

The last African metatherian

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Abstract

Morotodon aenigmaticus **gen. et sp. nov.** (Mammalia, Metatheria, ?Herpetotheriidae) from the early or early-middle Miocene of equatorial Africa (Moroto II locality, Moroto District, northeastern Uganda) is characterized by a short anterior cingulum, a buccal shelf, a well-developed hypoconulid in a central position, and a trigonid and talonid with similar mesio-distal lengths. Its small size and morphology suggest mostly insectivorous-faunivorous feeding habits. The faunal association of Moroto II, as well as previous palaeoenvironmental analyses, suggest that *Morotodon* lived in open woodland and bushland areas surrounded by grasses. *Morotodon aenigmaticus* shows several features reminiscent of early herpetotheriids, such as *Golerdelphys stocki* (late Paleocene of North America), and *Amphiperatherium ambiguum* (Eocene of Europe); this suggests an origin for its lineage previous to the Oligocene. In summary, its affinities lie with Northern Hemisphere herpetotheriids, and, most probably, with European ones.

Key Words

Africa, Herpetotheriidae, Metatheria, Miocene, Moroto II, Uganda

Introduction

The record of extinct African metatherians is scarce and, up to now, restricted to the Paleogene of its northernmost portion (Fig. 1; Table 1); in addition, the identity nature of several putative African metatherians has been contested (Gheerbrant 1995; Gunnell 2010; see a review in Crespo and Goin 2021). Unambiguous metatherians include *Peratherium africanum* Simons & Bown, 1984, from the Early Oligocene (Rupelian) of Egypt, and *Kasserinotherium tunisiense* Crochet, 1986 from the early Eocene of Chambi, Tunisia. *P. africanum* was originally described from remains found at Fayum Quarry M in

northern Egypt; subsequently, it was also recognized at similarly aged sediments at Taqah, Oman (Simons and Bown 1984; Crochet et al. 1992). Originally assigned to *Peratherium* (Herpetotheriidae), it was later referred to a new genus, *Qatranitherium* (Peradectidae; Crochet et al. 1992). More recently Hooker et al. (2008), while describing new material from Quarry M, argued in favour of the close affinity of this taxon with the European species *Peratherium laverghense* Crochet, 1979; thus, the generic name *Peratherium* was retained.

The other undisputed African metatherian, *K. tunisiense*, is solely known from two upper molars, and was included by Crochet (1986) within the Peradectidae.

McKenna and Bell (1997) placed this genus as an enigmatic taxon in the Supercohort Theria, without arguing on their taxonomic decision. Gunnell (2010) stated that there is no compelling reason to believe it represents a marsupial. To us, there is no compelling reason to believe it is not a metatherian (see also Hooker et al. 2008; Crespo and Goin 2021). Several authors have previously noted similarities between *Kasserinotheri-*

um and other Southern Hemisphere metatherians: Goin and Candela (2004) suggested affinities between *Kasserinotherium* and *Wirunodon chanku*, from the late Eocene Santa Rosa local fauna in Peru, while Beck (2013) noted similar dental features among *Kasserinotherium*, *Wirunodon*, and *Archaeonothos henkgodhelpi*, from the early Eocene Tingamarra fauna of Northern Queensland, Australia.

