Enigmatic new mammals from the late Eocene of Egypt

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with 4 figures

Abstract: A new mammalian genus and species from the earliest late Eocene of Egypt is represented by a lower jaw fragment and two isolated lower molars. A rare combination of features and the fragmentary nature of the materials make their taxonomic assignment to either Marsupialia or Chiroptera uncertain. The holotype of the new genus is the best-preserved specimen in the sample, a dentary fragment with two molars that have uncompressed trigonids, weak buccal cingulids, and a nyctalodont arrangement of the hypocristid. Some traits appear to more clearly support marsupial, as opposed to chiropteran, affinities for this species, including the very likely presence of four molars in the dentary. The enamel of an additional lower molar assigned to this species consists of a single layer of radial enamel without any prism decussation, an enamel type that characterizes marsupials as well as chiropterans. A second taxon is represented by two isolated upper molars. Some traits appear to more clearly support marsupial, as opposed to chiropteran, affinities for these species, including the orientation of pre- and postprotocristae, the moderately slender lingual portion of the trigon, and the absence of any talon expansion. As some of these features can be found in various bat clades, chiropteran affinities for these species cannot be ruled out, but we propose that the new taxa are more likely to represent specialized 'didelphimorphian' marsupials.

Keywords: Africa • Fayum • Metatheria • Didelphimorphia • Chiroptera • Biogeography • Enamel

Kurzfassung: Aus dem untersten Ober-Eozän von Ägypten liegen ein Unterkiefer-Fragment und zwei isolierte untere Molaren einer neuen Säugetier-Gattung und -Art vor. Die ungewöhnliche Merkmalskombination und der fragmentarische Erhaltungszustand der Stücke lassen eine Zuordnung zu den Marsupialia oder Chiroptera möglich erscheinen. Das Unterkieferfragment (Holotyp) enthält zwei Molaren mit unkomprimierten Trigoniden, schwach entwickelten buccalen Cinguliden und einer nyctalodonten Anordnung des Hypocristids. Der Kiefer hat ursprünglich vermutlich vier Molaren besessen, was für eine Zuordnung zu den Marsupialiern spräche. Der Schmelz eines der neuen Art zugeordneten isolierten unteren Molaren besteht aus einer einfachen Lage von Radialschmelz (ohne Prismenüberkreuzung), ein Schmelztyp, der sowohl bei den Marsupialia als auch bei den Chiroptera vorkommt. Ein zweites Taxon ist durch zwei einzelne obere Molaren repräsentiert. Auch hier sprechen manche Merkmale eher für eine Zuweisung zu den Marsupialia, unter anderem die Anordnung der Prä- und Protocristae, der mäßig schlanke linguale Teil des Trigons und das Fehlen einer Talon-Ausweitung. Da einige dieser Merkmale auch bei verschiedenen Fledermäusen auftreten, kann eine Zugehörigkeit zu den Chiroptera nicht ausgeschlossen werden, obwohl wir zu der Auffassung tendieren, dass es sich bei beiden neuen Taxa eher um spezialisierte „didelphomorphe" Beuteltiere handelt.

Schlüsselwörter: Afrika • Fayum • Metatheria • Didelphimorphia • Chiroptera • Biogeographie • Schmelz

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Introduction

Palaeogene deposits exposed in the Fayum Depression of northern Egypt are the primary source of terrestrial mammals from the early Cenozoic of Afro-Arabia. Discoveries in the Fayum area have greatly contributed to our understanding of anthropoid origins and a variety of other fundamental issues in mammalian evolution (SIMONS 1995; SIMONS & RASMUSSEN 1990; HOLROYD et al. 1996). Recently, the oldest terrestrial mammals from Egypt have been recovered from the earliest late Eocene (~37 Ma) Birket Qarun Locality 2 (BQ-2) (SEIFFERT et al. 2003, 2005). Here we report on new fossil mammals from BQ-2 that increase the diversity of mammals from this time and place in Africa.

The new material includes isolated molars and a partial dentary. All specimens are unique in their combination of features, precluding a definitive assessment of their affinities; both species exhibit a number of morphological features that have evolved convergently in various living and extinct marsupials as well as chiropterans and a number of other dentally dilambdodont placentals. Marsupials are known to have existed in Africa between the early or early middle Eocene (CROCHET 1986) and the early Oligocene (BOWN & SIMONS 1984). The short taxonomic history of these forms has already been controversial, however – early Eocene *Garatherium*, originally described as a peradectine marsupial, has since been reinterpreted as either a placental adapisoriculid (GHEERBRANT 1995) or as a herpetotheriine marsupial (MCKENNA & BELL 1997), whereas CROCHET et al. (1992) argued that the early Oligocene Fayum marsupial *Peratherium africanum* is not a member of *Peratherium* and transferred that species to a new genus, *Qatranitherium*. HOOKER et al. (in press) confirmed the herpetotheriid status of *P. africanum* based on new material. Chiropterans are represented in the Palaeogene of Africa by a rhinolophoid from the early Eocene of Tunisia (SIGÉ 1991); an indeterminate "microbat" from the early middle Eocene of Tanzania (GUNNELL et al. 2003); emballonurids, hipposiderids, and nycterids from a latest Eocene or earliest Oligocene locality (Taqah) in Oman (SIGÉ et al. 1994); and philisid vespertilionoids from the early Eocene of Tunisia (SIGÉ 1991), the early Oligocene of Egypt (SIGÉ 1985), and the Omani Taqah locality (SIGÉ et al. 1994). Recently G. GUNNELL et al. (in prep.) have identified philisids and rhinopomatids at locality BQ-2, and a megadermatid and a vespertilionid at a younger late Eocene locality in the Fayum sequence (Quarry L-41).

