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The oldest and youngest records of afrosoricid placentals from the Fayum Depression of northern Egypt

ERIK R. SEIFFERT



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Tenrecs (Tenrecoidea) and golden moles (Chrysochloroidea) are among the most enigmatic mammals alive today. Molecular data strongly support their inclusion in the morphologically diverse clade Afrotheria, and suggest that the two lineages split near the K-T boundary, but the only undoubted fossil representatives of each superfamily are from early Miocene (~20 Ma) deposits in East Africa. A recent analysis of partial mandibles and maxillae of *Eochrysochloris*, *Jawharia*, and *Widanelfarasia*, from the latest Eocene and earliest Oligocene of Egypt, led to the suggestion that the derived “zalambdomorph” molar occlusal pattern (i.e., extreme reduction or loss of upper molar metacones and lower molar talonids) seen in tenrecoids and chrysochloroids evolved independently in the two lineages, and that tenrecoids might be derived from a dilambdomorph group of “insectivoran-grade” placentals that includes forms such as *Widanelfarasia*. Here I describe the oldest afrosoricid from the Fayum region, ~37 Ma *Dilambdogale gheerbranti* gen. et sp. nov., and the youngest, ~30 Ma *Qatranilestes oligocaenus* gen. et sp. nov. *Dilambdogale* is the most generalized of the Fayum afrosoricids, exhibiting relatively broad and well-developed molar talonids and a dilambdomorph arrangement of the buccal crests on the upper molars, whereas *Qatranilestes* is the most derived in showing relatively extreme reduction of molar talonids. These occurrences are consistent with a scenario in which features of the zalambdomorph occlusal complex were acquired independently and gradually through the later Paleogene. Phylogenetic analysis places *Dilambdogale* and *Widanelfarasia* as sister taxa to the exclusion of crown afrosoricids, but derived features that these taxa share with early Miocene *Protenrec* hint at the possibility that both taxa might be stem tenrecoids. Late Paleocene *Todralestes* and *Afrodon* from Morocco are similarly placed as stem afrosoricids, indicating that African adapisoriculids (including *Garatherium*) might also be relevant to the origin of the tenrecoid and chrysochloroid clades.

Key words: Mammalia, Adapisoriculidae, Tenrecidae, *Garatherium*, *Widanelfarasia*, Eocene, Oligocene, Egypt.

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Introduction

Paleocene and Eocene mammals of Afro-Arabia are very poorly documented relative to those of other major landmasses. Among the more rarely recovered members of Paleogene African mammal faunas are a variety of diminutive insectivorous placentals—generally represented solely by isolated teeth—that were originally placed in higher-level taxa such as Cimolesta and Lipotyphla, and the families Adapisoriculidae, Chambilestidae, Cimolestidae, Palaeoryctidae, and Todralestidae (e.g., Gheerbrant 1992, 1994, 1995; Gheerbrant et al. 1998). Lipotyphla are now widely considered to be diphyletic on the basis of nucleotide and other genomic data (Springer et al. 1997; Madsen et al. 2001; Murphy et al. 2001; Amrine-Madsen et al. 2003; Asher et al. 2003; Springer et al. 2004; Asher and Hofreiter 2006; Seiffert 2007; Asher 2007), and two former members of that group—the Afro-Malagasy tenrecs (herein treated together

as a superfamily, Tenrecoidea, containing a monophyletic Potamogalidae (African otter-shrews) and Tenrecidae (Malagasy tenrecoids); see Asher and Helgen 2010, for an alternative classification, and African golden moles (Chrysochloroidea, Chrysochloridae) have come to be placed in their own order, Afrosoricida, within a larger endemic African clade, Afrotheria (Stanhope et al. 1998), that also includes elephants, sea cows, hyraxes, aardvarks, and sengis (Fig. 1). Molecular divergence estimates suggest that crown afrosoricids last shared a common ancestor in the latest Cretaceous or Paleocene (Douady and Douzery 2003; Springer et al. 2003), opening up the possibility that afrosoricid origins might be traced back to some of the poorly known “cimolestean” and/or “lipotyphlan” fossils that have been recovered from the Paleocene and Eocene of North Africa (Seiffert 2010).

At present there is, however, no unambiguous fossil evidence for this hypothesis. The crux of the issue is that all ex-

tant afrosoricids have a “zalambdomorph”^{*} occlusal pattern on their molars—i.e., a condition in which upper molar metacones and lower molar talonids are greatly reduced or absent altogether (see also Asher and Sanchez-Villagra 2005). Optimization of zalambdomorphy onto a cladogram of extant placentals alone (e.g., Springer et al. 2004) would reconstruct this dental pattern as having been present in the last common ancestor of tenrecs and golden moles (Fig. 1). If this ancestor was in fact ~66–63 Ma in age as estimated by molecular sequence data—and if Afrosoricida is indeed an endemic African clade—then zalambdodomorph fossil afrosoricids should have been present in Afro-Arabia during the time periods for which there is paleontological coverage on that landmass (i.e., latest Paleocene, early Eocene, early middle Eocene, late Eocene, and early Oligocene). Zalambdomorph species, are, however, completely absent from Afro-Arabian mammal faunas of these time periods (Seiffert 2010) suggesting that either (i) afrosoricids were not present in Afro-Arabia during the Paleogene, (ii) zalambdomorph afrosoricids were present in Afro-Arabia during the Paleogene, but not in the areas that have been sampled thus far, (iii) tenrecs and golden moles diverged much later (e.g., in the Oligocene) than suggested by molecular data, or (iv) zalambdodomorphy was not present in the last common ancestor of tenrecs and golden moles, and evolved convergently later in the Paleogene.

There is now a small but growing body of fossil evidence that has been interpreted by Seiffert et al. (2007) as supporting the latter scenario. The oldest definitive euzalambdomorph tenrecoids and chrysochlorids (i.e., forms that completely lack upper molar metacones) are from the early Miocene of Kenya and Uganda (Butler and Hopwood 1957; Butler 1969, 1984), but Seiffert et al. (2007) have recently identified tribosphenic latest Eocene (~34 Ma; Seiffert 2006; Seiffert et al. 2007) *Widanelfarasia* and early Oligocene *Jawharia* as stem tenrecoids, and early Oligocene *Eochrysochloris* as a stem chrysochlorid (see Fig. 2). Because these genera all retain well-developed molar metacones and/or lower molar talonid basins, these identifications would require that euzalambdomorphy evolved convergently within Afrosoricida. In particular, *Widanelfarasia*’s combination of a dilambdomorph M1 and protozalambdomorph M2–3 would suggest that the stem lineage leading to crown Tenrecoidea either passed through a dilambdodomorph phase prior to acquisition of zalambdomorphy, or that *Widanelfarasia*’s dilambdomorphy is autapomorphic. Furthermore, it has long been known that the extant potamogalid tenrecoid *Pota-*

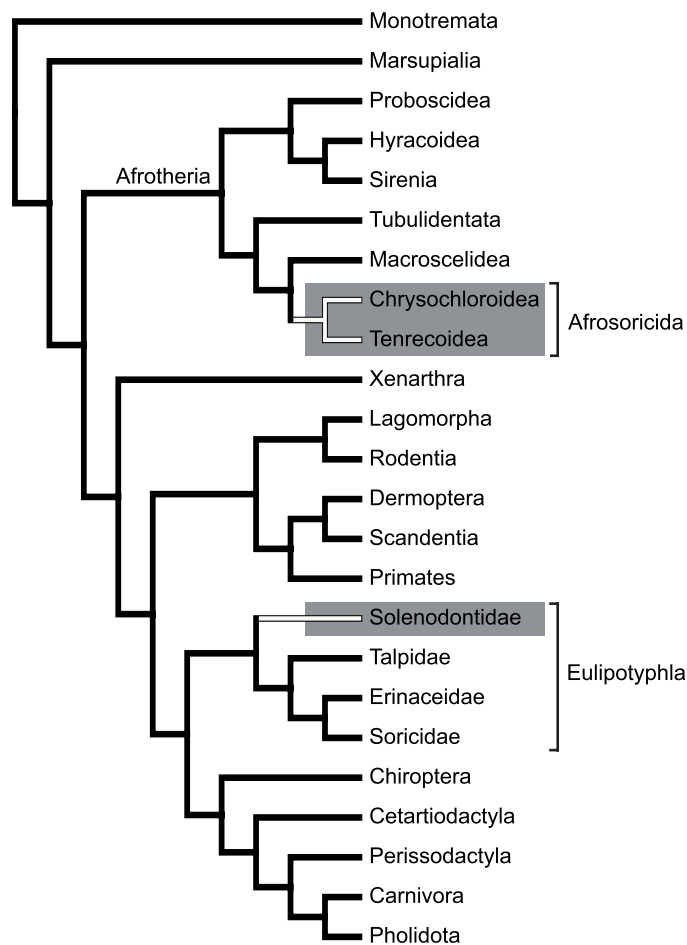


Fig. 1. Relationships of extant placental mammalian orders, based on the analysis of Roca et al. (2004), with zalambdomorph groups (Afrosoricida and Solenodontidae) highlighted.

mogale is protozalambdomorph (McDowell 1958; Butler 1972, 1988), lending additional support to the hypothesis that this condition might be plesiomorphic within Afrosoricida. Alternatively, this condition is simply an autapomorphy of *Potamogale*; this possibility is supported by the observation that the molar metacones of *Potamogale*’s sister taxon, the smaller genus *Micropotamogale*, vary from being very reduced to absent.

Here I present additional evidence that contributes to the debate surrounding the homology of zalambdomorphy in tenrecs and golden moles. Recent work at the earliest Priabonian (earliest late Eocene, ~37 Ma) Birket Qarun locality 2 (or BQ-2) has led to the recovery of the oldest Fayum afro-

^{*} In what follows I employ the terminology recently proposed by Lopatin (2006), which is useful for distinguishing important differences between taxa that have been termed “zalambdodont” and “dilambdodont” (Gill 1883). The broad category of “zalambdomorphy” is defined by Lopatin (2006: S215) as follows: “the trigon of the upper molars is formed by a large lingually located paracone, a paracrista that is V-shaped in projection, and styles; the metacone and protocone are considerably reduced or absent, the conules are absent ... in this pattern, the lower molars are characterized by reduced talonids and excessively developed trigonids, including the formation of the oblique paracristid and a very high and broad transverse protocristid”. “Euzalambdomorphy”, which is present in most extant afrosoricids, is described as “complete loss of the metacone and protocone, the lingual displacement of the paracone to the position of the protocone, excessive development of the stylar shelf, and appearance of supplementary cingular elements ... the talonid is extremely reduced and resembles a postcingulid” (Lopatin 2006: S215) while in “protozalambdomorphy”, which occurs in extant *Potamogale* and early Miocene *Protenrec*, “the metacone is considerably reduced (however, its rudiment is preserved between a shortened centrocrista and postmetacrista), the paracone is displaced to the center, the protocone and talonid are reduced” (Lopatin 2006: S215).

soricids, including a new genus described below that is evidently even more generalized than *Widanelfarasia*, and that appears to document an even more primitive dilambdomorph phase in either stem afrosoricid or stem tenrecoid evolution. The material also provides a clearer look at the upper molar and P4 morphology of a primitive afrosoricid, previously known solely from 3-D reconstructions derived from micro-CT scans of a damaged *Widanelfarasia* maxilla (Seiffert et al. 2007). A distal humerus from BQ-2 is also attributed to the new genus described here, providing the first look at one aspect of postcranial morphology in this poorly documented evolutionary radiation. In addition, less informative tenrecoid fossils that were collected in the 1960s at one of the youngest vertebrate fossil localities in the Fayum area (~29.5–30 Ma Quarry I; Fig. 2) have recently been relocated in the collections of the Yale Peabody Museum, and these specimens are described, named, and figured here for the first time. Though fragmentary, it is clear that the Quarry I fossils more closely approximate the euzalambdomorph condition than any of the older afrosoricids from the succession, and provide support for gradual acquisition of zalambdomorphy through the later Paleogene.