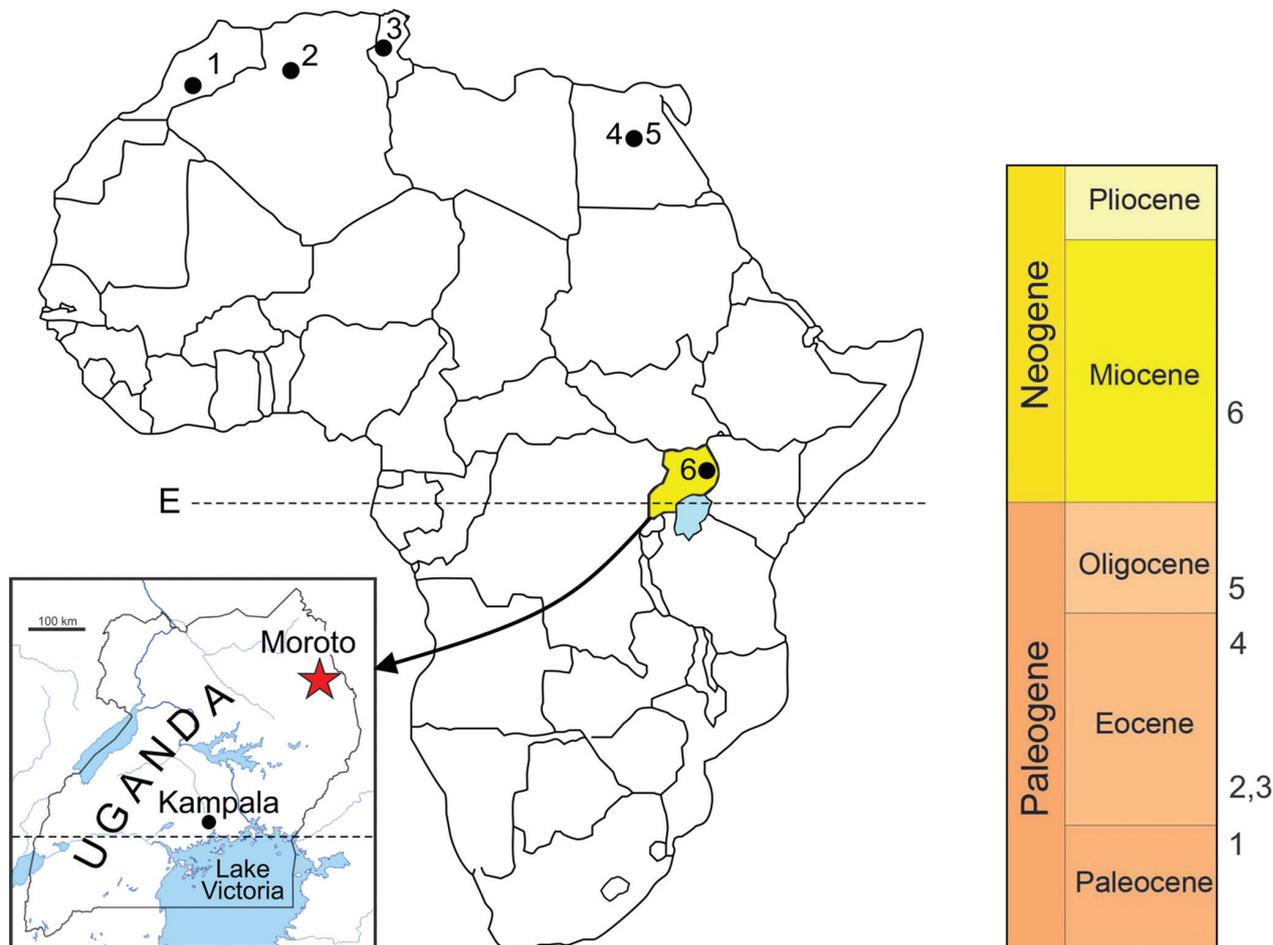


Figure 1. Map of Africa indicating the occurrences of extinct metatherians, or taxa previously regarded as Metatheria. Bottom left, map of Uganda indicating the Moroto II locality. Right, geologic time column indicating the age of each taxon. References: E, Equator; 1, *Garatherium todrae*; 2, *Garatherium mahboubii*; 3, *Kasserinotherium tunisiense*; 4, *Ghamidtherium dimaiensis*; 5, *Peratherium africanum*; 6, *Morotodon aenigmaticus* gen. et sp. nov. See the text and Table 1 for more information on these taxa.

Other extinct African taxa referred to the Metatheria are more probably eutherians (see Table 1). *Garatherium mahboubii* Crochet, 1984 from the Early Eocene of El Kohol (Algeria) was described as a peradectid by Mahboubi et al. (1983) and Crochet (1984). Later, Gheerbrant (1995), describing a new species from the Paleocene of Morocco (*Garatherium todrae* Gheerbrant, 1995), tentatively referred it to *Garatherium* and argued that both species actually represent adapisoriculid eutherians. Its referral to the Adapisoriculidae is currently maintained (De Bast et al. 2012; Crespo and Goin 2021).

Ghamidtherium dimaiensis Sánchez-Villagra, Seiffert, Martin, Simons, Gunnell, & Attia, 2007 was recovered from the Late Eocene of the Fayum Depression (Quarry

L-41; Egypt). Sánchez-Villagra et al. (2007) described *Ghamidtherium* from a partial jaw with m2-3, and referred to this species as an isolated molar, probably an m1. They regarded it as a possible marsupial, noting the difficulty in distinguishing these materials from those of various chiropteran groups. Additional material (two upper molars) was also described as belonging to enigmatic mammals of uncertain affinities. To the authors (Sánchez-Villagra et al. 2007: 413), the upper molars could be "... either a marsupial with some bat-like dental features, or a bat with marsupial-like dental features". Later, other authors such as Gunnell (2010) and Simmons et al. (2016) argued that both *Ghamidtherium* as well as the still unnamed upper molars are more probably referable to the Chiroptera (see also Crespo and Goin 2021).

Table 1. Cenozoic African metatherians (or putative metatherians) described up to now. The type localities of all these taxa are shown in the map of Fig. 1.

Species	Family	Age and locality	Author	Observations
1 <i>?Garatherium todrae</i>	Adapisoriculidae (Eutheria)	Late Paleocene, Morocco	Gheerbrant et al. (1998)	See Seifert (2010), De Bast et al. (2012)
2 <i>Garatherium mahboubii</i>	Adapisoriculidae (Eutheria)	Early Eocene, Algeria	Mahboubi et al. (1983); Crochet (1984).	See Gheerbrant (1995); De Bast et al. (2012)
3 <i>Kasserinotherium tunisiense</i>	?Peradectidae (Metatheria)	Early Eocene, Tunisia	Crochet (1986)	See Goin and Candela (2004); Beck (2013)
4 <i>Ghamidtherium dimaiensis</i>	?Chiroptera, fam. indet. (Eutheria)	Late Eocene, Egypt	Sánchez-Villagra et al. (2007)	See Gunnell (2010); Simmons et al. (2016)
5 <i>Peratherium africanum</i>	Herpetotheriidae (Metatheria)	Early Oligocene, Egypt and Oman	Simons & Bown (1984)	See Hooker et al. (2008)
6 <i>Morotodon aenigmaticus</i> gen. et sp. nov.	Herpetotheriidae (Metatheria)	Early-middle Miocene, Uganda	This work	See Pickford and Mein (2006)

Here we describe a third taxon unambiguously referable to the Metatheria, on the basis of a single, isolated lower molar. It has two unusual features: it comes from equatorial Africa (Uganda), and represents the youngest African metatherian so far known (early Neogene). The specimen was previously studied by Pickford and Mein (2006), together with all other small mammals from the type locality. These authors argued that the specimen belongs to a possible marsupial (Metatheria), discarding it as referable to the Tenrecidae or Chrysochloridae (Eutheria) on the basis of the number of the cuspids in the talonid. They also noted (Pickford and Mein 2006: 364) that the specimen “...belongs to a hitherto undescribed insect-eating mammal but the material is too restricted for us to be able to determine its precise affinities.” Later, Crespo and Goin (2021) mentioned the specimen and commented briefly on its metatherian nature and its possible herpetotheriid affinities. Here we provide a description of the new taxon, together with comparisons with both eutherian and metatherian lineages, and a discussion of its possible affinities, origins and biogeographical significance.

Institutional abbreviation

UM MOR II Uganda Museum, Kampala, Moroto II locality.

Methods

The type specimen was obtained while screen-washing sediments at the Moroto II locality. Comparisons were made with original specimens, casts, photographic stereopairs, drawings, photographs, and SEM micrographs provided in the literature. Measurements were done with a microscope with measuring table to 0.01 mm resolution. Dental terminology is provided in Fig. 4. For some species, their respective m4 have not been found for the purpose of a correct comparison with the holotype of *Morotodon*: *Peradectes chesteri*, *P. californicus*, *Asiadidelphis* (= *Indodelphis*) *luoi*, *Thylacodon montanensis*, *Herpetotherium merriami*, *H. tabrumi*, *H. valens*, and *Peratherium cuvieri*.