The quotation marks in "Didelphimorphia" signify the likely paraphyletic nature of this taxon (KIRSCH et al. 1997; SANCHEZ-VILLAGRA et al. 2007). We followed VAN VALEN (1966) and CROCHET (1980) for dental nomenclature. Abbreviations used in the text are: DPC = Duke Lemur Center, Division of Fossil Primates, CGM = Cairo Geological Museum, m = lower molar, M = upper molar.

Locality and association of material

All specimens were collected from an area of 30–40 square meters at Birket Qarun Locality 2 (BQ-2), which is situated 183 m below the contact of the Qasr el-Sagha and Jebel Qatrani formations north of Birket Qarun in the Fayum Depression, northern Egypt (SEIFFERT et al. 2003). Paleomagnetic reversal stratigraphy suggests that BQ-2 is about 37 million years old or earliest late Eocene (earliest Priabonian) in age (SEIFFERT et al. 2005; SEIFFERT 2006). Vertebrate fossils preserved at BQ-2 have been recovered primarily through quarrying and dry-sieving of intraclastic ironstone pebble and cobble conglomerates. In addition to the aforementioned chiropterans, BQ-2 also preserves remains of anthropoid (SEIFFERT et al. 2005), crown strepsirrhine (SEIFFERT et al. 2003), and adapiform primates, as well as proboscideans, hyracoids, herodotiines, ptolemaiids, creodonts, anomaluroid and hystricognathous rodents, and a number of "insectivoran-grade" placentals, but no anthracotheriid artiodactyls. The absence of anthracotheriids suggests that BQ-2 is at least slightly older than the Bir el Ater (Nementcha) locality that provides the first evidence for an anthracotheriid presence in Afro-Arabia (MAHBOUBI et al. 2003). The teeth described here differ in size and morphology from all other tribosphenic mammals at BQ-2, and therefore no reasonable attributions to other dental or cranial remains are possible following extensive collection of hundreds of isolated mammalian teeth from the locality.

Measurements

Tooth measurements follow CROCHET (1980: fig. 3). W (width) and L (length) of the specimens described and figured are as follows (mm). CGM 83699, m?2: L = 4.01, W = 2.03; m?3: L = 3.69, W = 2.12; DPC-BQ2-DPC 22442D m?1: W = 2.3; DPC 21498B, m1 or m2: L = 3.6, W = 1.72; DPC 21372A, M?2: L = 3.02, W = 3.74; DPC 21372B, M?3: L = 2.88, W = 3.64.

Systematic palaeontology

?Marsupialia ILLIGER, 1811
?"Didelphimorphia" GILL, 1872

Ghamidtherium n. gen.

Etymology: From *ghamid*, the Arabic word for mysterious, and Latin *therium*, derived from the Greek word *therion* for wild beast.

Type species: *Ghamidtherium dimaiensis* n. sp.

Locality and distribution: Locality BQ-2, earliest late Eocene (Priabonian), Birket Qarun Formation, northern Egypt.

Diagnosis: *Ghamidtherium* differs from other Paleogene Afro-Arabian mammals in combining the following features: molar trigonids relatively open and uncompressed, with a large angle between the proto-

and paracristids that decreases distally; molar metaconids low relative to protoconids, slightly taller than paraconids; lingually situated hypoconulid relatively small, connected to hypoconid (nyctalodont); weak buccal cingulids that are restricted to hypoflexids; well-developed precingulids; tooth mesial to the m?2 relatively large (about 90% the length of the m?2, based on spacing of alveoli), with mesial alveolus not offset buccally with respect to the distal alveolus.

Ghamidtherium dimaiensis n. sp.

Etymology: Refers to the nearby ruins of Dimai (Soknopaios Nesos).

Holotype: CGM 83699, a right dentary fragment including m?2-3, and alveoli for m?4 and one tooth anterior to m?2 (Figs. 1A–D).

Hypodigm: The type specimen and DPC 22442D, a partial right lower molar (m?1), preserving the trigonid and about half of the talonid (Figs. 1, 2, 3).

Locality and **distribution:** As for the genus.

Diagnosis: As for the genus.

Description of the holotype: The two preserved molars are two-rooted. Molar trigonid width increases distally, with the talonid being wider on both molars. The paracristid (= paralophid) extends between protoconid and paraconid without recurving lingually, and there is no marked carnassial notch in the paracristid. Relative heights of the molars are, on trigonids, protoconid > metaconid > paraconid; on talonids, hypoconid > entoconid > hypoconulid. In buccal view the protoconid rises well above the hypoconid. Well-developed entocristids enclose the talonid basins lingually, while the oblique cristids, which are connected to the middle portion of the postvallid (to the posterior wall of the trigonid), descend well below the level of the entocristids so that the lingual and buccal margins of the talonid are of different heights. As in "Didelphimorphia" (MARSHALL et al. 1990) and many other mammals (THENIUS 1989), hypoconulids are lower than the entoconids. Short postentocristids on the distal faces of the entoconids terminate lingual to the hypoconulids. The m?3 is shorter than the m?2, in contrast to the opposite condition in species of *Peratherium*.