Institutional abbreviations.—CGM, Egyptian Geological Museum, Cairo, Egypt; DPC, Duke Lemur Center Division of Fossil Primates, Durham, North Carolina, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Systematic paleontology

Supercohort Afrotheria Stanhope, Waddell, Madsen, de Jong, Hedges, Cleven, Kao, and Springer, 1998

Order Afrosoricida Stanhope, Waddell, Madsen, de Jong, Hedges, Cleven, Kao, and Springer, 1998

Suborder ?Tenrecomorpha Butler, 1972

Genus *Dilambdogale* nov.

Type species: *Dilambdogale gheerbranti* sp. nov., see below.

Etymology: From Greek *di*, two and *lambda*, eleventh letter of the Greek alphabet (L)—in reference to the dilambdomorph arrangement of the buccal crests on the genus' first upper molar; and *gale*, weasel—a common suffix in generic names of extant tenrecoids.

Diagnosis.—Same as for the species.

Dilambdogale gheerbranti sp. nov.

Figs. 3–7.

Etymology: In honor of the French paleontologist Emmanuel Gheerbrant, for his numerous contributions to the study of Paleogene Afro-Arabian placental mammals, including “insectivoran-grade” placentals.

Holotype: CGM 66005, a maxillary fragment preserving the distal alveolus for P3, the crowns of P4 and M1, the mesiobuccal root of M2, and the infraorbital foramen (Fig. 3).

Type locality: Birket Qarun locality 2 (BQ-2), northern Egypt.

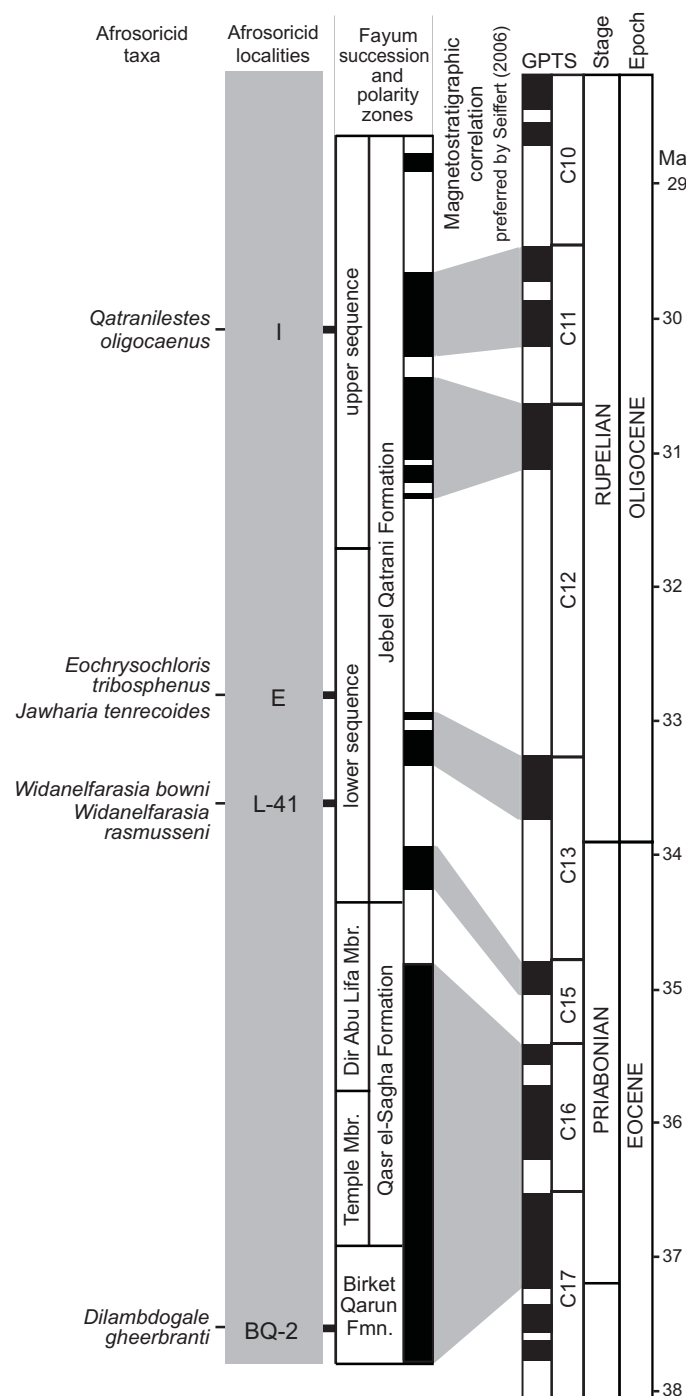


Fig. 2. Stratigraphic placement of afrosoricid-bearing localities in the later Paleogene rocks exposed in the Fayum area, and proposed correlation of local polarity zones to the Geomagnetic Polarity Timescale (GPTS), following Seiffert (2006) and Seiffert et al. (2008). Locality BQ-2, which yielded the remains of *Dilambdogale gheerbranti* described here, is estimated to be ~37 Ma; Quarry I, which produced remains of *Qatranilestes oligocaenus*, is estimated to be ~29.5–30 Ma.

Type horizon: Earliest Priabonian (earliest late Eocene), Umm Rigi Member of Birket Qarun Formation.

Material.—The type specimen; DPC 23306E, left M2; DPC 23307A, right M3; DPC 23007H, left m2; DPC 23736A, right mandibular fragment with m1 and talonid of p4; DPC

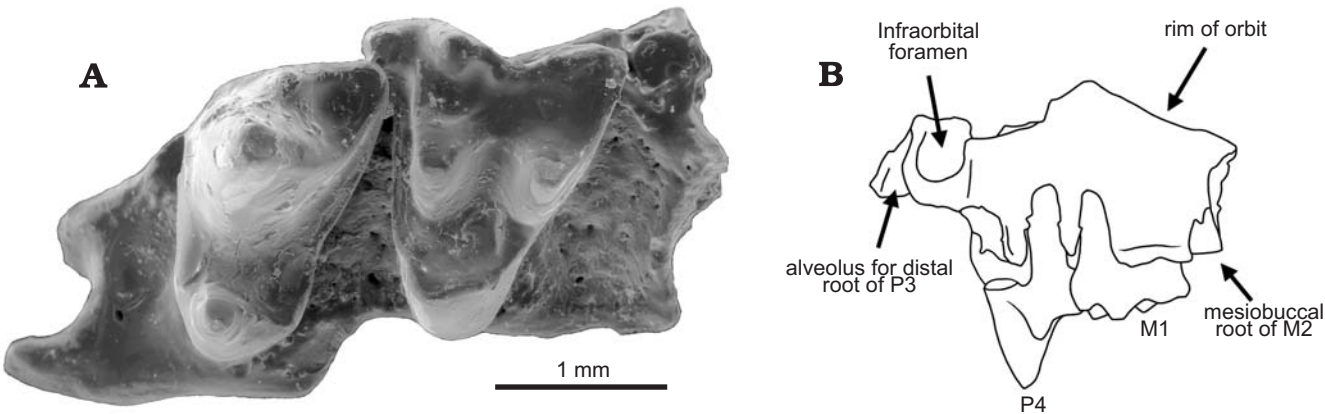


Fig. 3. Holotype maxilla of the afrosoricid placental *Dilambdogale gheerbranti* gen. et sp. nov., from the earliest late Eocene (earliest Priabonian) locality BQ-2, Birket Qarun Formation, Fayum Depression, northern Egypt. **A.** Occlusal view of CGM 66005, left maxillary fragment preserving the alveolus for the distal root of P3, crowns of P4–M1, and partial alveoli for the mesiobuccal and lingual roots of M2. **B.** Line drawing of CGM 66005 in lateral view, showing the position of the infraorbital foramen and the orbital rim.

23780C, left m2; DPC 23784D, right M1; DPC 23983C, right mandibular fragment with p4–m1; DPC 24001A, left P4; DPC 24081B, right mandibular fragment with p2–4; DPC 24103A, right mandibular fragment with m1–3; uncatalogued specimens at the CGM.

Diagnosis.—Differs from Miocene-to-Recent tenrecoids primarily in retaining a well-developed metacone and protocone on M1–3, small conules on M1–2, a cusate (rather than crestiform) stylocone on M1–3, and well-developed talonid and hypoconulid cusps on the lower molars. Further differs from tenrecoids other than *Protenrec* in having the distal root of P3 placed lingual to the mesiobuccal root of P4. Differs from *Widanelfarasia* in having a relatively well-developed P4 ectostyle; a shorter postmetacrista on M1; well-developed and cusate (rather than crestiform) metacone, stylocone, and parastyle on M3; a cusate, rather than crestiform, stylocone on M2; and in having an m1 with a relatively broad talonid and more buccally placed cristid obliqua, delimiting a relatively poorly-developed hypoflexid. Differs from late Paleocene *Todralestes* in having a “w”-shaped arrangement of the buccal crests on M1–2, relatively broad stylar shelves, no pre- or postcingula on M1–3, and a P4 ectostyle, -crista, and -fossa. Differs from late Paleocene *Afrodon chleuhi* in having a dilambdodont M2, relatively broad stylar shelves, and slightly taller molar trigonids. Differs from *?Garatherium todrae* (known only from upper molars) in lacking distinct upper molar premetaconule cristae and postpara- and premetacristae that contact the mesostyle buccally.

Description.—The dental morphology of *D. gheerbranti* is known from four upper tooth loci (P4, M1, M2, M3) and six lower tooth loci (p2, p3, p4, m1, m2, m3) (Figs. 3–6). Measurements for upper and lower teeth are provided in Table 1 and Table 2, respectively. The holotype partial maxilla (CGM 66005, Fig. 3) contains P4–M1 and preserves the infraorbital foramen, the alveolus for the distal root of P3, and the mesial halves of the lingual and mesiobuccal alveoli for M2; P4, M1, M2, and M3 are also known from isolated

Table 1. Measurements (in mm) of upper teeth of *Dilambdogale gheerbranti* gen. et sp. nov. BL, buccolingual breadth; MD, mesiodistal length.

Specimen	Locus	Maximum MD length [“Lab” in Gheerbrant (1992)]	Mesial BL width [“IM” in Gheerbrant (1992)]	Distal BL width [“ID” in Gheerbrant (1992)]	Width from base of paracone to protocone apex [“Iproto” in Gheerbrant (1992)]	MD length of trigon [“Lmd” in Gheerbrant (1992)]
DPC 23306E	M2	1.75	2.25	2.15	0.30	0.90
DPC 23307A	M3	1.13	2.50	1.55	0.35	0.80
DPC 23780C	M2	1.58	2.28	2.28	0.20	0.88
DPC 24001A	P4		1.70			
DPC 27784D	M1	1.58	2.05	2.05	0.25	0.90
CGM 66005	P4		1.75			
CGM 66005	M1	1.58	1.95	1.95	0.25	0.83

Table 2. Measurements (in mm) of lower teeth of *Dilambdogale gheerbranti* gen. et sp. nov. MD, mesiodistal length.