Locality, geology and age

The series of fossil localities of Moroto II are located near Kogole Hill, north of Nakiloro Village, in Moroto District, northeastern Uganda (Fig. 1). These sites have been well known since the 1960s, and contain an abundant and diverse mammal assemblage. The first field trip to these sites was carried out by a team led by William (Bill) Bishop; later in the 1980s, and until nowadays, field trips (as the Uganda Palaeontology Expedition of 1985) have been carried out by a team led by one of us (M.P.). The fauna of Moroto II has been intensively studied, especially the hominoids, as well as many other mammalian groups (e.g., eulipotyphlans, bats, anthracotheriids and the metatherian here described; see Pickford et al. 2017; Pickford 2020 and references therein).

The area of the geological succession is in the vicinity of Kogole; it is underlain by basement complex gneisses (Mozambique Belt; Fleuty 1968) and has small outcrops of Neogene deposits comprising Miocene sediments infilling valleys cut into the Precambrian gneisses and schists (Bishop 1958, 1964; Bishop et al. 1969; Pickford and Tassy 1980; Musalizi et al. 2009). They are capped by basalt lava presumably from the Mount Moroto volcano (Horne 1953; Varne 1966, 1967; Fleuty 1968). The fluvial deposits that comprise the mammal-bearing levels are dominated by clays and silts, with less frequent grits and conglomerates (Pickford et al. 2017).

The age of Moroto II is controversial, with two different opinions in the literature: one, based on the geology, dates the locality as 21–20 Ma (early Miocene), around the transition between the Aquitanian and the Burdigalian; it is regarded as older than Napak (Uganda, Faunal Set I, ca 20.5–19.5 Ma; Gebo et al. 1997; Werdelin 2010) (or 19.2 after Van Couvering and Delson 2021). A second view is based on the chronological significance of the faunal assemblage, which suggests an early-middle Miocene age (16.5–15.5 Ma, or late Burdigalian; Ogg et al. 2016); the latter is regarded by us as the most likely age for the mammal-bearing levels of Moroto II.

Systematic palaeontology

Mammalia Linnaeus, 1758

Metatheria Huxley, 1880

?Herpetotheriidae Trouessart, 1879

Morotodon gen. nov.

<http://zoobank.org/68CAD3FD-63A1-411F-8F4F-8287DAEA716E>

Type species. *Morotodon aenigmaticus* gen. et sp. nov.

Morotodon aenigmaticus gen. et sp. nov.

<http://zoobank.org/916A2124-80EE-4B16-A2FF-D7E4A48C529A>

Etymology. “The mysterious tooth from Moroto”. Moroto II is the fossil locality where this taxon was found; “-odon”, from *odontos*, genitive of *odous*, ancient Greek for tooth; gender is masculine; *aenigmaticus*, from the Latin *aenigma* (mystery), refers to the unexpected finding of a metatherian near the Equator in the Neogene of Africa.

Holotype. UM MOR II, 48'04, a last lower left molar (m4; Figs 2, 3; Suppl. material 1 and Suppl. material 2).

Measurements. Total length, 1.63 mm (1 mm trigonid length, 0.63 talonid length); trigonid width, 0.93 mm; talonid width, 0.94 mm (from Pickford and Mein 2006).

Locality and age. Moroto II, north of Nakiloro Village, Moroto District, northeastern Uganda (Fig. 1). Late early Miocene, upper Burdigalian (16.5–15.5 Ma).

Diagnosis. ?Herpetotherid metatherian with lower molars having a short anterior cingulid, a buccal shelf, and a trigonid and talonid with subequal length and width; the m4 has a vertical, well-developed hypoconulid in a central position. The specific diagnosis extends to the genus by monotypy.

Description. Specimen UM MOR II, 48'04 is bi-rooted, both roots being subcircular in section; the anterior root is smaller than the posterior one. The anterior cingulid is short and relatively wide at its central portion. The trigonid is open. The main cusps of the trigonid are well-developed. The paraconid is mesio-lingually positioned. The protoconid is the largest cusp of the tooth, and is slightly anteriorly placed with respect to the metaconid. The paracristid and metacristid are notched. The talonid is bucco-lingually compressed in its anterior half; at its posterior face its width is almost the same as that of the trigonid. The entoconid is broken; apparently, it was bucco-lingually compressed; the pre-entocristid is straight and ends in at posterolingual edge of the metaconid. The hypoconulid is separated from the entoconid; it is well-developed and is centrally placed on the posterior edge of the tooth; it is a vertical cusp (i.e., it is not posteriorly oriented or dorso-ventrally compressed). The hypoconid is only moderately developed; it is also buccally salient, but does not exceed buccally the level of the protoconid. The oblique cristid joins the posterior wall of the trigonid at the labiolingual midpoint of the tooth, below the metacristid notch. There is a well-developed buccal