The ventral border of dentary is gently curved, with excavated masseteric fossa, as is typical for opossums and many other mammals. No mental foramina are present in the preserved portion of the dentary.

Enamel microstructure of DPC 22442D: For enamel microstructure investigation, the molar was embedded in polyester resin for easier handling. After hardening of resin, the specimen was cut transversely and longitudinally with a low speed saw. Subsequently, the section planes were ground smooth (1200 corundum slurry on glass plate), dried, and etched for 2–4 seconds with 7 % (2N) HCl to make morphological details visible. After ultrasonic cleansing and rinsing with distilled water, the specimens were dried, mounted on SEM stubs and sput-

tercoated with gold (4–6 min). The specimens were studied by SEM at magnifications from 120 to 2100x.

The enamel consists of a single layer of radial enamel without any prism decussation. In the protoconid, prisms run straight from the enamel-dentine junction (EDJ) to the outer enamel surface (OES) and are moderately inclined apically (15–25°). The crystallites of the IPM are oriented perpendicularly to the EDJ or slightly antapically; due to the prism inclination, they are arranged at an angle of 20–30° to the prism long axes (Fig. 2). In the paraconid, prism cross sections are rounded and well developed prism sheaths separate prisms and IPM. Although very distinct, prism sheaths often are incomplete leaving a connection between prism and IPM (Fig. 3B), resembling the horse-shoe type of prism cross section. IPM is comparatively thick and a prismless external layer of about 10 μm thickness is present. The enamel is quite thick, 200 μm on the labial side of the protoconid and 120 μm on the lingual side. Enamel tubules are not detectable.

Body mass estimation: Regression equations of didelphid lower tooth dimensions on body mass (GORDON 2003) provide estimates of 519, 295, and 393 g for *Ghamidtherium dimaiensis* n. sp. based on the length, width, and area of the presumed m2, and estimates of 336, 322 and 329 g, respectively, for the presumed m3.

A lower molar (DPC 21498B) of *G. dimaiensis* n. sp. or a close relative

Another isolated tooth from BQ-2, DPC 21498B (Fig. 1E), may be a right m?1 of *Ghamidtherium dimaiensis* or represent a closely related species. DPC 21498B appears to continue morphological trends being expressed in the molars preserved in CGM 83699. For instance, when compared with the m?2 of CGM 83699, the angle between the paracristid and protocristid is even larger, the trigonid is narrower when compared with the width of the talonid. DPC 21498B was two-rooted although just one root is preserved, most features are like those of CGM 83699. In fact, this tooth fits well in the empty alveolus for m1 of CGM 83699, making it conceivable that this tooth belongs to the same taxon. However, the hypocristid (or posthypocristid) is directed towards the entoconid (meeting at the postentocristid base) and not towards the hypoconulid, while the same crests reaches the hypoconulid in CGM 83699. DPC 21498B has then an entoconid notch, lacking in CGM 83699. The metaconid is located posterior to the protoconid, as in the molars preserved in CGM 83699.

Upper molars belonging to another mammalian taxon from BQ-2 locality

Material: DPC 21372A (Fig. 4A), an isolated left upper molar (M?2) and DPC 21372B (Figs. 4B, C), an isolated right upper molar (M?3).
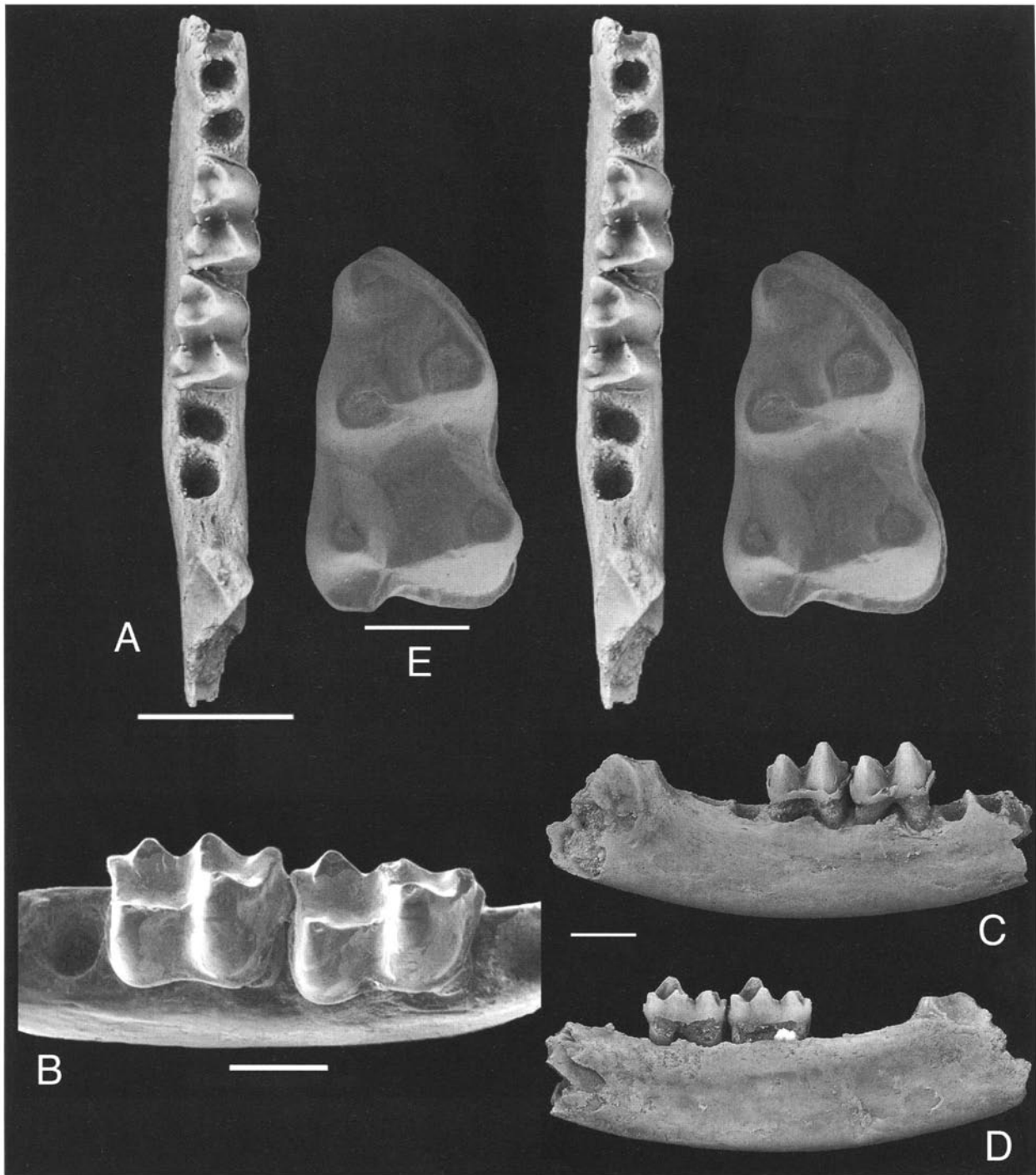
Fig. 1. A–D: *Ghamidtherium dimaiensis* n. gen., n. sp. CGM 83699, right dentary fragment including m?2–3 and alveoli for m?1 and m?4. A. Stereopair of occlusal view, anterior to top [?], scale = 5 mm; B. Occlusal/buccal view, scale = 2 mm; C. Buccal view, scale = 3 mm; D. Lingual view. – E: DPC 21498B, right m1 in occlusal view, probably referable to *Ghamidtherium dimaiensis*; stereopair, scale = 1 mm.