Specimen	Locus	MD length	Trigonid width	Talonid width
DPC 23307H	M2	1.70	0.98	0.90
DPC 23736A	M1	1.60	0.95	0.95
DPC 23783B	M2	1.60	1.03	0.85
DPC 23783B	M3	1.63	1.03	0.80
DPC 23983C	P4	1.60	0.85	
DPC 23983C	M1	1.53	0.90	
DPC 24081B	P2	1.20	0.50	
DPC 24081B	P3	0.83	0.60	
DPC 24081B	P4		0.80	
DPC 24103A	M1	1.50	1.00	0.93
DPC 24103A	M2	1.60	1.05	0.93
DPC 24103A	M3	1.53	0.90	0.75

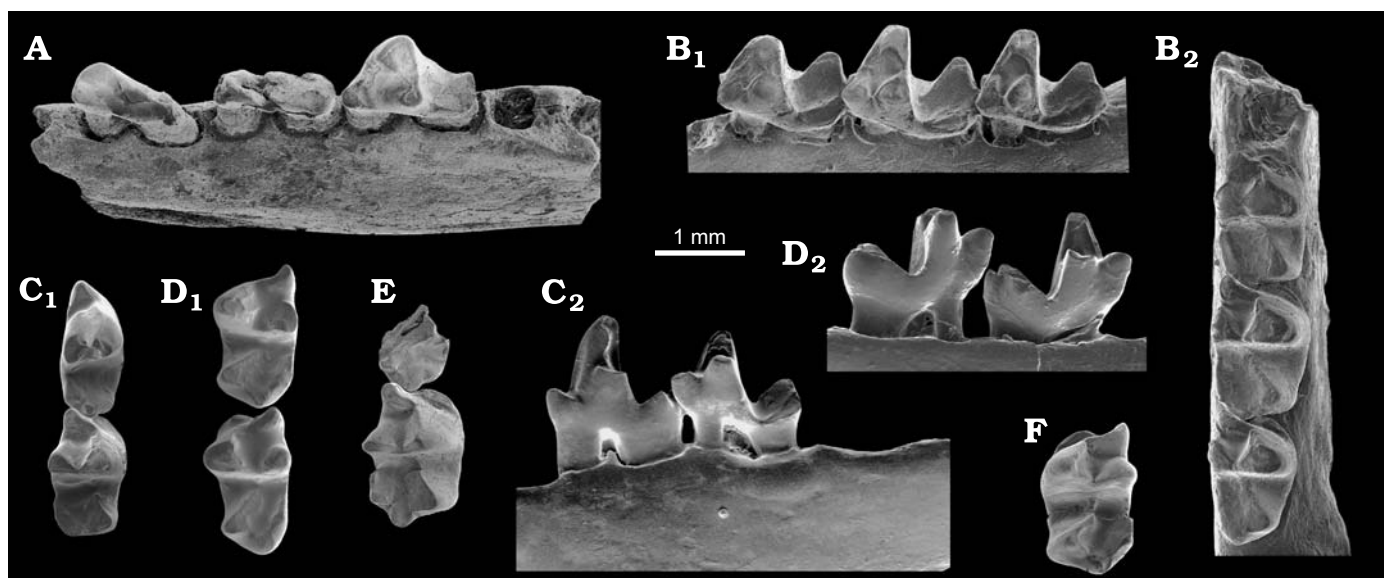


Fig. 4. Lower dentition of the afrosoricid placental *Dilambdogale gheerbranti* gen. et sp. nov. from the earliest late Eocene (earliest Priabonian) locality BQ-2, Birket Qarun Formation, Fayum Depression, northern Egypt. **A.** Oblique lingual view of DPC 24081B, a right mandibular fragment preserving the alveolus for the lower canine and the crowns of p2–4. **B.** DPC 24103A, right mandibular fragment preserving the worn crowns of m1–3 in oblique lingual (**B₁**) and occlusal (**B₂**) views. **C.** DPC 23983C, a right mandibular fragment preserving p4–m1 in occlusal (**C₁**) and lingual (**C₂**) views. **D.** DPC 23783B, a left mandibular fragment preserving m2–3 in occlusal (**D₁**) and lingual (**D₂**) views. **E.** Occlusal view of DPC 23736A, a right mandibular fragment preserving the talonid of p4 and the complete crown of m1. **F.** DPC 23307H, a left m2 in occlusal view.

teeth (Fig. 6). Partial mandibles together preserve p2–m3 in place (Figs. 4, 5), and most of these loci are also known from isolated teeth (Table 1). Though found in isolation, the M2–3 are assigned to this species because (i) they are of similar size to, and occlude well with, the m2–3 in the hypodigm, and (ii) they bear a strong resemblance to the upper teeth of younger *Widanelfarasia*, P2–M3 of which are preserved in place in a single maxilla (Seiffert et al. 2007).

A partial alveolus that is preserved mesial to the double-rooted p2 (Fig. 4A) is relatively large, and, as in *Widanelfarasia*, was presumably for the lower canine. If this interpretation is correct, then (d)p1 was absent in *Dilambdogale*, as in *Widanelfarasia* and all extant afrosoricids (Seiffert and Simons 2000). The p3 and p4 both bear tall protoconids; that of p3 is mesially inclined, and has a long postprotocristid on its gradually sloping distal face. There is a tiny paraconid at the base of the p3 protoconid which is slightly lingual to the

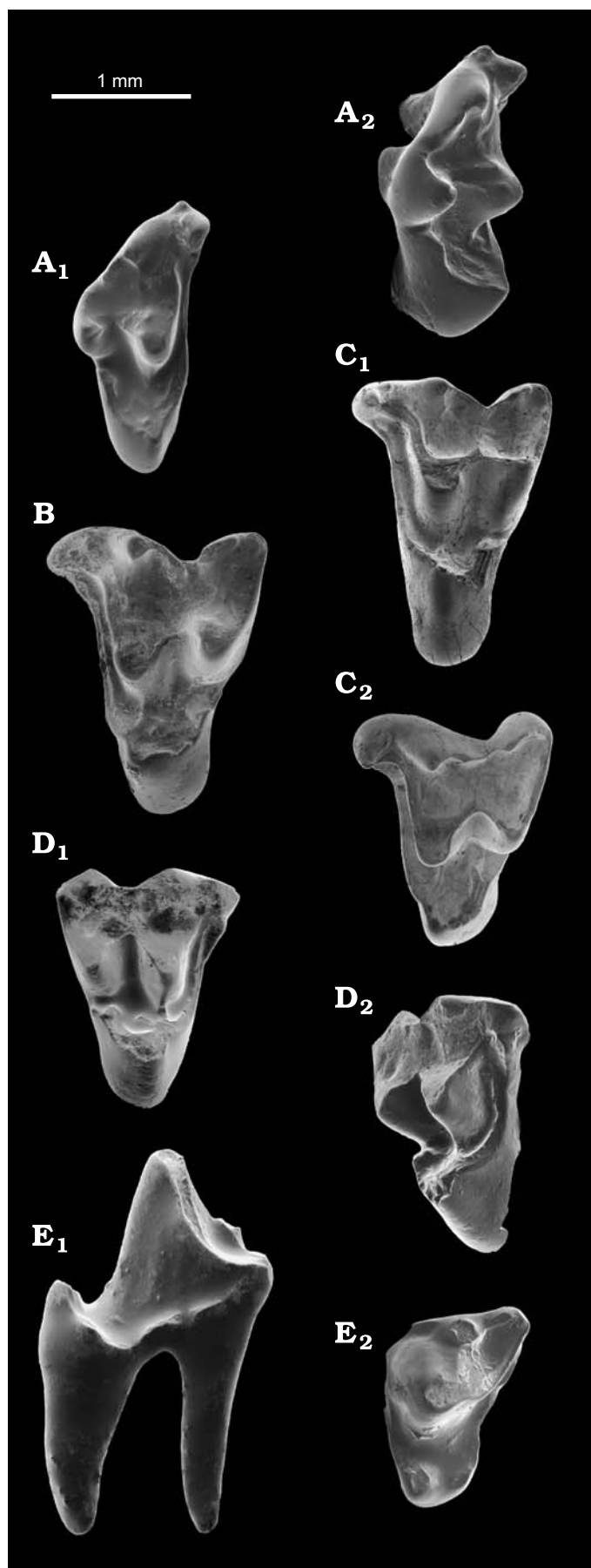
mesiodistal long axis of the tooth, and a larger hypoconid that is present at the distal terminus of the postprotocristid. There is a very faint and short lingual cingulum just distal to the paraconid, but it does not continue across the rest of the crown. The base of the crown is somewhat staggered with respect to the alveolar plane; the distal aspect of the crown base, above the distal root, extends closer to the alveolar plane than the mesial part of the crown base.

The p4 also has a small paraconid at the base of the protoconid (Fig. 4A, C); this cusp is relatively large and robust when compared with the p3 paraconid, but is nevertheless still very small in comparison to the tall p4 protoconid (Fig. 4C₂). The metaconid is approximately half the height of the protoconid (Fig. 4C₂), and is placed lingual, and slightly distal, to that cusp (Fig. 4C). A faint protocristid extends from the protoconid to the metaconid. Distinct and closely situated entoconid and hypoconid cusps are present on the lingual aspect of the talonid, with the hypoconid being slightly larger than the entoconid. There are very faint entocristid and hypocristid crests, but no cristid obliqua, and the p4 hypoflexid is deep. There are no lingual or buccal cingulids.

On m1 (Fig. 4B, C, E), the paraconid is large, mesially oriented, and is placed slightly buccal and far mesial to the metaconid. There is no premetacristid descending mesially from the metaconid, leaving the trigonid broadly open lingually. The paraconid is connected to the protoconid by an elongate paracristid that bears a distinct notch along its midpoint. The protocristid connecting the metaconid and protoconid varies from being perpendicular to the long axis of the tooth, to being slightly oblique. The metaconid is slightly



Fig. 5. Buccal view of DPC 23783B, a left mandibular fragment of the afrosoricid placental *Dilambdogale gheerbranti* gen. et sp. nov., from the earliest late Eocene (earliest Priabonian) locality BQ-2, Birket Qarun Formation, Fayum Depression, northern Egypt, preserving m2–3.



lower than the protoconid. The talonid is preserved on DPC 23736A (Fig. 4E); the basin is subequal in width to the trigonid, has a relatively shallow hypoflexid, and distinct entoconid, hypoconid, and hypoconulid cusps, the latter of which projects distally. The cristid obliqua meets the posterior wall of the trigonid slightly buccal to its midpoint. The m2–3 (Fig. 4B, D) differ from m1 in having oblique cristids that terminate midway between the protoconid and metaconid cusps, protocristids that are consistently transversely oriented, and relatively deep hypoflexids. All lower molars have talonids that are slightly longer than trigonids, oblique cristids and hypocristids that meet at a sharp angle, and distinct precingulids.

The mesiobuccal aspect of P4 is missing on all of the specimens that have been recovered thus far, but the alveolus for the mesiobuccal root is placed mesial to the preserved part of the crown, suggesting that *Dilambdogale* probably had a prominent parastyle on P4, as has been documented for *Todralestes* (Gheerbrant 1991b) and *Widanelfarasia* (Seiffert et al. 2007). The P4 bears a tall paracone cusp and a very small and mesially placed protocone. Like many crown tenrecoids, *Dilambdogale* also has a distinct ectostyle cusp distal and buccal to the apex of the paracone. DPC 24001A has a very faint ectocrista descending from the buccal face of the paracone to meet the ectostyle. Together with the elongate postparacrista, these structures delimit a shallow distolabial ectofossa. The P4 has no conules and no pre- and postcingula, but a tiny crestiform hypocone is present, and is connected to the protocone by a weak postprotocrista. Though the parastylar region is missing, it is clear that it would have protruded from a very low point on the mesial face of the paracone.