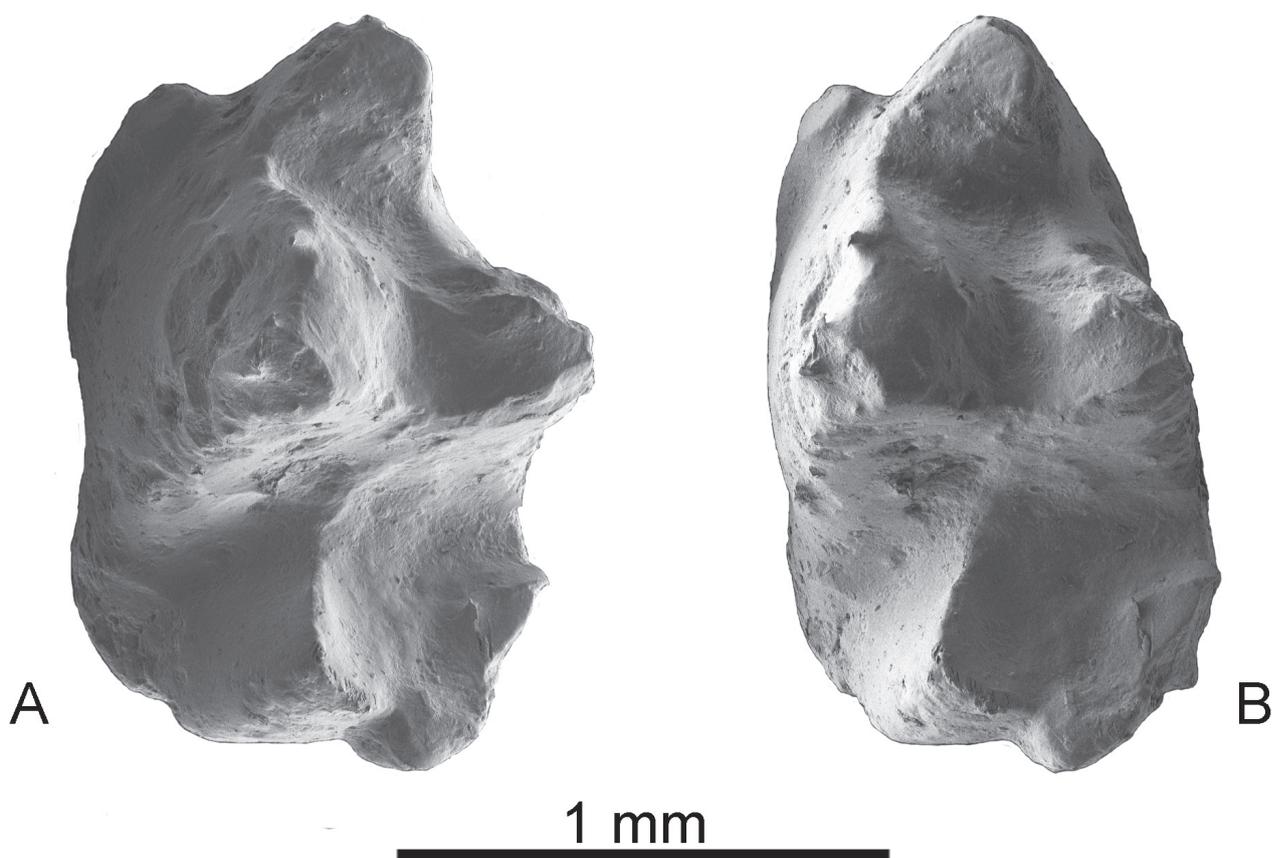


Figure 2. *Morotodon aenigmaticus* gen. et sp. nov. SEM images of specimen UM MOR II, 48'04 (an isolated left m4) in occluso-labial (A) and occlusal (B) views. Scale bar: 1 mm.

shelf, or cingulid, at the base of the crown, running from the base of the hypoconid to the posterobuccal edge of the protoconid. The tooth shows soil corrosion.

Comments. The specimen was originally described as a m1 or m2 (Pickford and Mein 2006). The reduced (laterally compressed) talonid at its anterior half, only moderately developed hypoconid, relatively central position of the hypoconulid, as well as the quite oblique orientation of the oblique cristid, allow us to reassign the specimen to an m4. This kind of reduction in the m4's talonid appears in several metatherians (e.g., *Peradectes russelli* Crochet, 1979 or *Amphiperatherium giselense* (Heller, 1936)).

Comparisons. Specimen UM MOR II, 48'04 is clearly not a deciduous tooth, due to the size and shape of its roots and the angle at which they would be inserted into the mandible. Several eutherian lineages have molar morphologies that are superficially similar to that of *Morotodon aenigmaticus*: afrotheriid “insectivores” (Afrotheria), bats (Chiroptera), some eulipotyphlans (Laurasiatheria, Eulipotyphla), and adapisoriculids (Euarchonta). Early afrotherians include *Ocepeia*, from the late Paleocene of Morocco, which is strikingly different from *Morotodon*. *Ocepeia* has bunoid, almost inflated lower molars with low protoconid, paraconid close to the metaconid; enclosed, deep trigonid basin; the metacristid is not vertical but gently sloping; talonids are multicuspid (up to five cusps), with a reduced hypoconulid. Among the Afroinsectiphilia, macroselidians can also be discarded: for instance, the middle-late Eocene *Nemenchatherium* has very low cusps, the paraconid is close to the protoconid and the hypoconulid, if present, is almost indistinguishable. *Chambius*, from the early or early middle Eocene of Tunisia, has its lower molars rounded in profile, with an indistinguishable hypoconulid, indistinct paraconid, and the talonid narrower than the trigonid.

Afrotheriids such as tenrecs and golden moles (of which at least members of the former were contemporaneous with *Morotodon*), were already discarded on the basis of the number of talonid cusps, three in metatherians and a single, elongated one in tenrecs (Pickford and Mein 2006). Effectively, tenrecids such as *Promicrogale*, from the Miocene of Namibia (Pickford 2018) or *Nanogale* from the Eocene of Namibia (Pickford 2019), have quite different lower molars in which the talonid is much smaller than the trigonid and lacks a hypoconulid, the paraconid in m2-3 is low and close to the metaconid, and the protoconid is proportionally very large; the talonid basin is much lower than that of the trigonid. Chrysochlorids have highly derived molars, of which the lower ones lack the talonid, while the paraconid and metaconid are reduced and twinned.

Chiropterans can also be ruled out because of the morphology and position of the hypoconulid, which in *Morotodon* is more developed and more centrally placed at the distal edge of the tooth; additionally, chiropterans have a buccal shelf or cingulid which is mesiodistally complete, linking the anterior and posterior cingulids. *Morotodon* differs from the probable chiropteran *Ghamidtherium dimaiensis* Sánchez-Villagra, Seiffert, Martin, Simons,

Gunnell, & Attia, 2007 in that the anterior cingulid is shorter and does not extend distally at the crown base; the metaconid is anteriorly positioned with respect of the protoconid; the entoconid is less developed; it lacks a posterior cingulid; the hypoconulid is larger, higher and less dorso-ventrally compressed, and it is not placed immediately distal to the entoconid but instead buccal to it; finally, the oblique cristid in *Morotodon* is less parallel to the dental axis.

