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

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

ABSTRACT.

Numerous avian eggshells and one well-preserved small ovoid-shaped egg (32 x 28 mm) were collected in the Gour Lazib area, western Algeria from three localities from the Glib Zegdou Formation dated from the late early or early middle Eocene. This material was associated with a rich vertebrate fauna. The scanning electron microscopy (SEM) study of the eggshells led to attribute them to neognathous birds; they are characterized by a thin shell (less than 0.5 mm thick) with a prismatic trilaminate microstructure. The occurrence of an avian carpometacarpus belonging to the Presbyornithidae from HGL50, which is located one meter below the HGL 51 level, suggests that the egg remains may be referred to this bird family, which is so far unknown in the Palaeogene of the Afro-Arabian continent.

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1. Introduction

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

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

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

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

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

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

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

3. Geological context.

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

Institutional abbreviations

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

4. Results

4.1. Osteological fossils

Order Galliformes Temminck, 1820

Indeterminate family, genus and species

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

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

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

Order Anseriformes Wagler, 1831

Family Presbyornithidae Wetmore, 1926

Indeterminate genus and species

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

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

Description and comparisons

The morphological characteristics of the carpometacarpus of the Presbyornithidae have been given by Howard (1955) for the genus *Telmabates*, and by Ericson (2000) for the genera *Telmabates* and *Presbyornis*. Then two other genera have been described, *Teviornis* from the late Cretaceous of Mongolia (Kurochkin et al. 2002) and *Wilaru* from the Late Oligocene and early Miocene of Australia (De Pietri et al., 2016). One of the main characteristics is that the dorsal crest of the carpal trochlea extends as far or slightly farther caudally as the ventral crest in *Telmabates* and *Teviornis*, and extends well caudally farther in *Presbyornis*. In *Wilaru* both rims of the carpal trochlea extend caudally and distally to about the same level. In the Glib Zegdou specimen, the dorsal crest of the trochlea extends as far caudally as the ventral crest (Fig. 2 e).

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

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

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

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

4.2. Oological fossils

Order Neognathes Pycraft, 1900

Ornithoid-prismatic morphotype Mikhailov, 1997

Indeterminate oofamily, oo-genus and species

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

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

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

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

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

5. Discussion and conclusion

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

Fossil eggs can be attributed unequivocally to a taxon only by identifiable embryonic bones or hatchlings found inside or in association of the eggs (Hirsh and Quin, 1990). Very few examples have been reported for neognaths (Schweitzer et al., 2002) but the co-occurrence of eggs with monospecific adult bones in an autochthonous fossil assemblage allows indirect correlations. It is on this point that Leggitt and Buchheim (1997) have assigned the avian eggshells coming from nesting sites (Eocene, Wyoming) rich in *Presbyornis* remains, to this bird taxon. This report suggests that the egg remains with the same features, found on the Gour Lazib area may thus be referred to the Presbyornithidae, which were so far unknown in the Paleogene deposits of the Afro-Arabian continent. In fact, this extinct waterfowl family, found in very large numbers in lacustrine environments (bones sometimes associated with eggshell fragments (Leggitt and Buchheim, 1998) was particularly recovered in Upper Cretaceous to Paleogene deposits from both North America and Asia (Ericson, 2000; Kurochkin et al., 2002; Kurochkin and Dyke, 2010; Eberle and Greenwood 2012; Mayr, 2009).