A relatively unworn M1 is present in the holotype specimen (Fig. 3). This locus is also represented by an isolated tooth with a more worn stylar region (DPC 23784D; Fig. 6D). The M1 resembles *Widanelfarasia* in having a “W”-shaped arrangement of the pre- and postparacristae and pre- and postmetacristae. In mesial and distal view, the paracone, metacone, and protocone are approximately equal in height. The paracone and metacone show some “fusion” of their bases. The stylar region of the M1 in the holotype specimen exhibits some wear, but it is clear that the stylocone would have been the largest and tallest cusp on the buccal aspect of the tooth, followed by the parastyle. It appears that there was also a very small mesostyle at the trough of the ectoflexus, and a similarly small cusp “D” on the periphery of the metastylar lobe. This interpretation is supported by the clear presence of these cusps on M2 (see below). The trigon is restricted due to encroachment of the centrally placed para- and metacone and is bor-

Fig. 6. Upper dentition of the afrosoricid placental *Dilambdogale gheerbranti* gen. et sp. nov. from the earliest late Eocene (earliest Priabonian) locality BQ-2, Birket Qarun Formation, Fayum Depression, northern Egypt. A. DPC 23307A, right M3, in occlusal (A₁) and distal (A₂) views. B. DPC 23306E, left M2, in occlusal view. C. DPC 23780C, left M2, in occlusal (C₁) and buccal (C₂) views. D. DPC 23784D, right M1, in occlusal (D₁) and mesial (D₂) views. E. DPC 24001A, left P4, in distal (E₁) and occlusal (E₂) views.

dered lingually by distinct pre- and postprotocristae. A small, lingually-placed paraconule is present and bears a postparaconule crista on DPC 23784D but not on CGM 66005; the preprotocrista bypasses the lingual aspect of the paracone and is continuous with the parastylar area. There is a short but distinct hypoparacrasta that connects the paraconule and the lingual face of the paracone on DPC 23784D, but this is absent on the holotype specimen. A small metaconule is present but is more buccally placed than the paraconule. A distolabially oriented postmetaconule crista leaves the trigon open distally on DPC 23784D, but this crest is not present on CGM 66005. There is no premetaconule crista, and no pre- or postcingula, on either specimen.

M2 is represented by two isolated specimens (DPC 23306E, Fig. 6B; DPC 23780C, Fig. 6C). The M2 is much broader (buccolingually) than M1. Of the two primary buccal cusps, the paracone is closest to the protocone (and is placed farther from the buccal margin than is the metacone). In lingual and buccal view, the paracone is taller than the metacone (Fig. 6C₂). When compared with M1, the protocone is relatively prominent, but the trigon is more constricted mesiodistally. The styler shelf bears a tall and distinct stylocone and a much smaller mesostyle and cusp “D” (Fig. 6C₂). The parastyle is prominent, and the parastylar lobe forms a prominent mesial “hook” which, based on the placement of the mesiobuccal root of M2 implanted in the holotype partial maxilla, would have curved around the buccal aspect of the metastylar lobe of M1, as in *Widanelfarasia* (Seiffert et al. 2007). A paraconule is not evident on DPC 23780C, but is present, though minute, on DPC 23306E; on the latter specimen the paraconule is connected to the base of the paracone by a short postparaconule crista. As on M1, the paraconule is situated closer to the protocone than is the metaconule, there is no premetaconule crista, and there are no pre- or postcingula.

M3 (represented solely by DPC 23307A, Fig. 6A) has well-developed paracone and metacone cusps, the postpara- and premetacristsae of which are slightly buccally oriented in a weakly “W”-shaped arrangement. The metacone is smaller than the paracone, both in height and in volume. The postmetacrasta is buccally (rather than distally) oriented and is continuous with the buccal aspect of a very broad styler shelf. The stylocone and parastyle are distinct and well-developed, and, at least on DPC 23307A, an accessory cuspule is present on the buccal face of the tooth just distal and labial to the parastyle. A crestiform metaconule is present but no paraconule is evident, perhaps due to wear. It is clear that there is no postparaconule crista and no pre- or postcingula.

Various fragments of the mandibular corpus are preserved (see, e.g., Figs. 4A, B, 5). The corpus is fairly shallow, being only slightly taller than trigonid height, and bears a mental foramen below m1 (Fig. 5) and p2. Little is preserved of the distal part of the mandible but the anterior part of the masseteric fossa appears to have been well-developed.

Humerus.—A small distal humerus (Fig. 7) from locality BQ-2 (DPC 24108A) is attributed to *Dilambdogale gheerbranti*

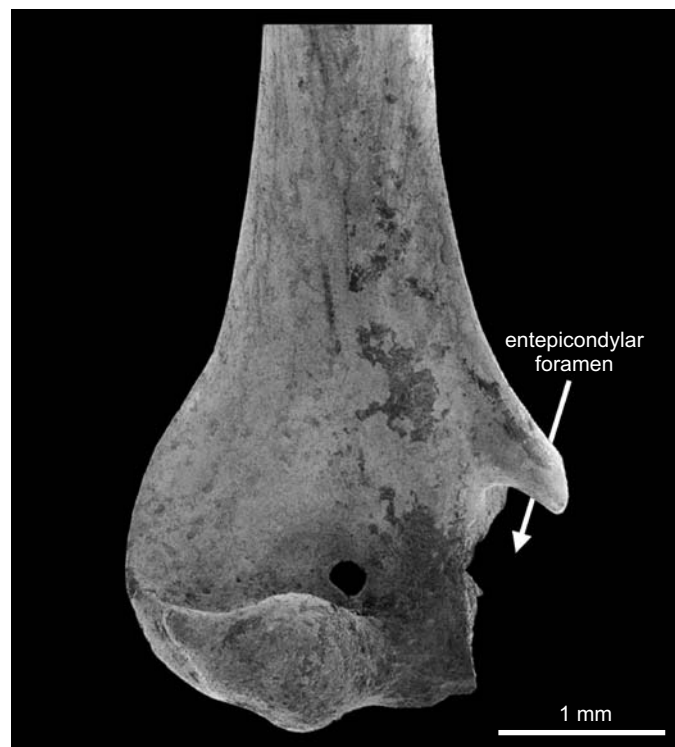


Fig. 7. DPC 24108A, right distal humerus attributed to the afrosoricid placental *Dilambdogale gheerbranti* gen. et sp. nov., from the earliest late Eocene (earliest Priabonian) locality BQ-2, Birket Qarun Formation, Fayum Depression, northern Egypt.

branti on the basis of size, morphology, and relative abundance. The only other small mammals known from BQ-2 that the humerus could be attributable to (on the basis of size alone) is the chiropteran *Qarunycteris* (Gunnell et al. 2008) and the anomaluroid rodent *Shazurus* (Sallam et al. 2010a). DPC 24108A exhibits none of the distinctive derived features of chiropteran distal humeri (see, e.g., Simmons and Geisler 1998), excluding the possibility that the specimen is attributable to *Qarunycteris*. The morphology of a distal humerus of the large anomaluroid *Kabirmys* from BQ-2 (Sallam et al. 2010b, c) is radically different from that of DPC 24108A, suggesting that its smaller relative *Shazurus* is unlikely to exhibit the morphology observable on DPC 24108A.

DPC 24108A does bear clear morphological resemblance to the distal humeri of some extant tenrecoids, particularly species of *Microgale*, which lends additional support for its attribution to *Dilambdogale*. Features shared with many species of *Microgale*, such as the presence of an entepicondylar foramen, a moderately developed brachioradialis flange, a deep radial fossa, a shallow olecranon fossa, and an ovoid capitulum with a proximodistally tall but laterally tapering capitular tail, are, however, presumably primitive within Afrosoricida, and possibly within Afrotheria. Perforation of the bony lamina separating the olecranon and radial fossae, as occurs in DPC 24108A, also occurs variably in species of *Microgale* (Salton and Sargis 2008). The medial aspect of the trochlea is missing, but in distal view there is a distinct notch separating the capitulum from the lateral aspect of the tro-

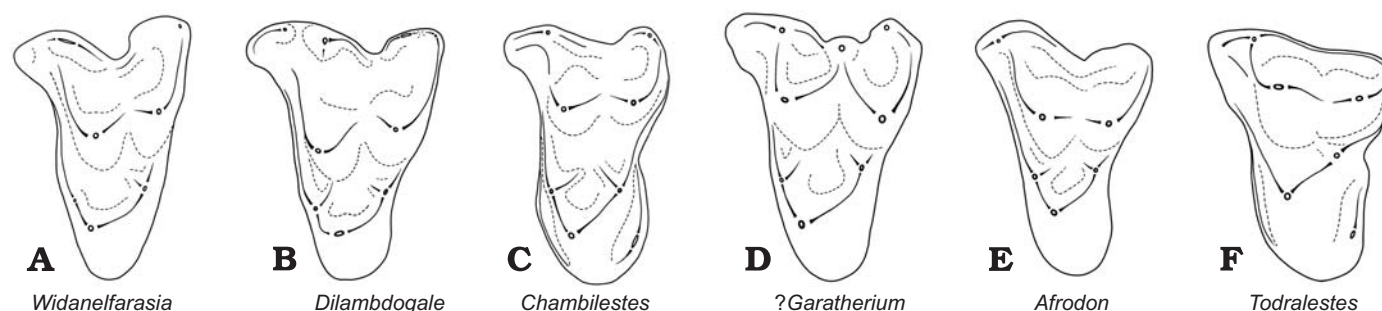


Fig. 8. Comparison of occlusal morphology of the upper second molar (scaled to the same approximate buccolingual width) in a series of Paleogene African mammals with possible afrosoricid affinities. **A.** *Widanelfarasia bowni* (latest Eocene, Jebel Qatrani Formation, Egypt), based on Seiffert et al. (2007). **B.** *Dilambdogale gheerbranti* (earliest late Eocene, Birket Qarun Formation, Egypt). **C.** *Chambilestes foussanensis* (late early or early middle Eocene, Chambi, Tunisia), based on Gheerbrant and Hartenberger (1999). **D.** *?Garatherium todrae* (late Paleocene, Jebel Guersif Formation, Morocco), based on Gheerbrant et al. (1998). **E.** *Afrodon chleuihi* (late Paleocene, Jbel Guersif Formation, Morocco), based on Gheerbrant (1988). **F.** *Todralestes variabilis* (late Paleocene, Jbel Guersif Formation, Morocco), based on Gheerbrant (1991b).

chlea, as in species such as *Microgale talazaci*. DPC 24108A also preserves the distal part of a sharp deltopectoral crest, the more proximal part of which trends laterally. DPC 24108A bears no special resemblance to the humeri of Malagasy *Geogale* and African potamogalids, which are likely to be autapomorphic in lacking entepicondylar foramina and having relatively reduced brachioradialis flanges. The humeri of golden moles reflect their highly fossorial existence in having features such as elongate medial epicondyles, globular capitula, mediolaterally long trochleae, and humeral shafts that are strongly laterally canted relative to the long axis of the distal articulation (e.g., Asher and Avery 2010). None of these features are seen in DPC 24108A.

The morphology of DPC 24108A is consistent with *Dilambdogale* having been a very generalized terrestrial quadruped. The combination of a shallow olecranon fossa and a deep radial fossa suggest that *Dilambdogale* habitually maintained postures in which the forearms were typically held in acute flexion. DPC 24108A bears none of the structural features of the distal humerus that are typically correlated with saltatory locomotion, habitual fossoriality, arboreality, or dedicated aquatic behavior in extant mammals.

Comparisons.—As already noted, the fossil record of small mammals is relatively poor in Afro-Arabia (Seiffert 2010), and as such it is rare for “insectivoran-grade” placentals (sensu Asher 2005) to be documented by more than a few tooth loci. Therefore *Dilambdogale*, despite being represented solely by P4–M3 and p2–m3 and a distal humerus, actually allows for more extensive comparisons than many other important taxa from Afro-Arabian Paleogene, some of which are only documented by upper teeth (e.g., *Garatherium*, *Chambilestes*).