Morotodon differs from the Eulipotyphla in the presence and morphology of the hypoconulid. In their lower molar morphology representatives of the Soricidae and Talpidae have some similarities with *Morotodon*. However, the anterior cingulid in soricids is better developed and may continue posteriorly towards the buccal surface of the crown, and in the talonids the hypoconulid is reduced (or, if not reduced, is placed very low regarding the entoconid) and located immediately posterior to the entoconid. Generalized erinaceids such as *Galerix* lack a hypoconulid, and, in the last molar, the paraconid is crest-like, and the oblique cristid is parallel to the dental axis. Among other more derived soricomorphs, the living *Solenodon*, for instance, has extremely reduced talonids and mesio-distally compressed trigonids.

Being more similar in overall morphology (but see below), a more detailed comparison of *Morotodon* with individual adapisoriculid taxa is worthwhile. *Morotodon* differs from *Afrodon gheerbranti* De Bast & Smith, 2017 in having a more lingual paraconid, more developed protoconid, presence of a buccal shelf (or cingulid), better developed hypoconid and entoconid, and a more centrally placed hypoconulid. It differs from *Afrodon chleuhi* Gheerbrant, 1988 in having a longer trigonid, a better developed protoconid, trigonid and talonid of similar width, and a less developed, more anteriorly placed hypoconulid. It differs from *Bustylus marandati* (Crochet and Sigé 1983) in having a narrower anterior cingulum, longer trigonid, more centrally placed metaconid, a developed buccal shelf, a larger entoconid, and an independent hypoconulid. It differs from the todralestid *Todralestes variabilis* Gheerbrant, 1991 in having a less reduced talonid, the presence of a buccal shelf, and a larger hypoconulid.

Comparisons with early Marsupialiformes. *Morotodon aenigmaticus* compares best with metatherian mammals, especially with Marsupialiformes (most metatherians except the early clade Deltatheridia). The best known early marsupialiform (i.e., non deltatheroid) metatherian is *Kokopellia juddi* Cifelli, 1993, from the medial Cretaceous of Utah in North America (see Cifelli and Muizon 1997 for a detailed description of the dentition of *Kokopellia*). Molars of *Kokopellia* represent the generalized condition for almost all Cenozoic metatherians. *Morotodon aenigmaticus* differs from *Kokopellia juddi* in that its m4 lacks a posterior cingulid, and a shorter talonid (clearly longer in *Kokopellia* in all lower molars), a less posteriorly placed metaconid, a smaller hypoconulid (in *Kokopellia* it is larger and closer to the entoconid), and a smaller and less anteriorly placed hypoconid. Both *Morotodon* and *Kokopellia* share a

well-developed buccal shelf (or cingulid), and a similarly oriented oblique cristid, which ends anteriorly at a point below the metaconid notch.

Comparisons with Peradectidae. Most Cenozoic Holarctic metatherians belong either to the Peradectidae or to the Herpetotheriidae, so a detailed comparison with species of these two groups is needed in order to clarify the affinities of *Morotodon aenigmaticus*. Most representatives of both families are known from the Northern Hemisphere. In North America, peradectids and herpetotheriids are known from the Late Cretaceous to the Miocene, while in Eurasia they span the early Eocene to the Miocene (in Europe, peradectids are restricted to the Eocene). In Africa, peradectids had been known only for the early Eocene (*Kasserinotherium*), while herpetotheriids are known for the early Oligocene (*Peratherium*). Our allocation of *Morotodon* to herpetotheriids expands the group to the Miocene.

Peradectes. *Morotodon aenigmaticus* differs from *Peradectes lousi* Crochet, 1979 in having a proportionally longer talonid, less difference in height between the trigonid and the talonid, and in that the hypoconid is more salient. Differs from *Peradectes californicus* (Stock, 1936) (m4 of this species is unknown) in that the metaconid is more anteriorly placed than the protoconid, and the talonid is proportionally narrower. Differs from *Peradectes chesteri* Gazin, 1952 (although the m4 of this species is unknown) in having a larger paraconid which is not as close to the metaconid, and a proportionally larger hypoconulid. Differs from *Peradectes coprexeches* Williamson & Taylor, 2011 in having a narrower trigonid, the oblique cristid is not subparallel to the preentocristid (in such a way that the talonid is anteriorly narrower), the hypoconulid is more developed and less paired to the entoconid; finally, a buccal cingulid is present. Differs from *Peradectes minor* Clemens, 2006 and *Peradectes mutigniensis* Crochet, 1979 in having a paracristid which is less transverse to the dental axis, the hypoconulid is farther from the entoconid, it lacks a posterior cingulid and has a buccal shelf or cingulid. Differs from *Peradectes pauli* (Gazin, 1956) in having a more salient hypoconid, while the oblique cristid is less parallel to the dental axis. Differs from *Peradectes protinnominatus* McKenna, 1960 in having a longer talonid, a larger hypoconulid which is farther from the entoconid, and in that the oblique cristid is less parallel to the dental axis. Differs from *Peradectes russelli* Crochet, 1979 in that the paraconid and metaconid are less close to each other, the entoconid is smaller, the hypoconulid is farther from the entoconid, and the oblique cristid is less parallel to the dental axis.

Mimoperadectes. Differs from *Mimoperadectes labrus* Bown & Rose, 1979 in having a less developed anterior cingulid, a shorter trigonid, a paraconid that is farther from the metaconid and the hypoconulid and the entoconid are more detached (for this reason, the talonid is wider posteriorly).

Nanodelphys. Differs from *Nanodelphys hunti* (Cope, 1873) in having a narrower trigonid and shorter talonid, a hypoconulid that is set farther from the entoconid, and the oblique cristid not being subparallel to the preentocristid.