Locality and **distribution**: Locality BQ-2, earliest late Eocene (Priabonian), Birket Qarun Formation, northern Egypt (same as for *Ghamidtherium dimaiensis* n. sp.).

Main features: Differs from other Paleogene Afro-Arabian mammals in having a dilambdodont arrangement of the buccal crests; ectoflexi on either side of a distinct

stylar cusp C; postparacrista and premetacrista meet at stylar cusp C on M?2; premetacrista continuous with stylar cusp C on M?3; small parastyles; stylocones very small or absent; metacones that are placed farther from the buccal margin than the paracones; no paraconules or associated cristae; no metaconule on M?3; pre- and postprotocristae that meet the lingual faces of the para-
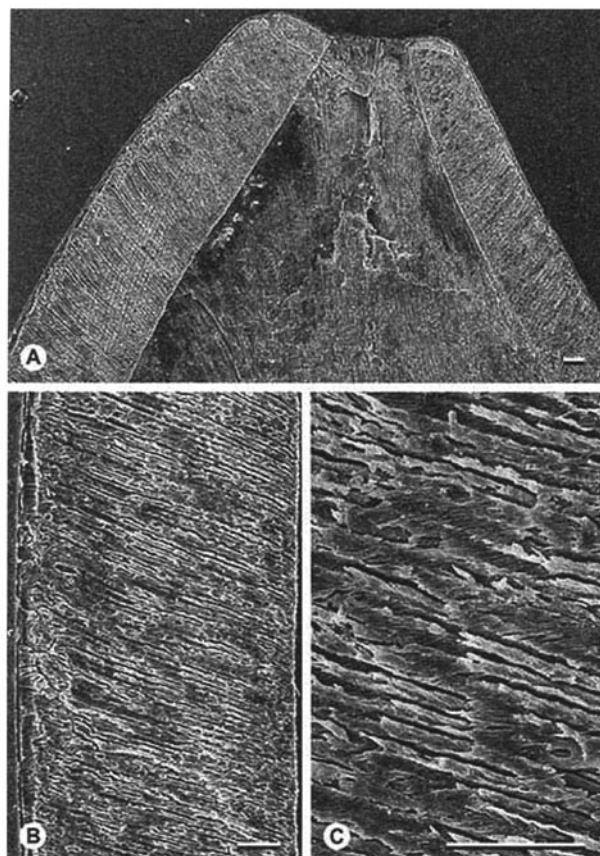
Fig. 2. *Ghamidtherium dimaiensis* n. gen., n. sp. Enamel longitudinal sections of the protoconid of DPC 22442D; in all sections, the occlusal surface is to the top. Scale bars = 30 μm. **A.** Tip of the protoconid, labial side to the left. **B.** enamel of the labial side of the protoconid, EDJ to the right. **C.** Detail of the inner enamel zone of B.

more pronounced, just mesial to stylar cusp C, and a less marked concavity distal to that cusp. The distal ectoflexus is more pronounced in DPC 21372B than in DPC 21372A, as would be expected in a more distal molar of the M1–M3 series (see CROCHET 1980: 30). Furthermore, the mesial ectoflexus of DPC 21372A is more pronounced than that of DPC 21372B.