The genus that is best-documented from older horizons in Africa is latest Paleocene *Todralestes variabilis* (Gheerbrant 1991b, 1994). *Todralestes* differs from *Dilambdogale* in retaining upper molar features which, based on their occurrence in other afrotherians (e.g., Seiffert 2007), may be primitive within that clade—e.g., relatively narrow styler shelves, short

prepara- and postmetacristae, linear centrocristae, absence of deep ectoflexi, presence of pre- and postcingula, and, in some individuals, small hypocones on M1–2 (Fig. 8F). Styler cusps are also poorly-developed and crestiform in *Todralestes*, but are much more prominent in *Dilambdogale*, and *Todralestes* lacks an ectostyle on P4, whereas this cusp is very prominent in *Dilambdogale*. The morphology of P4 in *Todralestes* is otherwise also very similar to that of *Dilambdogale* in having a long postparacrista and a very low, small, and mesially positioned protocone. *Dilambdogale* is more similar to *Todralestes* in the lower dentition, differing primarily in having larger para- and hypoconid cusps on p3, an entoconid on p4, relatively broad lower molars with more distinct talonid cusps, and molar protocristids that tend to be less obliquely oriented with respect to the long axis of the molar crown.

Seiffert et al. (2007) noted that *Todralestes*, *Widanelfarasia*, and *Protenrec* all have an odd configuration of the maxilla and P3–4 complex, in which the distal root of P3 is lingually placed, being mesial to the lingual root of P4, rather than being mesial to the mesiobuccal root as in other afrotherians. This feature is also seen in *Dilambdogale* (Fig. 3). This morphology appears to be related to the placement of the rostral aperture of the infraorbital foramen; in all of the aforementioned taxa, the rostral aperture is placed just dorsal to the mesiobuccal root of P4, and the alveolar process of the maxilla lateral to the P3 is similarly offset medially, leading to a distinctive constriction of the palate at the junction between P3 and P4. This morphology is also seen in the extant Malagasy tenrec *Geogale* (Butler 1984), and, interestingly, the early Eocene hyaenodontid *Koholia* from Algeria (Crocket 1988). These taxa also all have a greatly enlarged paracone on P4, a mesiobuccal root of P4 that is widely exposed in lateral view, and, in those taxa that preserve a P3 in place (*Widanelfarasia*, *Protenrec*, and *Geogale*) there is a distinctly “stepped” transition from the apex of the P4 to that of P3 (Fig. 3). This surely would have also been the case in *Dilambdogale* and *Todralestes*, given the small size of the occluding p3, and the position of the distal P3 alveolus far dorsal to the base of the P4 crown. As strange as this overall

pattern may be, its presence in a variety of early Paleogene African mammals with very different dental morphology suggests that this condition may be plesiomorphic at a high taxonomic level within Afrotheria.

The upper dentition of the alleged adapisoriculid *Afrodon chleuhi*, from the same latest Paleocene deposits that yielded remains of *Todralestes variabilis* (Gheerbrant 1988, 1995; Gheerbrant et al. 1998), is more similar to *Dilambdogale* than is *Todralestes* in having relatively broad styler shelves, longer and more buccally oriented prepara- and postmetacristae, more pronounced ectoflexi, a relatively lingually placed paraconule, and absence of pre- and postcingula. However *A. chleuhi* is not as derived as *Dilambdogale* in that it retains a linear centrocrista and a styler shelf that is not as broad (Fig. 8E); the styler cusps are also more crestiform in *A. chleuhi*. The lower molars and p4 of *A. chleuhi* are also relatively broad, with deep hypoflexids (as in *Dilambdogale*), and its p4 talonid is more complex than that of *Todralestes*. *Afrodon tagourtensis*, from the earliest Eocene of Morocco (Gheerbrant 1993; Gheerbrant et al. 1998), is even more similar to *Dilambdogale* than is *A. chleuhi* in having a relatively elongate buccal margin on M1, and, on p4, a distinct entoconid.

Of all other older Afro-Arabian mammals, *Dilambdogale* is most similar in its occlusal morphology to *Garatherium mahboubii* from the early Eocene of Algeria (Crochet 1984; Mahboubi et al. 1986). A similar species that has been referred to as *?Garatherium todrae* is also known from the latest Paleocene localities that preserve remains of *Afrodon chleuhi* and *Todralestes variabilis* (Gheerbrant et al. 1998). Unlike *Afrodon* and *Todralestes*, but as in *Dilambdogale*, *Garatherium* exhibits well-developed dilambdomorphy, with a “W”-shaped arrangement of crests connecting the paracone and metacone (Fig. 8D). Like *Dilambdogale*, *Garatherium* has distinct parastyle, stylocone, mesostyle, and “D” cusps along the buccal margin, but in *Garatherium* the mesostyle and cusp “D” are even more prominent, and the mesostyle is met by the postpara- and premetacristae. Further resemblances include the lack of pre- and postcingula. At present no lower teeth or upper premolars have been attributed to *Garatherium*, limiting comparisons with *Dilambdogale*, however the distinctive upper molar features shared by the two taxa increase the likelihood that the two species may be closely related, and that *G. mahboubii* is indeed a placental as argued by Gheerbrant (1991a), and not a peradectine marsupial as was initially suggested (Crochet 1984; Mahboubi et al. 1986).

The enigmatic genus *Chambilestes* from the early or early middle Eocene of Tunisia (Gheerbrant and Hartenberger 1999; Fig. 8C) differs from *Dilambdogale* in having distinct pre- and postcingula, small hypocones on M1–2, well-developed postpara- and premetaconule cristae, and a relatively narrow styler shelf. On the basis of predicted occlusal relationships, Seiffert and Simons (2000) suggested that *Chambilestes* might have affinities with *Widanelfarasia*, but now that the upper dentition of *Widanelfarasia* is known (Seiffert et al. 2007), this possibility appears remote. *Chambilestes* might be

more closely related to *Todralestes* (Seiffert 2010), specifically early Eocene *Todralestes butleri* (Gheerbrant 1993).

Of all Paleogene Afro-Arabian taxa, *Dilambdogale* is most similar to latest Eocene *Widanelfarasia* (Seiffert and Simons 2000; Seiffert et al. 2007). The upper and lower teeth of these genera exhibit a series of striking resemblances, but *Dilambdogale* appears to be more primitive in having relatively broad lower molar talonids (Fig. 9), a larger metacone on M2, and a distinct and cusped metacone on M3. In each of these features, *Dilambdogale* is similar to early African “adapisoriculids” such as *Afrodon*, while *Widanelfarasia* exhibits derived features that arguably align the genus with later tenrecoids (Seiffert et al. 2007).

Stratigraphic and geographic range.—Earliest Priabonian, northern Egypt.

Suborder Tenrecomorpha Butler, 1972

?Superfamily Tenrecoidea Gray, 1821

Genus *Qatranilestes* nov.

Type species: *Qatranilestes oligocaenus* sp. nov., see below.

Etymology: From Arabic *qatran*, tar—in reference to the dark basalt capping the Jebel Qatrani Formation, cobbles of which drape the hills north of Quarry I and which give that Formation its name (Jebel Qatrani = “tar hill”), and from Greek *lestes*, robber—a common suffix in generic names of insectivoran-grade placentals.

Diagnosis: Same as for the species.

Qatranilestes oligocaenus sp. nov.

Figs. 10, 11B.

Holotype: YPM 24203, a right mandibular fragment preserving the talonids of m2–3 (Fig. 10B).

Etymology: In reference to the Oligocene age of the species.

Type locality: Quarry I, northern Egypt.

Type horizon: Late early Oligocene, upper sequence of Jebel Qatrani Formation, northern Egypt (~29.5–30 Ma).

Diagnosis.—Small species (about 65% the size of *Dilambdogale gheerbranti*) that differs from other Fayum afrosoricids (*Dilambdogale*, *Widanelfarasia*, and *Jawharia*) in having relatively reduced talonid basins and capacious hypoflexids on m2–3 (Figs. 9, 10); differs from *Dilambdogale* in having very reduced molar entoconids.

Description.—*Qatranilestes* is only known from very fragmentary material, notably the holotype mandible preserving

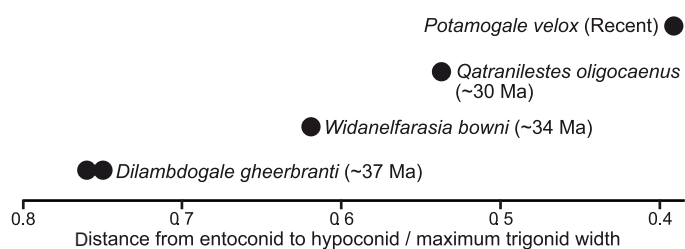


Fig. 9. Relative talonid breadth in Paleogene afrosoricids. Plot of the distance from the entoconid to hypoconid on m2 divided by the maximum breadth of the m2 trigonid. Note that relative talonid breadth decreases through the later Paleogene.