Armintodelphys. Differs from *Armintodelphys dufraini* Smith & Smith, 2013 in having a wider anterior cingulid, a less reduced paraconid, a slightly posteriorly placed paraconid (relative to the protoconid), a less straight oblique cristid, a hypoconulid that is farther from the entoconid, and in the presence of a buccal shelf. Differs from *Armintodelphys dawsoni* Krishtalka & Stucky, 1983 in having a more developed paraconid which is less mesio-distally compressed, and a narrower talonid. Differs from *Armintodelphys blacki* Krishtalka & Stucky, 1983 in having an anteriorly placed metaconid with respect to the protoconid, the anterior half of the oblique cristid not being parallel to the dental axis, a smaller hypoconulid that is farther from the entoconid, and a narrower talonid basin.

Comparisons with Herpetotheriidae. Asiadidelphis. *Morotodon aenigmaticus* differs from *Asiadidelphis zaissanense* Gabunia, Shevyreva, & Gabunia, 1990 (described in Ziegler et al. 2007; fig. 3.3) in having a wider anterior cingulid, oblique cristid less parallel to the dental axis, and a more buccally placed hypoconulid. Differs from *Asiadidelphis tjutkovae* Emry, Lucas, Szalay, & Tleuberdina, 1995 in its smaller size, a more centrally positioned hypoconulid on the posterior edge of the talonid, and a larger entoconid. Differs from *Asiadidelphis* (= *Indodelphis*) *luoi* (Bajpai, Kapur, Thewissen, Tiwari, & Das, 2005) in having a more developed anterior cingulid, a proportionally higher protoconid relative to the metaconid, a mesio-distally less compressed paraconid, a narrower talonid and oblique cristid that is less parallel to the dental axis.

Swaindelphys. Differs from *Swaindelphys encinensis* Williamson & Taylor, 2011 in having a shorter anterior cingulid, narrower trigonid and talonid, a less developed, lower hypoconulid, and, in occlusal view, a straight but not curved oblique cristid. Differs from *Swaindelphys cifelli* Johanson, 1996 in having a more developed anterior cingulid, in its hypoconulid which is farther from the entoconid, a smaller hypoconulid, and a talonid that is longer relative to the trigonid.

Thylacodon. Differs from *Thylacodon montanensis* Williamson, Brusatte, Carr, Weil, & Standhardt, 2012 in having (although the m4 was not preserved in the latter) a narrower entoconid, a hypoconulid that is farther from the entoconid, and in the absence of a posterior cingulid. Differs from *Thylacodon pusillus* (Archibald, 1982) in having a better developed anterior cingulid, smaller entoconid, and a hypoconulid that is not twinned to the entoconid.

Golerdelphys. Differs from *Golerdelphys stocki* Williamson & Lofgren, 2014 in lacking a posterior cingulid and in that the entoconid is proportionally smaller.

Copedelphys. Differs from *Copedelphys titanelix* (Matthew, 1903) in having a shorter and wider anterior cingulid, a proportionally smaller trigonid, a paraconid that is not mesio-distally compressed, an oblique cristid obliqua is not straight, a buccally more salient hypoconid, and in that the hypoconulid is less posteriorly projected. Differs from *Copedelphys stevensoni* (Cope, 1873) in having a shorter and wider anterior cingulid, a

less antero-posteriorly compressed paraconid, an oblique cristid obliqua that is less parallel to the preentocristid, and in the presence of a buccal shelf (or cingulid).

***Herpetotherium*.** Differs from *Herpetotherium youngi* (McGrew, 1937) in having a shorter anterior cingulid, an oblique cristid that meets the trigonid more lingually, a more developed hypoconulid that is not twinned to the entoconid, and a more salient hypocone. Differs from *Herpetotherium fugax* Cope, 1873 in having a shorter and wider anterior cingulid, a proportionally narrower trigonid, a paracristid that is less transversal to the dental axis, an oblique cristid that is not subparallel to the preentocristid, and a hypoconulid that is farther from the entoconid. Differs from *Herpetotherium comstocki* (Cope, 1884) in having a shorter anterior cingulid, an oblique cristid that is subparallel to the dental axis, a proportionally larger hypoconulid that is farther from the entoconid; in turn, this last cusp is proportionally smaller. Differs from *Herpetotherium edwardi* (Gazin, 1952) in having larger paraconid and hypoconulid, the latter smaller and farther from the entoconid, and an oblique cristid that is less parallel to the dental axis. Differs from *Herpetotherium marsupium* Troxell, 1923 in having a smaller entoconid, more buccal hypoconulid, and a straighter oblique cristid that is less parallel to the dental axis. Differs from *Herpetotherium merriami* (Stock & Furlong, 1922) in having (although the m4 was not preserved) a larger hypoconulid which is placed farther from the entoconid. Differs from *Herpetotherium tabrumi* Korth, 2018 in having (although the m4 is not present) a larger hypoconulid which is farther from the entoconid, a shorter preentocristid, and an oblique cristid that is less parallel to the dental axis. Differs from *Herpetotherium valens* (Lambe, 1908) in having (although the m4 was not preserved) a shorter and wider anterior cingulid, relatively narrower talonid, a paracristid that is less transversal to the dental axis, paraconid and metaconid clearly set apart from each other, a smaller entoconid and a proportionally larger hypoconulid that is farther from the entoconid.