Stylar cusps are weakly developed; aside from cusp C, only a small mesial cusp (A or stylocone) is present on DPC 21372A. This cusp is not present on DPC 21372B. The centrocrista is separated into two portions on DPC 21372B; the premetacrista extends from the metacone mesially and buccally up to stylar cusp C, with which it is continuous. The postparacrista extends from the paracone labially up to the wall just below the junction of the premetacrista with stylar cusp C. In 21372A the two portions of the centrocrista join buccally next to stylar cusp C. In both molars the preprotocrista extends toward the base of the paracone, joining a variably developed hypoparacrista (sensu GODINOT 1994) on the lingual face of the paracone (clearly developed only in DPC 21372B).

Among marsupials, the two most relevant comparative groups are the Herpethotheriinae (MARSHALL et al. 1990) and the Peradectinae (STORCH & QIU 2002). The
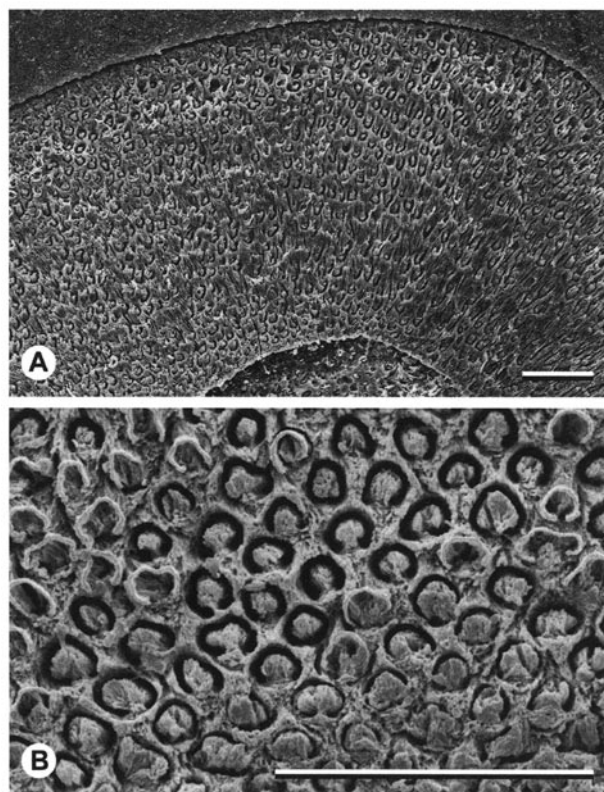
and metacones, respectively; and extensive mesial and distal cingula that do not meet lingually around the base of the protocone.

Description and comparisons: These upper teeth appear to be too small to occlude with the lower molars of *Ghamidtherium dimaiensis* and likely represent a different taxon. Differences between DPC 21372A and 21372B relate to tooth position and degree of wear. Locus cannot be positively established for these two upper molars. The teeth are assigned to the same taxon, under the assumption that the differences between them are the result of DPC 21372B and 21372A representing different positions - M?3 and M?2 respectively.

On both teeth, the apex of the paracone is relatively low when compared with that of the metacone. On DPC 21372A there is a very small metaconule situated on the postprotocrista, just lingual to the notch between this crista and the metacone. There is no metaconule on DPC 21372B, and no paraconule on either tooth. DPC 21372A has a distinct cingulum distal to the protocone. Both molars, especially DPC 21372B, have a wide trigon basin. On both molars, two ectoflexi are present, one

Fig. 3. *Ghamidtherium dimaiensis* n. gen., n. sp. Enamel cross sections of the paraconid of DPC 22442D. Scale bars = 30 μm. **A.** Overview of the lingual side, OES on top, EDJ at bottom. **B.** Detail of the distal side, close to the OES (towards bottom).
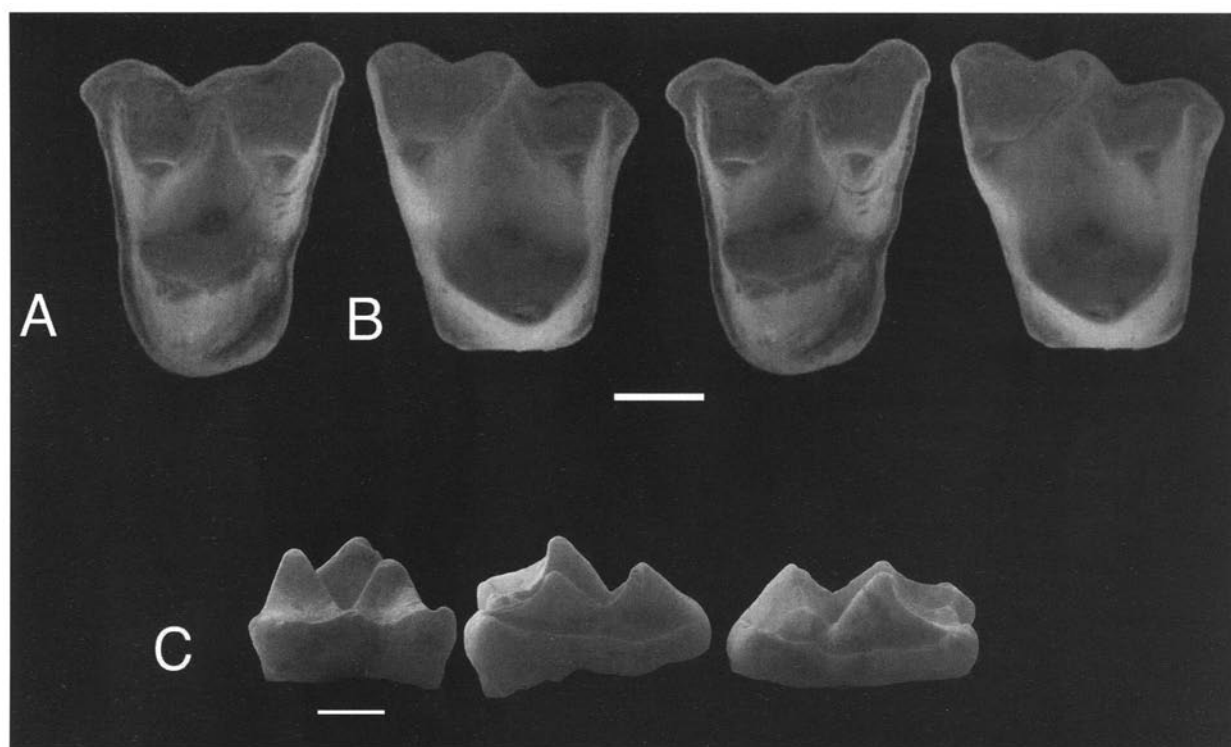
Fig. 4. Mammalia indet. **A**: DPC 21372A, left M?2. – **B**: DPC 21372B right M?3, stereopairs of occlusal views, scale = 1 mm. – **C**: DPC 21372B, buccal, mesial and distal views (left to right).