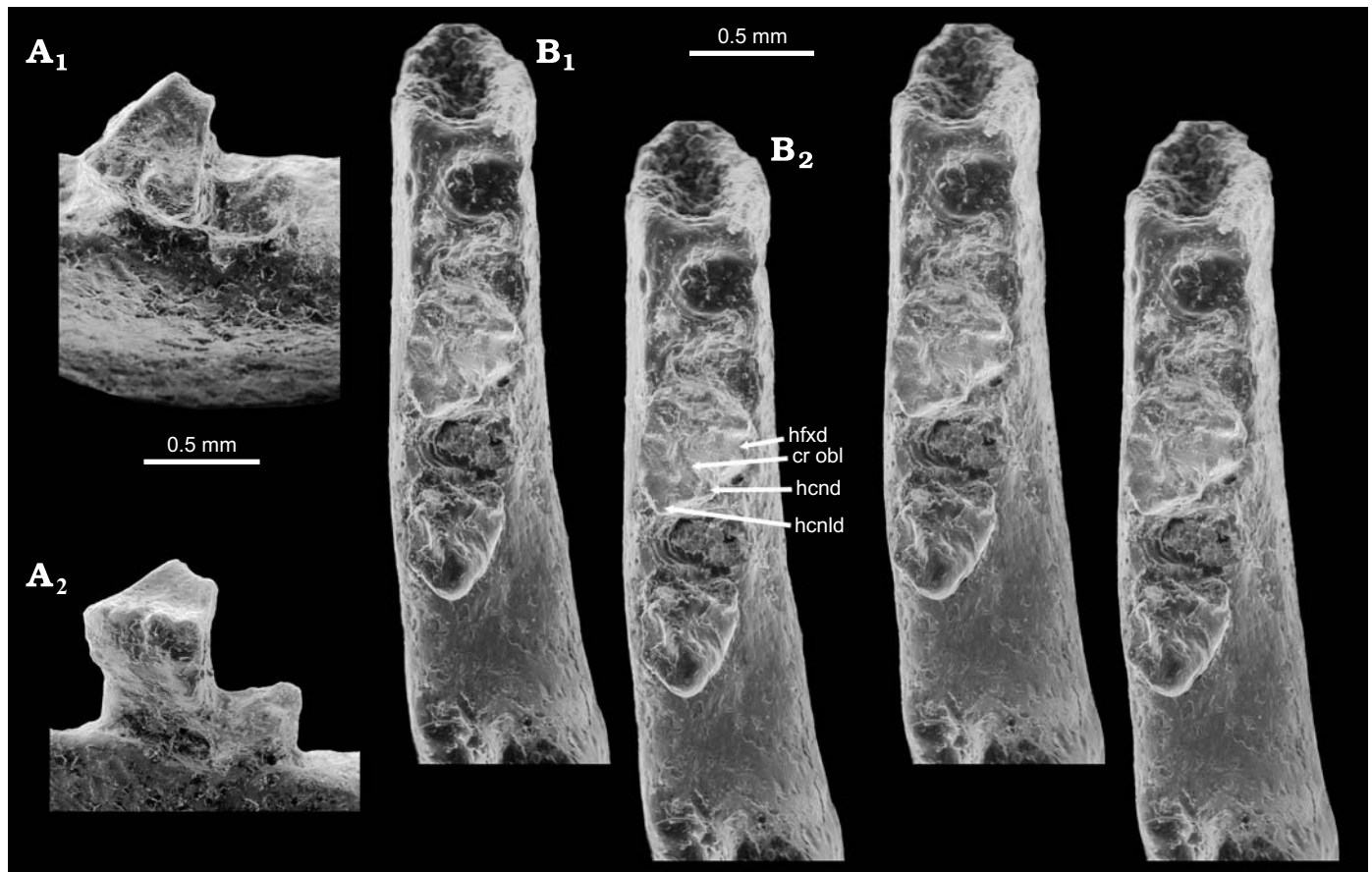


Fig. 10. Dental morphology of the afrosoricid placental *Qatranilestes oligocaenus*, gen. et sp. nov., from the late early Oligocene (late Rupelian) Quarry I, upper sequence of the Jebel Qatrani Formation, northern Egypt. **A.** YPM 24200, right mandibular fragment with crown of m3 in occlusal (A₁) and lingual (A₂) views. **B.** YPM 24203, holotype right mandible with talonids of m2–3 in occlusal stereo view (B₁ and B₂).

the talonids of m2–3, the horizontal ramus distal to p4, and the base of the ascending ramus (Fig. 10B). A complete but badly abraded and worn m3 is implanted in another partial mandible (YPM 24200, Fig. 10A). Even from such poorly preserved material, it is clear that *Qatranilestes* is unique among Fayum tenrecoids in having very reduced talonids (Figs. 9, 11) and capacious hypoflexids (m2 talonid width = 0.45 mm; m3 talonid width = 0.45 mm). The m2 talonid preserves a concave cristid obliqua and small hypoconid, hypoconulid, and entoconid cusps. The trigonid of m3 on YPM 24200 is very worn, but clearly would have had well-developed metaconid, paraconid, and protoconid cusps, and was elevated high above the very low and mediolaterally narrow talonid basin, which shows little clear differentiation of cusps aside from the hypoconid. The m3 of the holotype specimen is not as worn and damaged, but similarly shows only very small and indistinct talonid cusps, with the hypoconid and hypoconulid closely approximated. Relative to trigonid breadth, the m3 talonid of *Qatranilestes* is very reduced relative to those of *Widanelfarasia* and *Jawharia*. Seiffert et al. (2007) noted that *Widanelfarasia* exhibits slight external rotation of the long axis of the lower molar crowns, leading to an arrangement in which the lower molar paraconids are situated distal to the hypoconulid (rather than the entoconid) of the adjacent molar.

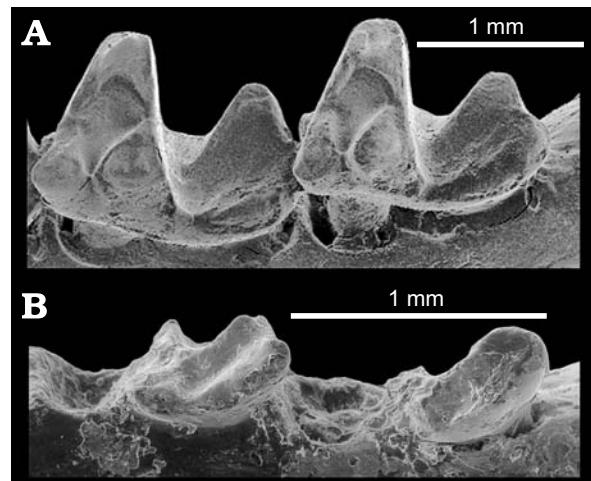


Fig. 11. Comparison of talonid morphology, in lingual view of two Egyptian afrosoricid placentals. **A.** *Dilambdogale gheerbranti* (DPC 24103A), from the earliest late Eocene (earliest Priabonian; ~37 Ma) locality BQ-2, Birket Qarun Formation, Fayum Depression, northern Egypt. **B.** *Qatranilestes oligocaenus* (YPM 24203), from the late early Oligocene (late Rupelian; ~30 Ma) Quarry I, upper sequence of the Jebel Qatrani Formation, northern Egypt. Specimens are scaled to the same approximate m2–3 length to facilitate comparison. Note the much larger hypoconid and relatively capacious and concave talonid basin in *Dilambdogale*. Also note that the m2 entoconid is broken in DPC 24103A, but is relatively well-developed in other specimens.

This orientation decreases the size of the trough for the occluding upper molar metacone, and increases the buccal exposure of the paracristid for occlusion with the upper molar postmetacrista. Judging from the orientation of the m2 talonid, *Qatranilestes* had a similar external rotation of the molar crowns. The preserved morphology and orientation of *Qatranilestes*' m2–3 suggests that the occluding M2 would have had a greatly enlarged paracone (to occlude in the large hypoflexid), a reduced metacone, and an elongate postmetacrista, and probably more closely approximated the “euzalambdomorph” occlusal pattern than did any of the older species that have been recovered thus far.

Phylogenetic analysis

Afrodon chleuhi, *Dilambdogale gheerbranti*, and *Todralestes variabilis* were added to the character–taxon matrix of afrotherian mammals that was originally compiled by Seiffert (2007), and which was recently augmented by Barrow et al. (2010). Although *Eochrysochloris*, *Jawharia*, and *Qatranilestes* may prove to be key taxa for understanding afrosoricid interrelationships, available specimens preserve too few characters to be included in the analysis. The matrix now includes 403 morphological characters, 18 369 nucleotide characters (from three mitochondrial genes and 20 nuclear genes) derived from the analysis of Amrine-Madsen et al. (2003), ten chromosomal association presence/absence characters derived from various analyses (Yang et al. 2003; Robinson et al. 2004; Kellogg et al. 2007), and eight SINE presence/absence characters derived from the analysis of Nikaido et al. (2003). See Seiffert (2007) for additional information, including character descriptions; the modified matrix, in NEXUS format, is available at <http://www.morphobank.org>.

The matrix was analyzed under two assumption sets using the maximum parsimony algorithm in PAUP* 4.0b10 (Swofford 1998); results are presented in Figs. 12 and 13. In one analysis (Fig. 12A), some multistate characters were ordered and scaled; in the other assumption set all multistate characters were unordered and equally weighted (Fig. 12B). Analysis of the matrix with some multistate characters ordered and scaled recovered a single tree of length 18745.188 (Fig. 12A). Despite very minor perturbations to the matrix of Seiffert (2007) in terms of character and taxon addition, afrotherian superordinal relationships are remarkably different from those recovered in his original analysis—i.e., instead of a ([Macroscelidea + Afrosoricida], [Tubulidentata + Paenungulata]) arrangement, Afrosoricida is instead placed as the sister group of all other afrotherians, a Macroscelidea + Tubulidentata clade is placed as the sister group of Paenungulata, and, within the latter group, Sirenia joins Hyracoidea rather than Proboscidea. These results reinforce Seiffert's (2007) conclusion that two bursts of superordinal cladogenesis—one at the base of crown Afrotheria, and one at the base of Paenungulata—occurred so rapidly that interordinal relationships might not be convincingly resolved by parsimony analyses of combined molecular-morphological data sets.

Within Afrosoricida, *Protenrec* was placed as the nearest sister group of chrysochloroids and tenrecoids, followed by a *Dilambdogale*–*Widanelfarasia* clade. *Todralestes* was placed as the most basal stem afrosoricid. Analysis of all characters unordered recovered 63 MPTs of length 19568 (Fig. 12B). The strict consensus of these trees provides no resolution among crown afrosoricids or Paleogene taxa, apparently due to Early Cretaceous *Prokennalestes* and *Montanalestes*, which acted as “wild-card” taxa by falling either as a sister group of placentals, or as a sister group of *Todralestes*, *Dilambdogale*, and *Widanelfarasia* across the 63 equally most parsimonious trees. An Adams consensus of the 63 MPTs reveals that a (*Todralestes*, [*Dilambdogale*, *Widanelfarasia*]) clade was nevertheless consistently placed with afrosoricids, though in various positions, and in most of the trees this clade was placed as the sister group of *Protenrec*, followed by *Potamogale*. When the poorly-known genus *Afrodon* was added to the matrix (Fig. 13), the phylogenetic relationships among afrotherians remained the same, and *Afrodon* was placed as a sister group of a *Dilambdogale*–*Widanelfarasia* clade whether certain multistates were treated as ordered and scaled, or as unordered.

Discussion

In many ways, the dentitions of *Dilambdogale* and *Widanelfarasia* are morphologically intermediate between those of the highly derived euzalambdomorph afrosoricids from the early Miocene of East Africa, and those of the much more generalized protodilambdomorph adapisoriculids and todralestids from the latest Paleocene of northern Africa. An intermediate phylogenetic position is supported by parsimony analyses with some multistate characters ordered and scaled (Figs. 12, 13), but analyses with all characters unordered sometimes nest *Afrodon*, *Dilambdogale*, *Todralestes*, and *Widanelfarasia* deep within Tenrecoidea as sister taxa of *Protenrec*, or alternatively as stem afrosoricids joined by Early Cretaceous *Montanalestes* and *Prokennalestes* (the latter of which are generally considered to be basal eutherians [e.g., Kielan-Jaworowska et al. 2004]). These results must be interpreted with considerable caution, because the matrix employed here was originally compiled in order to test hypotheses of superordinal relationships among the morphologically diverse afrotherian crown group, and might not be sufficiently detailed to accurately resolve relationships among stem and crown afrosoricids.