***Peratherium* (Fig. 3).** Differs from *Peratherium africanum* in having a shorter and wider anterior cingulid, deeper oblique cristid which is less parallel to the dental axis, a slightly sloping and not vertical posterior wall of the trigonid (the metacristid), and a more buccally placed hypoconulid. Differs from *Peratherium bretouense* Crochet, 1979 in having a shorter anterior cingulid, a less developed entoconid, a less bucco-lingually compressed hypoconulid that is placed farther from the entoconid, and lack of a posterior cingulid. Differs from *Peratherium cayluxi* Filhol, 1877 in having a shorter anterior cingulid, a more buccally salient hypoconid, and a smaller entoconid. Differs from *Peratherium constans* (Teilhard de Chardin, 1927) in having a wider and shorter anterior cingulid, a more buccally salient hypoconid, a smaller hypoconulid that is placed farther from the entoconid. Differs from *Peratherium cuvieri* (Fischer, 1829) in having (although the m4 was not preserved in the latter) a proportionally larger hypoconulid which is more buccally

placed, lack of a posterior cingulid, a smaller entoconid, and a longer talonid. Differs from *Peratherium elegans* (Aymard, 1846) in having a narrower anterior cingulid, a larger hypocone which is less rounded, a larger and more buccally placed hypoconulid of which the buccal slope does not form a continuum with the posthypocristid. Differs from *Peratherium laverghense* Crochet, 1979 in that the hypoconid is more buccally salient, the hypoconulid is larger and not placed immediately posterior to the entoconid. Differs from *Peratherium matronense* Crochet, 1979 in having a shorter anterior cingulid, a more anteriorly placed metaconid regarding the protoconid, and a hypoconulid that is not immediately distal to the entoconid. Differs from *Peratherium monspeliense* Crochet, 1979 in having a shorter anterior cingulid, and in that the oblique cristid is less parallel to the dental axis. Differs from *Peratherium perrierense* Crochet, 1979 in having a shorter anterior cingulid, an oblique cristid that is less parallel to the dental axis, and a hypoconulid that is farther from the entoconid. Differs from *Peratherium sudrei* Crochet, 1979 in that the hypoconulid is closer to the entoconid, and the entoconid and the hypoconid are at the same level (while in *P. sudrei* the entoconid is more anteriorly placed).

***Amphiperatherium* (Fig. 3).** Differs from *Amphiperatherium brabatense* Crochet, 1979 in having a wider anterior cingulid, and a proportionally larger and more buccally placed hypoconulid. Differs from *Amphiperatherium minutum* (Aymard, 1846) in having a less reduced talonid and in that the hypoconid is more buccally salient. Differs from *Amphiperatherium goethei* Crochet, 1979 in having a shorter anterior cingulid, a paraconid that is less close to the metaconid (therefore, the trigonid is less mesiodistally compressed), and an anteriorly slightly narrower talonid. Differs from *Amphiperatherium lamandini* (Filhol, 1876) in having a more salient hypoconid, larger hypoconulid which is farther from the entoconid, and in lacking a posterior cingulid. Differs from *Amphiperatherium frequens* (Meyer, 1846) in having a less reduced talonid, a shorter anterior cingulid, presence of a buccal cingulid, and the hypoconulid that is farther from the entoconid. Differs from *Amphiperatherium maximum* Crochet, 1979 in its smaller size, shorter anterior cingulid, a mesio-distally less compressed paraconid, a larger hypoconulid that is placed farther from the entoconid, and a smaller entoconid. Differs from *Amphiperatherium bastbergense* Crochet, 1979 in having a shorter anterior cingulid, a mesio-distally less compressed paraconid, a smaller entoconid, a larger hypoconulid that is farther from the entoconid, and in the absence of a posterior cingulid. Differs from *Amphiperatherium fontense* Crochet, 1979 in having a smaller anterior cingulid, an anteriorly narrower talonid, a proportionally smaller entoconid, and a hypoconulid that is larger and placed farther from the entoconid. Differs from *Amphiperatherium ambiguum* (Filhol, 1877) in having a shorter anterior cingulid and the hypoconulid being farther from the entoconid.

Differs from *Amphiperatherium exile* (Gervais, 1848–52) in having a shorter anterior cingulid, a mesio-distally less compressed paraconid and an anteriorly narrower talonid. Differs from *Amphiperatherium bourdellense* Crochet, 1979 in having a narrower talonid and a more

central position of the hypoconulid, which is placed farther from the entoconid. Differs from *Amphiperatherium giselense* (Heller, 1936) in having a mesio-distally less compressed paraconid, larger hypoconulid, anteriorly narrower talonid, and lack of a posterior cingulid.