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

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Figure legends

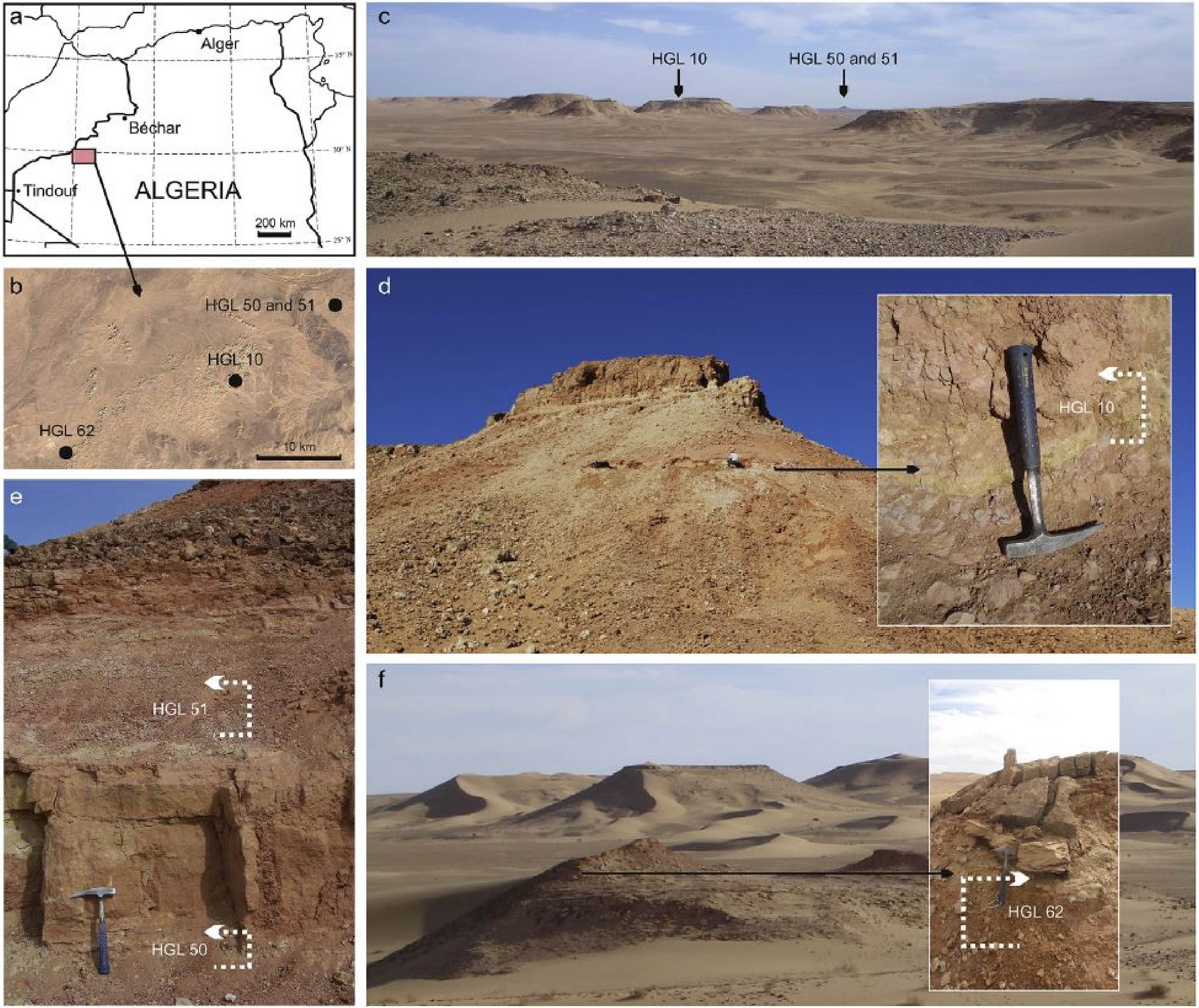
Figure 1. Gour Lazib location map and outcrops showing localities yielding avian egg and bone remains. (a-b) geographic location of the Gour Lazib in western Algeria and satellite image the four fossiliferous localities; (c) panoramic view of the Gour Lazib showing HLG 10 and HGL 50-51 localities; view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