Certain aspects of occlusal morphology in *Dilambdogale* and *Widanelfarasia* are somewhat unexpected given their position as possible “intermediate” taxa—for instance, despite exhibiting features that are typical of protozalambdomorphs (e.g., transversely broad molar crowns, broad stylar shelves with elongate and buccally oriented prepara- and postmetacristae, reduced metacones that are placed buccal to paracones, a deep ectoflexus on M1–2, and complete

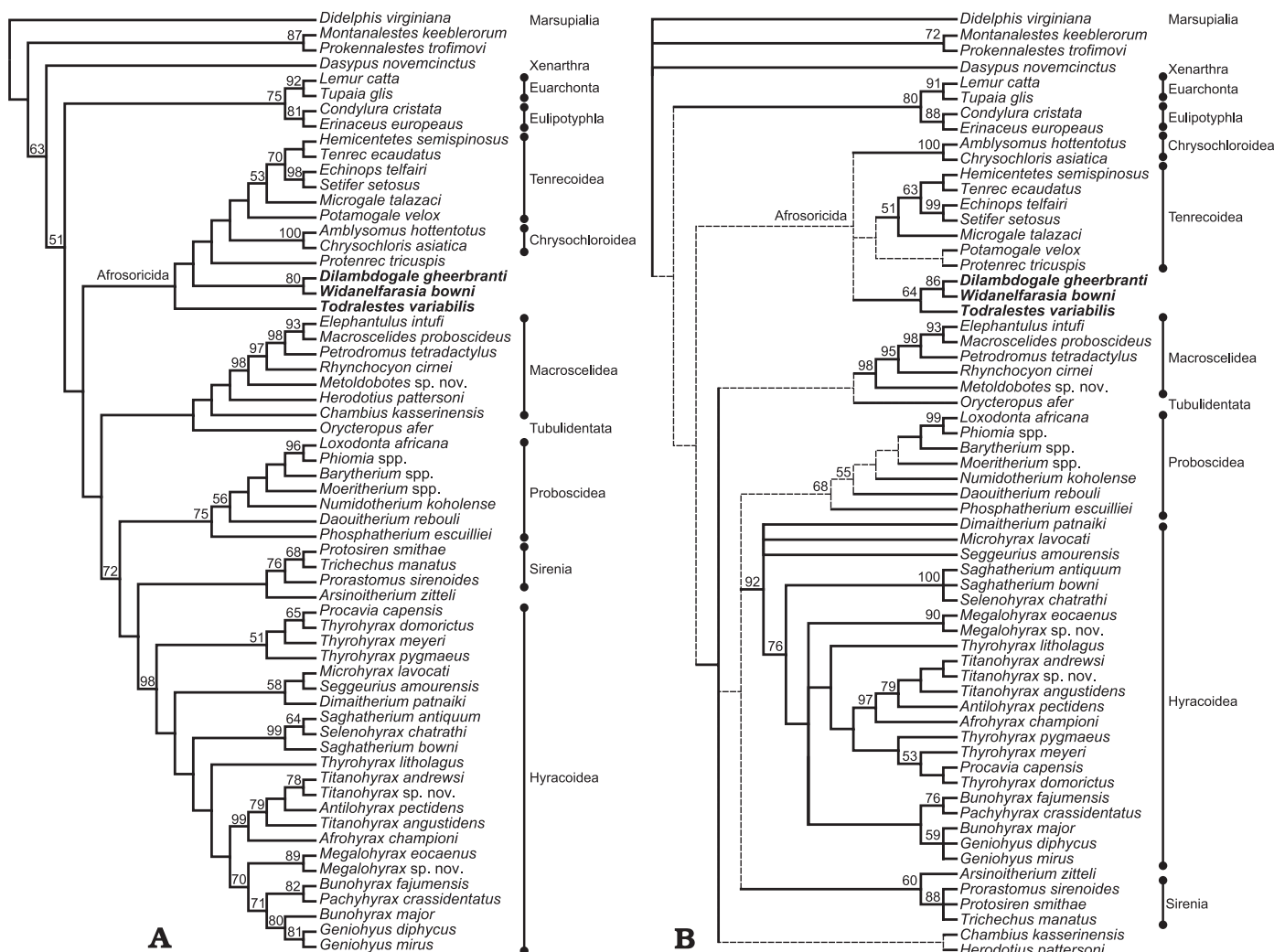


Fig. 12. Phylogenetic analysis of living and extinct afrotherians, with *Dilambdogale* and *Todralestes* added to a modified version of the matrices employed by Seiffert (2007) and Barrow et al. (2010). **A.** Single most parsimonious tree derived from analysis with some multistate characters ordered and scaled; tree length = 18746.434, consistency index excluding uninformative characters = 0.49, retention index = 0.44, rescaled consistency index = 0.28. **B.** Adams consensus of 63 equally parsimonious trees derived from analysis with all multistate characters unordered, and *Afrodon* excluded; tree length = 19579, consistency index excluding uninformative characters = 0.49, retention index = 0.44, rescaled consistency index = 0.28. Dashed lines indicate branches that are present in the Adams tree, but not in the strict consensus of all MPTs.

absence of pre- and postcingula), the buccal crests of the Fayum afrosoricids are nevertheless arranged in a typically dilambdomorph “W” shape. This odd combination of molar features either suggests that tenrecoid (or afrosoricid) zalam-bdomorphy is derived from dilambdomorphy, or that *Dilambdogale* and *Widanelfarasia* are merely highly derived sister taxa that are members of a dilambdomorph stem afrosoricid clade. By placing *Dilambdogale* and *Widanelfarasia* as sister taxa to the exclusion of all other afrotherians, parsimony analysis favors an interpretation in which their dilambdomorph arrangement of the buccal crests is simply a specialization of an extinct side branch (Figs. 12, 13).

Parsimony analyses provide a simple and straightforward directional explanation for the distribution of molar occlusal features among afrosoricids through time, and are also highly consistent with stratigraphic ordering of the taxa concerned

—i.e., older taxa generally exhibit primitive dental features, while successively younger taxa acquire features of the euzalambdomorph dental pattern through the later Paleogene. The only undoubted fossil afrosoricid in the analysis, early Miocene *Protenrec*—a genus that has consistently been interpreted as a tenrecoid, despite its relatively generalized dental morphology (Butler and Hopwood 1957; Butler 1969, 1972, 1978, 1984; Asher and Hofreiter 2006)—is surprisingly most parsimoniously placed as a sister taxon of crown Afrosoricida when some multistate characters are ordered and scaled (Figs. 12A, 13A). In the absence of contradictory evidence, a logical interpretation of this phylogenetic pattern would be that the absence of euzalambdomorphs in the Paleogene of Afro-Arabia is best explained by a very late divergence of chrysochloroids and tenrecoids, possibly in the later Oligocene.

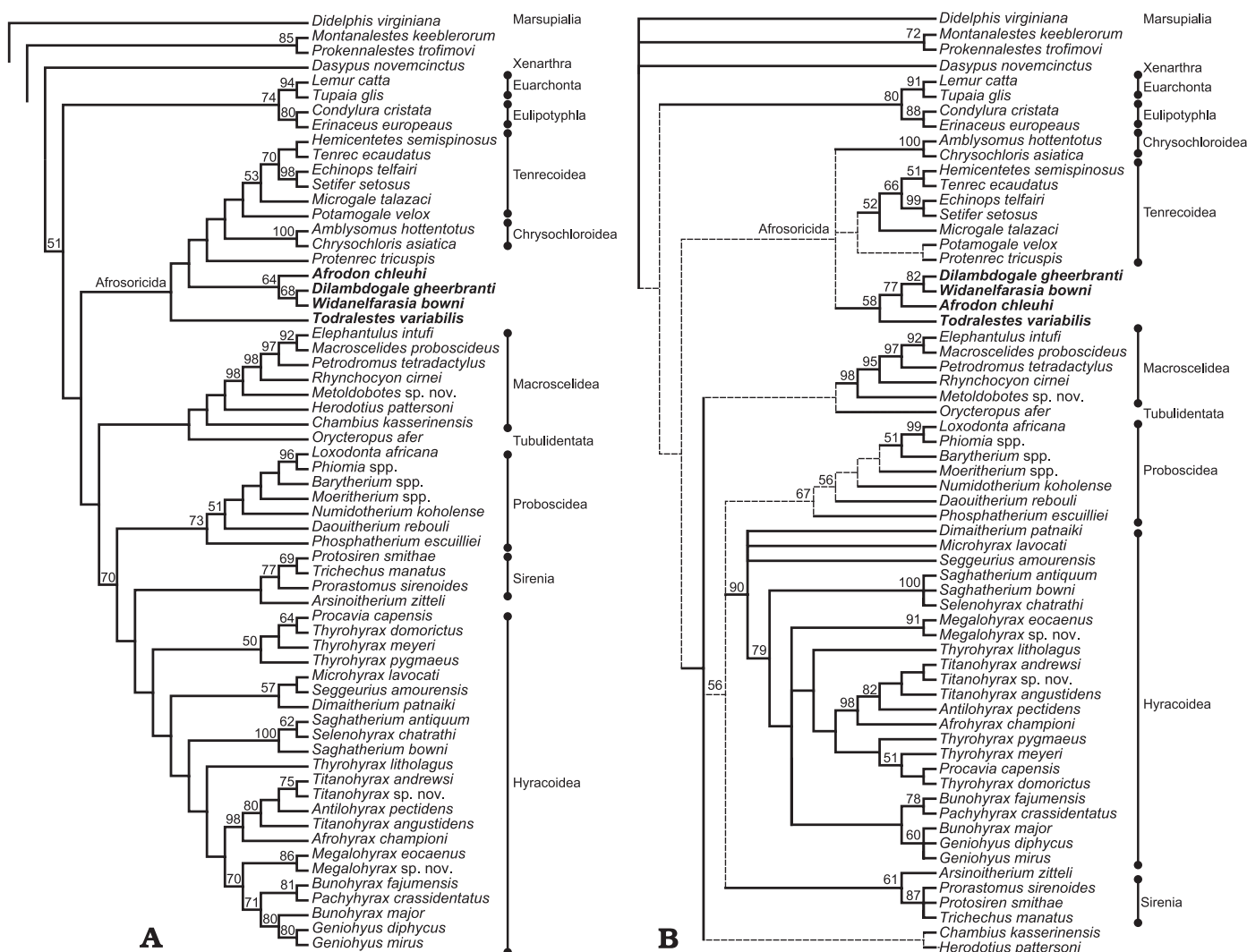


Fig. 13. Phylogenetic analysis with the poorly-known latest Paleocene genus *Afrodon* included. **A.** Single most parsimonious tree derived from analysis with some multistate characters ordered and scaled; tree length = 18748.435, consistency index excluding uninformative characters = 0.49, retention index = 0.44, rescaled consistency index = 0.28. **B.** Adams consensus of 97 equally parsimonious trees derived from analysis with all multistate characters unordered, and *Afrodon* included; tree length = 19582, consistency index excluding uninformative characters = 0.49, retention index = 0.45, rescaled consistency index = 0.28. Dashed lines indicate branches that are present in the Adams tree, but not in the strict consensus of all MPTs.

The possibility of such a late origin for crown Afrotheria is strongly contradicted, however, by molecular divergence estimates that place the chrysochloroid-tenrecoid split about 40 million years earlier—in either the latest Cretaceous or earliest Paleocene (Springer et al. 2003; Gilbert et al. 2006; Poux et al. 2008). Indeed, the relationship between tenrecs and golden moles is distant enough that the two have not consistently been recovered as sister taxa in molecular phylogenetic analyses (Murata et al. 2003; Waddell and Shelley 2003; Kitazoe et al. 2007; Arnason et al. 2008). It is unlikely that the timing of the chrysochloroid-tenrecoid divergence has been dramatically overestimated by these molecular analyses, because dating of other splits within Afrotheria, particularly those within Paenungulata, are generally remarkably consistent with that group's much better fossil record.

