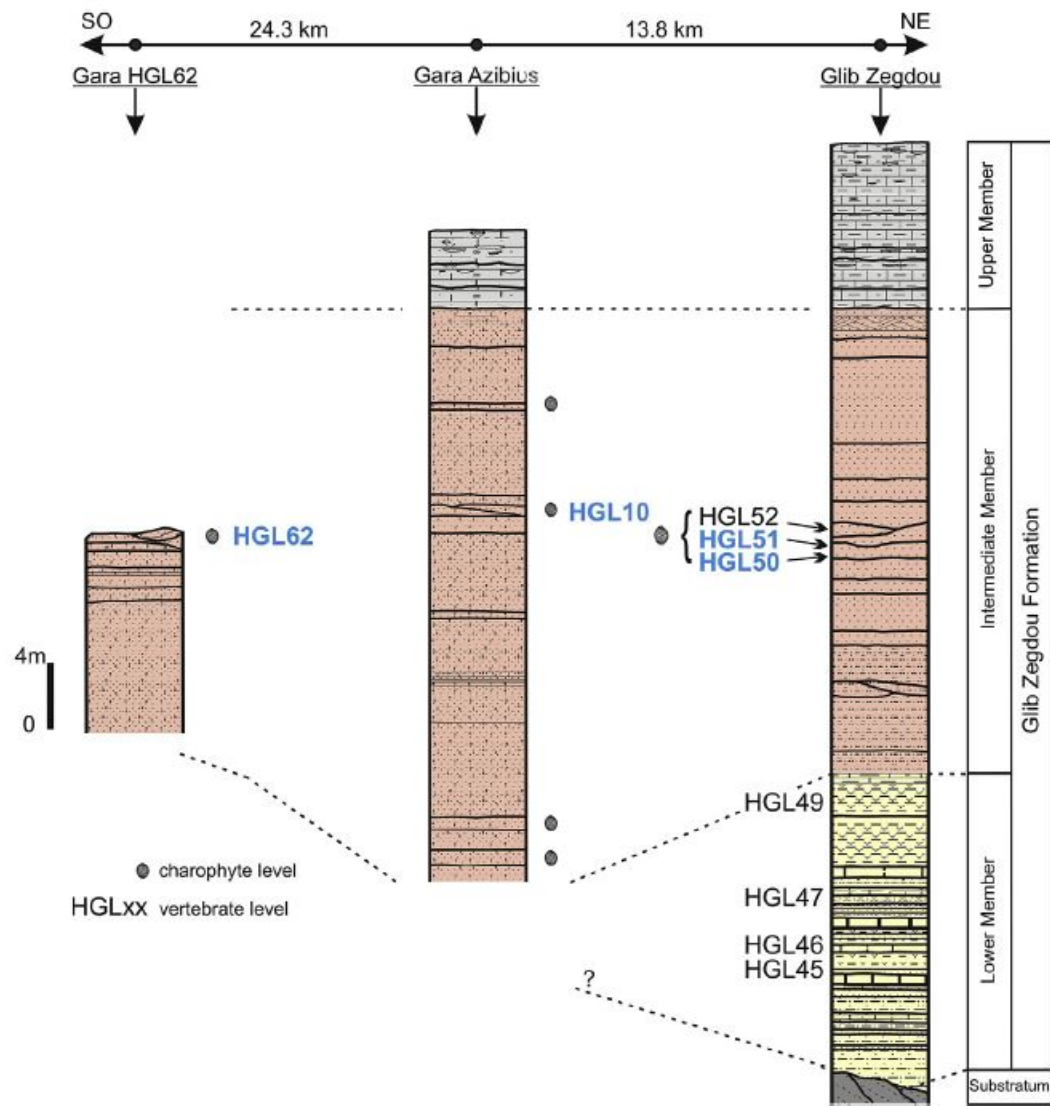
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550 Figure 4. (a) UM-HGL10A, a nearly complete egg with an ovoid shape, discovered  
551 isolated in the HGL10 locality. (b-d) SEM micrograph images of eggshells; (b) UM-  
552 HGL10-4a Circular pore orifices on the outer surface (arrows) x 180; (c) 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)



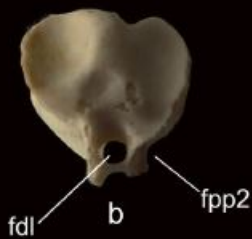
560 UM-HGL10B The mammillae are underlined by alterations and a possible canal pore  
561 is observable (black arrows) x 100. Scale bar 1 cm.







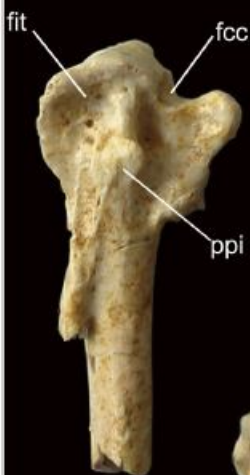
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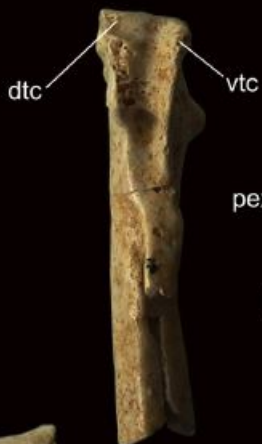
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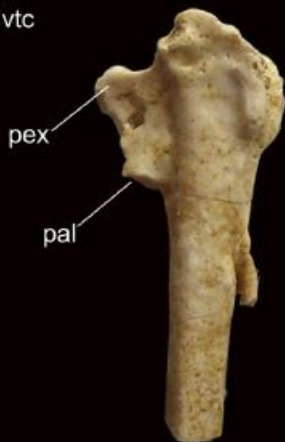
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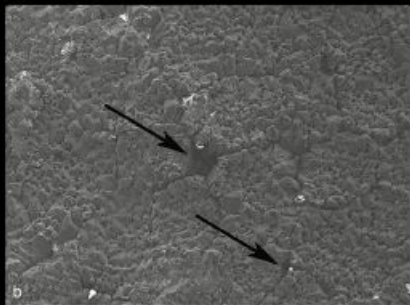
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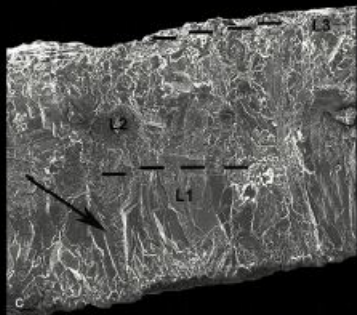
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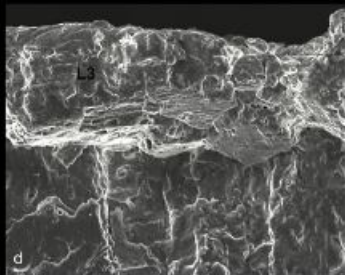
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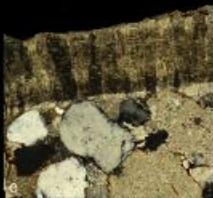
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