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

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

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

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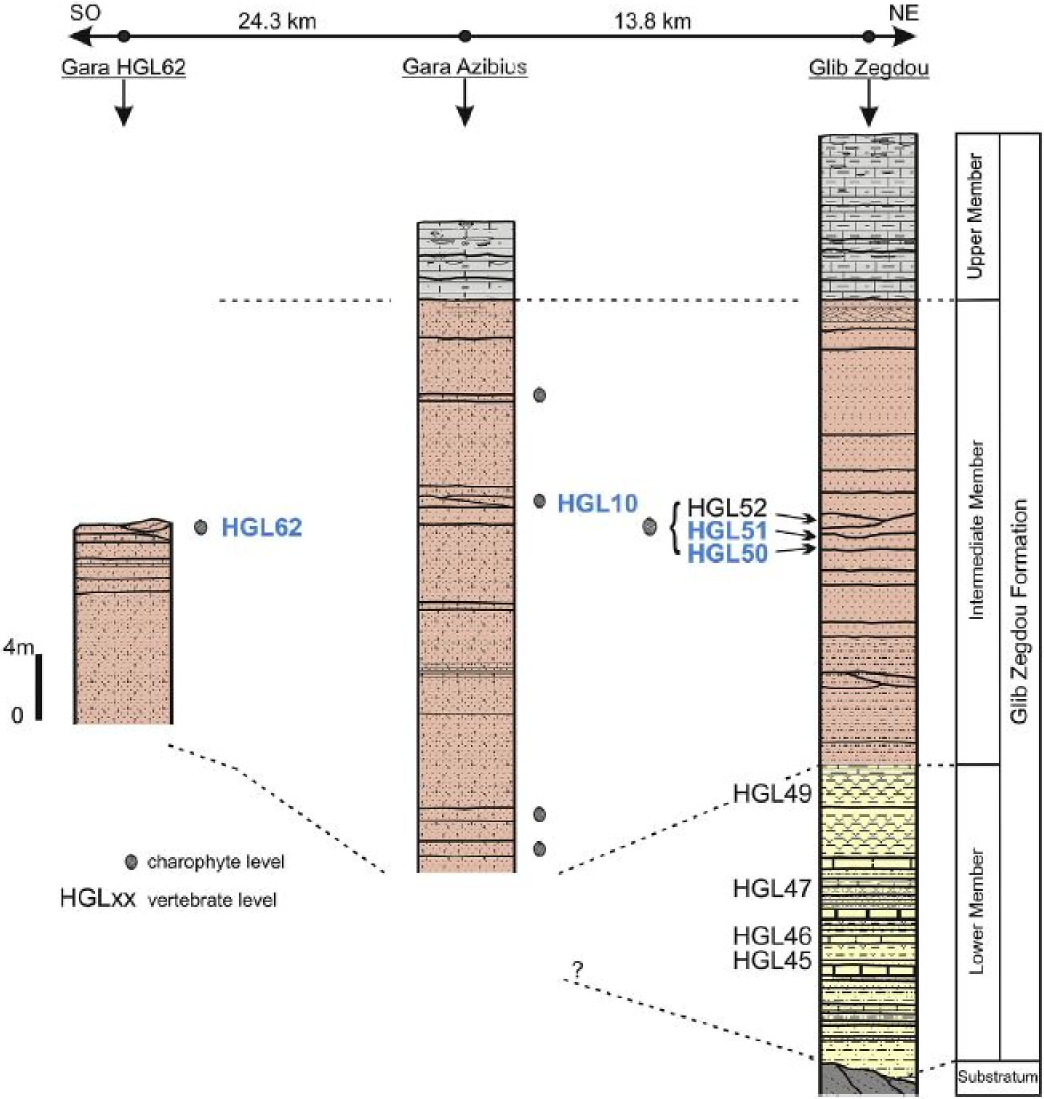