most diagnostic feature of the BQ-2 upper molars is the presence of a V-shaped centrocrista, which, among marsupials, is found in herpetotheriines and differs from the rectilinear centrocrista of peradectines; however a V-shaped centrocrista has arisen multiple times independently within Marsupialia (MUIZON & CIFELLI 2001). As in most members of the Herpetotheriinae, the apex of the V-shape centrocrista is close to stylar cusp C; in these upper molars the centrocrista even reaches that cusp ("talpidian dilambdodonty" sensu CROCHET 1980, also characteristic of derorhynchids and sternbergiids among marsupials, GOIN et al. 1999). A high degree of dilambdodonty is also attained by some protodidelphids from the Paleocene of South America (GOIN et al. 1998). In Paleocene–Eocene derorhynchids of South America and Antarctica, the V-shaped centrocrista intrudes into the stylar shelf to the point of approaching the stylar cusps, as in the BQ-2 upper molars (GOIN et al. 1999: 339). However in members of all of these other marsupial groups, the centrocrista does not extend so far buccally as it does in the BQ-2 upper molars.

In the BQ-2 upper molars there is no continuous crest uniting the stylar cusps as in *Kasserinotherium*. The difference in height between the metacone and paracone does not reach the extreme condition observable in the herpetotheriine *Asiadidelphis tjutkovae* (EMRY et al. 1995: fig. 2). One unusual, and less marsupial-like, feature is the relatively large and broad protocone, although this is seen in marsupials such as *Alphadon* and *Peradectes*. There are mesial and distal

cingula along the protocone, as in *Asiadidelphis*; these are absent in all peradectines aside from *Sinoperadectes*. The metacingulum is small and not shelf-like and flaring as in *Sinoperadectes*. While the preprotocrista joins the hypoparacrista in the BQ-2 upper molars, in herpetotheriines the preprotocrista courses mesially and buccally to terminate mesial to the base of the paracone (e.g., *Herpetotherium youngi*, KORTH 1992: fig. 3; *Asiadidelphys tjutkovae*, EMRY et al. 1995: fig. 2). In DPC 21372A there is no marked hypoparacrista as in DPC 21372B, but both teeth are similar in that the preprotocrista extends towards the base of the paracone, as opposed to coursing mesial to it as in *Herpetotherium*.

There are several similarities between DPC 21372B and the type of *Xenostylus peninsularis* (MLP 94-III-15-10), from the Eocene of Antarctica. These include the wide trigon basin, the shallow ectoflex flanking stylar cusp C, the relative size and location of the stylar cusps, and the relative height of the paracone and metacone. As pointed out to us by F.J. GOIN (pers. comm. January 2007), "marsupials lack a notch in the postparacrista, and typically either ends down towards the labial face of the crown, is subhorizontal, or goes slightly upwards. In DPC 21372B and in MLP 94-III-15-10, in contrast, the postparacrista goes first downwards following the paracone's disto-labial slope, and then turns upwards towards the stylar cusp C, thus shaping a notch".

The BQ-2 upper molars are very similar to the rhinolophoid chiropteran from Chambi (SIGÉ 1991) in hav-

ing pre- and postprotocristae that terminate near the base of the paracone and metacone, respectively; in having an ectoflexus mesial and distal to the apex of the centro-crista; and in having a small parastyle. Although the single upper molar of the Chambi rhinolophoid is damaged, it would appear from SIGÉ's (1991) figure 1 that it likely would have exhibited some expansion of the talon, and this is demonstrably absent in DPC 21372A. This distal expansion is also clearly present in a much younger rhinolophoid, *Hipposideros omani* from Taqah, Oman (SIGÉ et al. 1994). There is also a much more distinct stylar cusp C in the BQ-2 upper molars, whereas that cusp is not distinct in the Chambi rhinolophoid or in *H. omani*.