When one of the topologies recovered by the parsimony analyses presented here (Fig. 13A) is plotted against time within the context of a latest Cretaceous divergence of chrysochloroids and tenrecoids (Fig. 14), and rooted with the oldest known paenungulate, *Eritherium* (Gheerbrant 2009), the picture becomes much more complicated, and the topology arguably becomes far less likely, because such an ancient split implies extraordinarily long Paleogene “ghost lineages” for all of crown Afrotheria, and an unsampled >45 Ma-long interval for the lineage leading to *Protenrec*. The extremely short internodes along the afrotheric stem lineage also leave very little time for the evolution of zalambdomorphy. As such, when metacone loss is reconstructed within Afrotheria using a maximum likelihood approach on the time-calibrated phylogeny (Fig. 14), the last common ancestor of crown Afrotheria, and even

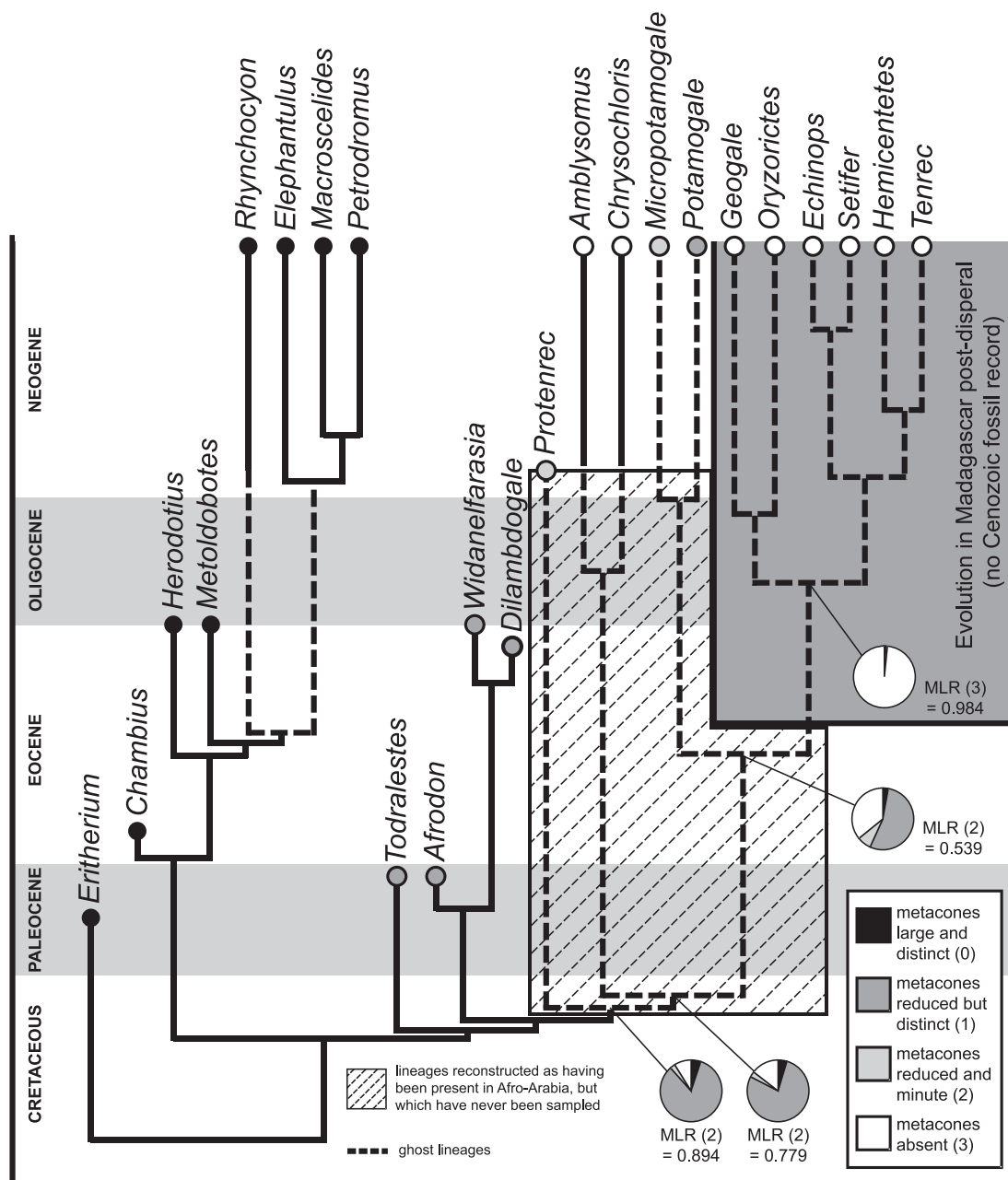


Fig. 14. Implied ghost lineages and maximum likelihood reconstructions of M2 metacone size (treated as an ordered character with four states), given one of the topologies (Fig. 12A) recovered by parsimony analysis of morphological data. Here the topology is plotted against time, with major divergences among clades with extant representatives based on the molecular estimates of Douady et al. (2003) for Macroscelidea, Poux et al. (2008) for Tenrecoidea, and Gilbert et al. (2006) for the origin of crown Chrysochloroidea. The depth of the *Potamogale*–*Micropotamogale* divergence has not been estimated using molecular data, and is here arbitrarily placed at half the time depth of Potamogalidae. An origin of crown Afrotheria at ~80 Ma is supported by various studies (e.g., Springer et al. 2003). Although parsimony reconstructs metacone loss as homologous in tenrecs and golden moles, note that when branch lengths are taken into account for maximum likelihood reconstructions (“MLR”, computed in Mesquite v. 2.72; Maddison and Maddison 2005), the common ancestors of crown Afrotheria and crown Tenrecoidea are reconstructed as having had a reduced but distinct M2 metacone, the former with high proportional likelihood (0.779). These data, combined with the numerous zambomorph Paleogene ghost lineages that are required by the parsimony-based topology, arguably call into question the likelihood of the topology itself.

the last common ancestor of crown Tenrecoidea, is optimized as having had distinct but reduced M2 metacones. Parsimony analysis cannot incorporate these considerations as background information, but such evidence calls into question the likelihood of the topology itself, at least as it relates to the origin of zambomorphy.

There are additional taxa from the Fayum succession that are currently too fragmentary to be included in the parsimony analysis, but that nevertheless might come to bear decisively on this issue should more material be recovered. Notably, the tiny species *Eochrysochloris tribosphenus*—at present represented solely by mandibular fragments, a partial p3, and

crowns of p4 and m2 (Seiffert et al. 2007)—exhibits an m2 talonid morphology in which the cristid obliqua is oriented only slightly lingually, leaving a relatively shallow hypoflexid for an occluding paracone when compared with those of *Dilambdogale*, *Widanelfarasia*, *Jawharia*, and *Qatranilestes*. *Eochrysochloris* also has a very tall trigonid, and the occlusal pattern of M2 is predicted to be associated with an occluding m2 that would be transversely broad, but not dilambdomorph (Seiffert et al. 2007). This poorly-known but very distinctive genus reveals that there are two groups of probable afrosoricids in the Paleogene of northern Africa, the other being represented by *Dilambdogale*, *Widanelfarasia*, *Jawharia*, and *Qatranilestes*, all of which have deep hypoflexids. It was previously argued by Seiffert et al. (2007) that the latter group documents gradual acquisition of tenrecoid zalambdomorphy from dilambdomorphy through the later Paleogene, while *Eochrysochloris* documents acquisition of chrysochloroid zalambdomorphy through a very different transformation of upper molar occlusal morphology. This scenario is, however, still highly speculative, and must be tested by the recovery of much more complete fossil material.

While it appears increasingly likely that the Fayum afrosoricids are of relevance for understanding the origins of Tenrecoidea and Chrysochloroidea, these taxa also provide some interesting clues that might help to explain the higher-level affinities of older insectivoran-grade placentals from Afro-Arabia such as *Afrodon*, *Garatherium*, and *Todralestes*. *Garatherium* was originally identified as a peradectine marsupial on the basis of an isolated upper molar from the early Eocene El Kohol locality in Algeria (Crochet 1984), but was subsequently reinterpreted as a dilambdomorph adapisoriculid (Gheerbrant 1991a, 1995). The well-developed dilambdomorphy seen on the M1 of *Dilambdogale* and *Widanelfarasia* is similar to, though less extreme than, that of *Garatherium*, and all three taxa have broad styler shelves, restricted trigons, elongate postmetacristae, no pre- or postcingula, and small conules. Like *Garatherium*, *Dilambdogale* has relatively distinct (as opposed to crestiform) styler cusps, and variably exhibits a postparaconule crista, which was not previously clearly present in the micro-CT reconstructions of *Widanelfarasia*. In many ways therefore *Dilambdogale* appears to be structurally intermediate between *Garatherium* and *Widanelfarasia*, while *Widanelfarasia* is in turn structurally intermediate between the older dilambdomorphs and tenrecoids. If *Garatherium* is an early stem tenrecoid, its age (~56–54 Ma) would be in line with molecular estimates for the timing of the chrysochlorid-tenrecoid divergence.

Dilambdogale's position as a morphological and phylogenetic intermediate between tenrecoids and adapisoriculids takes on new significance in light of a recent analysis that has suggested a close relationship between *Afrodon* and the enigmatic Late Cretaceous placental *Deccanolestes* from India (Prasad et al. 2010). Analysis of adapisoriculid tarsals from the late Paleocene of Europe has also suggested that *Deccanolestes* is closely related to European adapisoriculids (Smith et al. 2009). On the basis of tarsal morphology, *Deccanolestes*

has, however, been interpreted as a possible “archontan” or euarchontan (Prasad and Godinot 1994; Kielan-Jaworowska et al. 2004; Smith et al. 2009), and not as a possible afrotherian. If *Deccanolestes* is in fact allied with adapisoriculids as argued by Prasad et al. (2010), this interpretation would appear to be consistent with Storch's (2008) recent analysis of adapisoriculid humeri, which led him to suggest that the family has plesiadapiform (and hence euarchontan, and possibly even primate) affinities. Notable exceptions to the interpretation of *Deccanolestes* as a basal euarchontan are the studies of Wible et al. (2007), which placed *Deccanolestes* as a stem placental, and that of Rana and Wilson (2003), who considered *Deccanolestes* to be of uncertain affinities within Placentalia. Most recently, Boyer et al. (2010) described a distal humerus and proximal ulna of *Deccanolestes*, and concluded that its distal humerus is more primitive than the adapisoriculid humeri described by Storch (2008), and morphologically intermediate between Late Cretaceous *Protungulatum* and *Procerberus*, and definitive euarchontans. Breakage of the distal humerus that is here attributed to *Dilambdogale* does not allow for extensive comparison, but in preserved morphology the humeral morphology of *Dilambdogale* appears to be quite similar to that of *Deccanolestes*, and both are similar to generalized tenrecoids such as *Microgale*.

Given the enormous amount of homoplasy that has occurred in the dentition of placental mammals, the meaning of the occlusal similarities shared by *Deccanolestes*, adapisoriculids, and afrosoricids is by no means clear at the moment. There can be little doubt, however, that the dental morphology of *Deccanolestes* closely approximates the primitive morphotype for crown placentals; as was argued by Kielan-Jaworowska et al. (2004: 505): “molar morphology of *Deccanolestes* differs substantially from that of *Cimolestes* and similar taxa...mainly in the presumed retention of plesiomorphies”. Primitive adapisoriculids such as *Afrodon* and *Bustylus* are similarly generalized, to the extent that the latter was first described as a marsupial by Crochet and Sigé (1983). The fact that adapisoriculids have been proposed as possible marsupials, basal euarchontans, and herein as possible basal afrosoricids—the latter two of which are now known to be very distantly related within Placentalia (Fig. 1)—could indicate that many, if not most, aspects of dental morphology in *Afrodon*, *Bustylus*, and *Deccanolestes* were present in the last common ancestor of crown Placentalia (a hypothesis that is supported by the very basal placement of *Deccanolestes* in Wible et al.'s [2007] phylogenetic analysis), and that the most basal members of Afrotheria, Euarchontoglires, Laurasiatheria, and Xenarthra might be identified as “adapisoriculid” on the basis of dental features. This possibility is particularly compelling in light of the results of the phylogenetic analyses presented here, which consistently placed Afrosoricida as the sister group of all other afrotherians, rather than as the sister group of Macroscelidea and/or Tubulidentata as in many molecular studies (Fig. 1). This phylogenetic arrangement implies an insectivoran-grade (and perhaps dentally adapisoriculid-like), rather than condylarthran-grade, ancestor for crown Afrotheria (see

discussion in Seiffert 2002; Robinson and Seiffert 2004; Seiffert 2007; Tabuce et al. 2008; Asher and Seiffert 2010). Paleontological sampling in the Late Cretaceous of Africa, ideally from horizons near the estimated time of origin of Afrotheria (i.e., ~80 Ma, early to mid-Campanian) is now desperately needed to test these and other hypotheses bearing on afrotherian origins.

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