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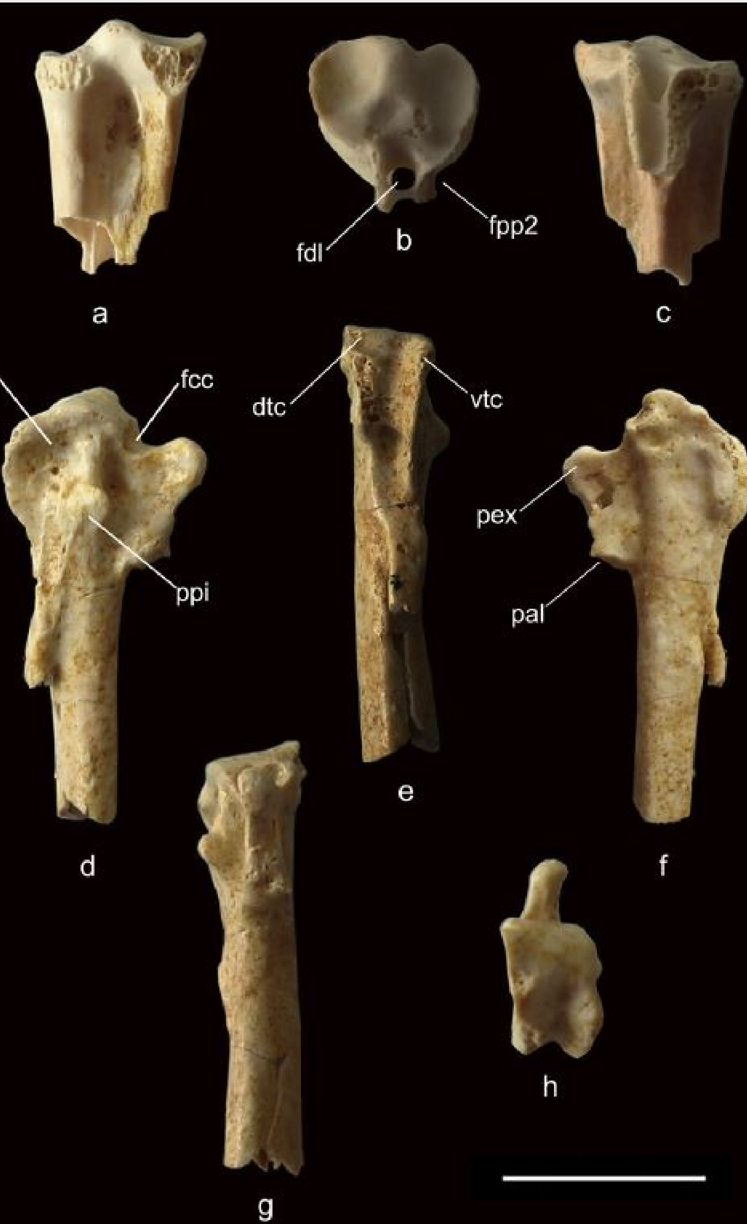
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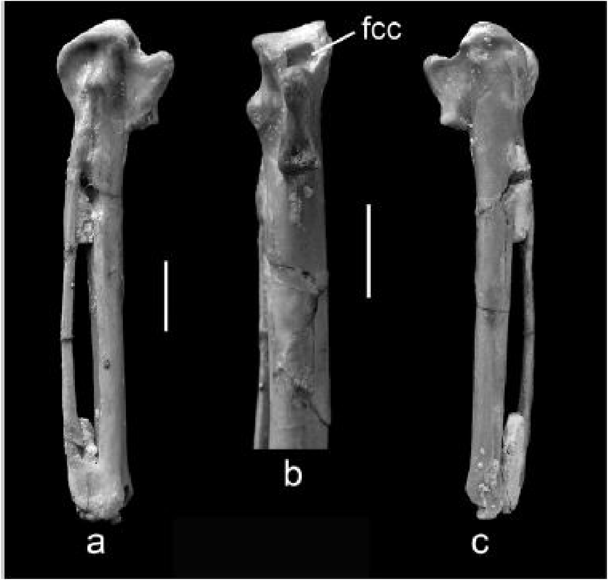
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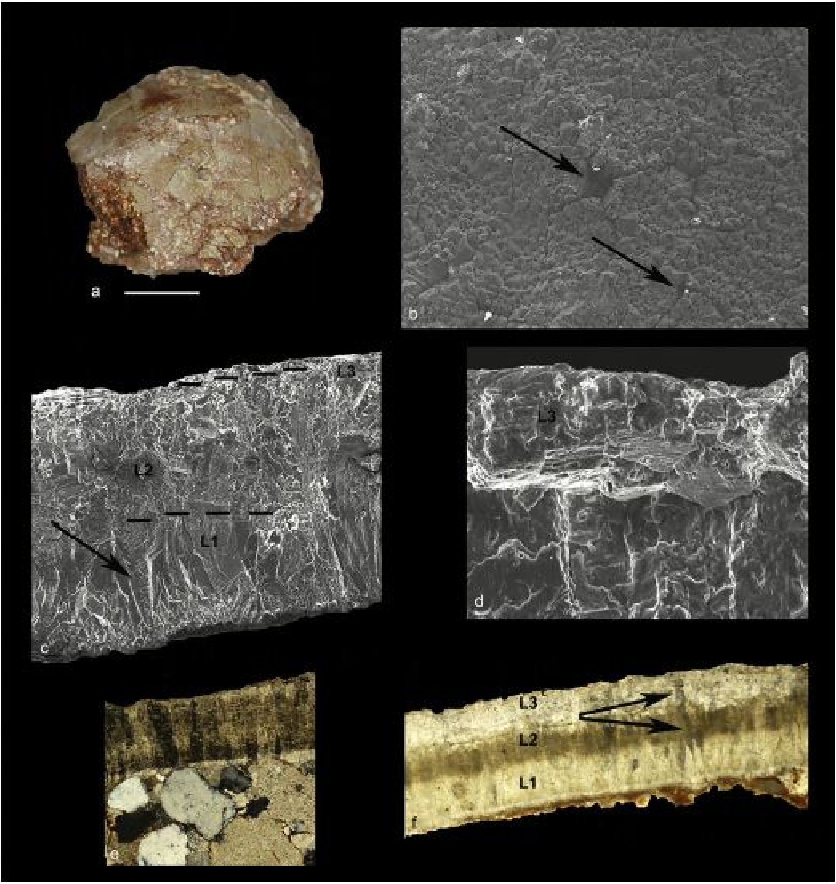
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