The lack of a talon expansion on the BQ-2 upper molars is seen in many vespertilionoids and is unlike rhinolophoids. The preprotocrista and postprotocrista reaching the base of the paracone and metacone, respectively, also is like the morphology of some vespertilionoids and some early Eocene bats, and unlike rhinolophoids. Most vespertilionids have the trigon basin slightly open distally, so that there is a little gap between the postprotocrista and metacone, but it is often a shallow separation and on cursory view can look like it is connected (N. CZAPLEWSKI, pers. comm. 2006).

Discussion

Molar morphology of *Ghamidtherium dimaiensis*

Although no single feature, in isolation, constitutes definitive evidence for allocating *Ghamidtherium dimaiensis* to Marsupialia (MUIZON 1994), we would argue that a mosaic of traits makes that the most parsimonious hypothesis. The most significant marsupial-like feature of the lower dentition is the inferred large size of the tooth mesial to m?2, which is unlike the condition seen in Palaeogene bats, which tend to have relatively short and compressed p4s. The mesial alveolus of the presumed m1 is positioned directly mesial to the distal alveolus, and is not offset buccally, as is seen in many bats with compressed p4s. Rhinolophoid bats have compressed p4s. Megadermatids have more elongate p4s than other rhinolophoids but m1 and m2 are distinctly different from one another in megadermatids, not like in *Ghamidtherium dimaiensis*. The uncompressed trigonid on m?2, with a large angle between the para- and protocristid, is also unlike the condition seen in other Palaeogene bats, and is similar to the condition seen in the possible late Cretaceous marsupial from Madagascar (KRAUSE 2001; but see AVERIANOV et al. 2003). The twinning of the hypoconulid and entoconid in *Ghamidtherium dimaiensis* is typical of marsupials, but is also present in many bats. *Ghamidtherium dimaiensis* exhibits the talonid structure that is most common in marsupials (nyctalodonty, in which the hypocristid con-

nects the hypoconid to the hypoconulid). Common Afro-Arabian Paleogene bats, such as late Eocene–early Oligocene philisid vespertilionoids are myotodont (the hypoconid connects directly to the entoconid and bypasses the hypoconulid), but the oldest philisid, early or early middle Eocene *Dizzya*, is nyctalodont (SIGÉ 1991). Overall, however, the lower molar structure of *Ghamidtherium dimaiensis* is quite different from that of other Paleogene Afro-Arabian bats, and bears little similarity to that of any member of the most diverse Paleogene Afro-Arabian chiropteran community described thus far (Taqah; SIGÉ et al. 1994). A more comprehensive comparison of these specimens with bats and marsupials could examine the angle shown by the trigonid cusps and its relation to the rest of the molar series.

Enamel microstructure

A single layer of radial enamel represents the plesiomorphic therian condition. It characterizes the teeth of basal Paleogene placentals as well as most Paleogene to modern lipotyphlans and chiropterans and is very widespread among marsupials (LESTER & HAND 1987; LESTER et al. 1988; KOENIGSWALD 1988, 1997; KOENIGSWALD et al. 1987). Above the size of a European hedgehog (*Erinaceus europaeus*), the molars of most placentals are characterized by decussating layers of prisms, the HUNTER-SCHREGER bands (HSB). HSB represent an adaptation to strengthen the enamel against increased chewing stresses and to prevent crack propagation (VON KOENIGSWALD et al. 1987; PFRETZSCHNER 1988). In contrast to the placentals, HSB are rare among marsupials and have only been recorded in borhyaenids and vombatids (VON KOENIGSWALD 1988, 1994; FERREIRA et al. 1989). In marsupials, other derived enamel types such as striped enamel and zipper enamel (VON KOENIGSWALD & GOIN 2000) were developed to strengthen the enamel that do not occur in placentals. Nevertheless, radial enamel is the dominant enamel type in marsupials, and even the molars of the rhinoceros-sized herbivore *Diprotodon* consist almost entirely of this enamel type (VON KOENIGSWALD 1994). In the molars of the much smaller placental *Erinaceus*, on the other hand, already incipient HSB are present (VON KOENIGSWALD 1997). LESTER & HAND (1987) and LESTER et al. (1988) have studied chiropteran enamel in great detail at the prism level, but did not refer to the enamel types. According to the figures and observations by VON KOENIGSWALD (1997), chiropteran enamel consists of a single layer of plesiomorphic radial enamel with the IPM mainly oriented parallel to the prisms. LESTER & HAND (1987) and LESTER et al. (1988) quoted horse-shoe shaped prism cross sections as typical for chiropterans. The presence of horse-shoe like prism cross sections in DPC 22442D might be valued as a chiropteran character. However, according to VON KOENIGSWALD & CLEMENS (1992), prism cross sections can be highly variable and the shape of the prism cross sec-

tion often changes in the course of the prism from the EDJ to the OES. The 20–30° angle between prism long axes and IPM, on the other hand, advocates for an attribution of DPC 22442D to Marsupialia rather than to Chiroptera. VON KOENIGSWALD & GOIN (2000: 141) observed angles of up to 45° between IPM and prisms in Paleogene peradectids, didelphimorphs and microbiotheriids, whereas in chiropterans there is apparently no or only a minor angle. With its plesiomorphic enamel condition, the attribution of DPC 22442D to either Marsupialia or Chiroptera remains ambiguous.

Taxonomic affinities of isolated upper molars

Of all available taxonomic options, it appears that the second taxon, represented only by upper molars) in the sample is either a marsupial with some bat-like dental features, or a bat with marsupial-like dental features. It can be referred to but not diagnosed as Marsupialia. Marsupial features of these upper molars include the absence of a hypocone (although DPC 21372A could be interpreted as having a hypocone swelling on the postcingulum), presence of a stylar cusp C, the relatively low paracone, and the moderately slender lingual portion of the upper molars. Many bats also have reduced (or absent) conules and a V-shaped centrocrista (SIGÉ 1991; HOOKER & WEIDMANN 2000), but do not otherwise present the suite of characters observable in these upper molars (SIGÉ 1985: fig. 3). DPC 21372A and DPC 21372B differ dramatically from Afro-Arabian Paleogene bats such as *Philisis* in being much less dilambdodont, in having mesiodistally broad trigons that are closed distally and pre- and postprotocristae that join the bases of the para- and metacones respectively. In all Paleogene Afro-Arabian and Laurasian bats that we have examined, the preprotocrista bypasses the paracone to connect with the parastylar region, and the postprotocrista ends before reaching the metacone, leaving the trigon basin open posteriorly (see, e.g., RUSSELL & SAVAGE 1973; HOOKER 2001). The BQ-2 upper molar described here (especially DPC 21372B) also have a more centrally placed protocone than other Paleogene Afro-Arabian bats. However, many modern Old World bat taxa do have strong postprotocristae closing off the trigon posteriorly. The BQ-2 upper molars differ from placentals that have marsupial-like molars, such as adapisoriculids (GHEERBRANT 1991, 1995), in the reduction of the paracone, relatively shorter preparacrista lacking a carnassial notch, reduced conules (STORCH & QIU 2002), and the presence of a V-shaped centrocrista (although the latter is present in *Remiculus*, *Adapisoriculus*, *Garatherium*, and *Wyonycteris*, GHEERBRANT 1991, 1995; SMITH 1995). The relatively large cingulum distal to the protocone of DPC 21372A and DPC 21372B is missing in most adapisoriculids (*Remiculus* has a postcingulum although it does not join the metacingulum) (GHEERBRANT 1991, 1995; GHEERBRANT & RUSSELL 1991).

The difficulty in assigning isolated dilambdodont molars to Marsupialia, Chiroptera, or some other taxon is exemplified by the taxonomic history of fossil marsupials reported from northern Africa. The first discovery of an extinct Afro-Arabian marsupial was from the early Oligocene of Egypt (*Peratherium africanum*; BOWN & SIMONS 1984). CROCHET (1984) described *Garatherium mahboubii* from the early Eocene of Algeria (see also MAHBOUBI et al. 1986), but the marsupial affinities of this species were contested by GHEERBRANT (1995), who placed *G. mahboubii* in the Adapisoriculidae, a group of enigmatic early Palaeogene placentals known entirely from dental remains (GHEERBRANT 1991). MCKENNA & BELL (1997) classified *Garatherium* within the Herpetotheriinae, a subgroup of the paraphyletic "Didelphidae" assemblage currently being used by most marsupial taxonomists working on isolated teeth from the Palaeogene of Laurasia and Africa (GOIN 1993). KIRSCH et al. (1997) presented a classification in which Herpetotheriidae was placed incertae sedis within "Didelphimorphia". The genus *Qatranitherium* was erected by CROCHET et al. (1992) to include a lower deciduous tooth (referred to dP3) from the late Eocene or early Oligocene of Oman as well as the *P. africanum* material described by BOWN & SIMONS (1984; but see HOOKER et al. in press). The only other Palaeogene African marsupial is early Eocene *Kasserinotherium tunisiense*, which is known by two upper molars recovered from Chambi in Tunisia; this species was referred to the Peradectinae by CROCHET (1986).

Afro-Arabian marsupials are poorly known. We conservatively place the new species in the paraphyletic group "Didelphimorphia" with a query, following the taxonomic use of some authors (KIRSCH et al. 1997), for lack of a better option. The presence of marsupials in Africa is significant, as it indicates faunal exchange with other continents (most likely Europe), because marsupials appear to have originated in Asia or North America and only later dispersed to Europe, South America, Antarctica, Australia, and Afro-Arabia (CIFELLI 1993; ROUGIER et al. 1998). The early Palaeogene Afro-Arabian mammal fauna is generally thought to be a mix of endemic afrotherians combined with a more limited component of immigrants from Europe and Asia. However, even the notoriously poor early–middle Eocene record of African mammal evolution has now produced scanty remains of anthropoid (GODINOT & MAHBOUBI 1992) and stem strepsirrhine (HARTENBERGER & MARANDAT 1992) primates, possible plesiadapiforms (TABUCE et al. 2004), zegdoumyid rodents (VIANEY-LIAUD et al. 1994), as well as marsupials (CROCHET 1986), all of which attest to a significant amount of trans-Tethyan dispersal from Europe and/or Asia into Afro-Arabia. GOIN & CANDELA (2004) pointed out several similarities between the Paleogene marsupial from Peru *Rumiodon inti* and European Herpetotheriidae, and more significantly, between the Peruvian *Wirunodon chanku* and *Kasserinotherium tunisiense*, a peradectid

marsupial (CROCHET 1986) from the lower Eocene of Tunisia. The systematic (and with it, the palaeobiogeographic) significance of such similarities remains to be tested. As the enigmatic fossils described here do not show clear affinities with other Afro-Arabian marsupials, they may provide additional evidence for dispersal into Afro-Arabia. In the absence of more complete fossil evidence, the ancestral source area for this mammalian lineage will, however, remain open.

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