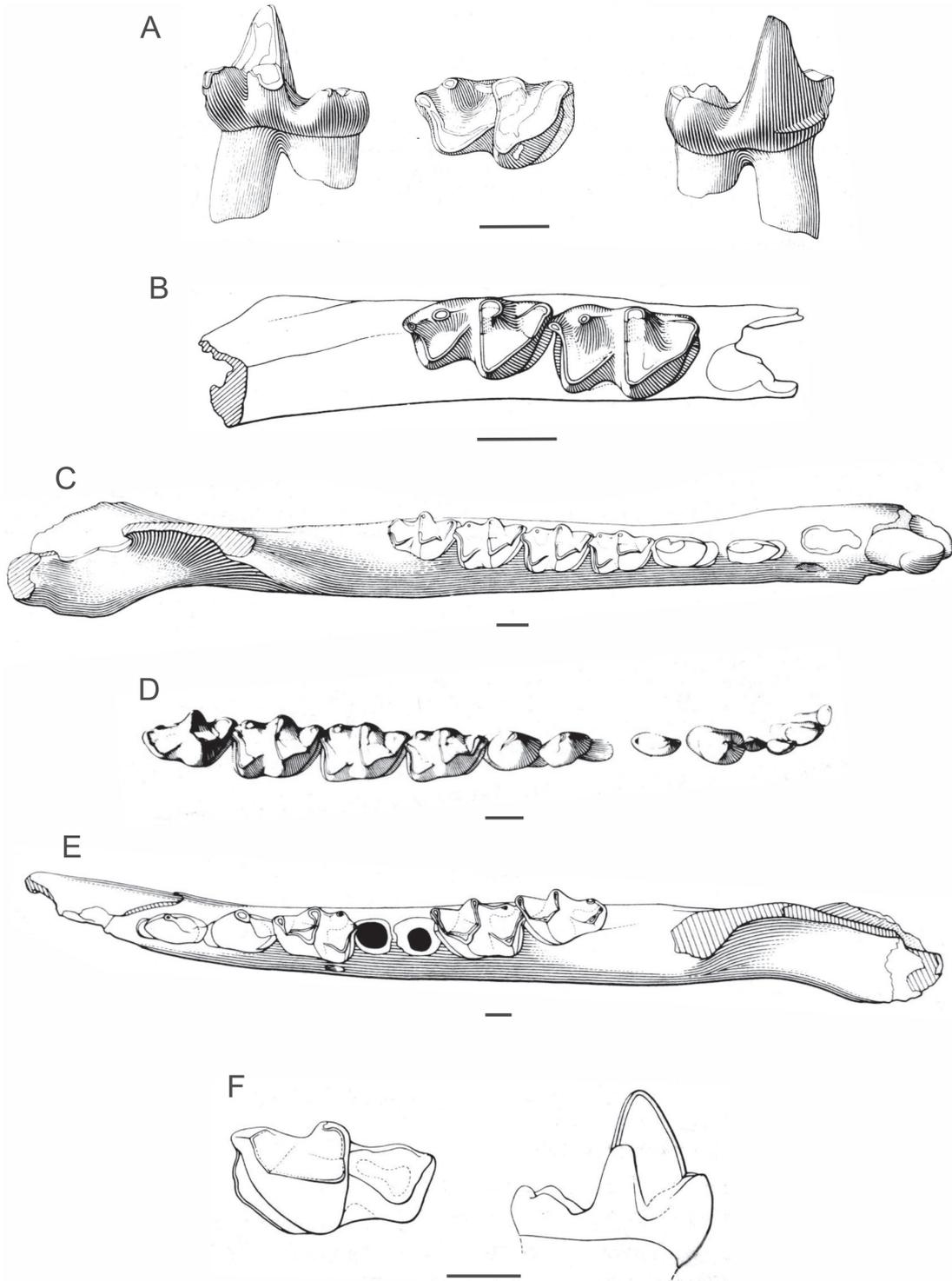


Figure 3. Lower molar series of various marsupial taxa belonging to Peradectidae (A) and Herpetotheriidae (B–F). **A.** *Peradectes russelli*, CB 1027 (CL), right m4 in lingual, occlusal, and labial views; **B.** *Amphiperatherium lamandini*, ECA 3104 (UM), fragment of right mandible with m3-4 in occlusal view; **C.** *Peratherium elegans* (type of *Peratherium agmardi* Filhol), QU 8216 (MNHN), right mandible with c and p1-m4 in occlusal view; **D.** *Peratherium perrierense* (holotype), PRR 2524, right mandible with i1-m4 in occlusal view; **E.** *Peratherium cayluxi*, QU 8217 (MNHN) (holotype), left mandible with p2-m1 and m3-4 in occlusal view; **F.** *Amphiperatherium ambiguum*, PLA 1042 (UM), left m4 in occlusal and lingual views. Figures after Crochet (1980). Scale bars: 1 mm.

Rumiodon. Differs from *Rumiodon inti* Goin & Candela, 2004 in having a wider anterior cingulid, distinct hypoconulid that is larger and not twinned with the entoconid, and an oblique cristid that is less parallel to the dental axis.

Comparisons with other Cenozoic Holarctic metatherians. *Estelestes.* Differs from *Estelestes ensis* Novacek, Ferrusquía-Villafranca, Flynn, Wyss, & Norell, 1991 (early Eocene; referred by the authors to the “Didelphidae”), in that it lacks a postcingulid (in *Estelestes* the postcingulid extends anteriorly forming a buccal cingulid basal to the hypocone), the hypocone is more buccally salient, the hypoconulid is farther from the entoconid and less posteriorly tilted; finally, an oblique cristid is less parallel to the dental axis.

Orhaniyeia. Differs from *Orhaniyeia nauta* Métais, Coster, Kappelman, Licht, Ocañoğlu, Taylor, & Beard, 2018 (middle Eocene of Turkey) in being much smaller, has less bunoid molars, the anterior cingulid is better developed, the paraconid is placed farther from the metaconid, the paracristid is less transverse to the dental axis, the talonid is shorter, the hypoconid is much more distally placed, an oblique cristid that is less parallel to the dental axis; finally, it lacks multiple cusps on the pre-entocristid.

Comparisons with South American “opossum-like” metatherians. *Morotodon aenigmaticus* differs from the Protodidelphidae (early to middle Eocene) in being much smaller, has less bunoid molars, and smaller and narrower talonids. Differs from the Derorhynchidae (Paleogene of South America and Antarctica) in having a longer talonid, no posterior cingulid, smaller entoconid and larger hypoconulid. Differs from species of *Gaylordia* (early Eocene) in having a less developed anterior cingulid, longer talonid, less lingually placed paraconid; finally, an oblique cristid that is less parallel to the dental axis. Differs from species of *Marmosopsis* (early Eocene) in lacking a posterior cingulid and an oblique cristid that is less subparallel to the dental axis. Differs from species of *Minusculodelphis* (Eocene) in its larger size, better developed talonids and hypoconid, and in the persistence of the hypoconulid. Differs from species of *Monodelphopsis* (early Eocene) in having a narrower talonid, an oblique cristid that is less subparallel to the dental axis, and better developed entoconid and hypoconulid which are less closely set to each other. Differs from species of *Carolopaulacoutoia* (early Eocene) in its shorter talonid, less parallel oblique cristid to the dental axis, more salient hypoconid, and smaller and more centrally placed hypoconulid. Differs from species of *Itaiboraidelphys* (early Eocene) in having a poorly developed anterior cingulid, the paraconid is more distant from the metaconid, an oblique cristid that is less parallel to the dental axis, and the hypoconulid is more centrally placed. Differs from species of *Didelphopsis* (Paleocene-early Eocene) in having a shorter anterior cingulid, proportionally longer trigonid, the paraconid is placed farther from the metaconid, an oblique cristid that is less parallel to the dental axis, and the hypoconulid is larger and farther from the entoconid. Differs from *Pucadelphys andinus* Marshall & Muizon, 1988 (early Paleocene) in having a larger hypoconulid and an oblique cristid that is less parallel to the dental axis.

Discussion

Affinities of *Morotodon aenigmaticus* gen. et sp. nov.

With only two exceptions (the deltatheroidan *Gurbanodelta kara*, from the Paleocene of China, and the

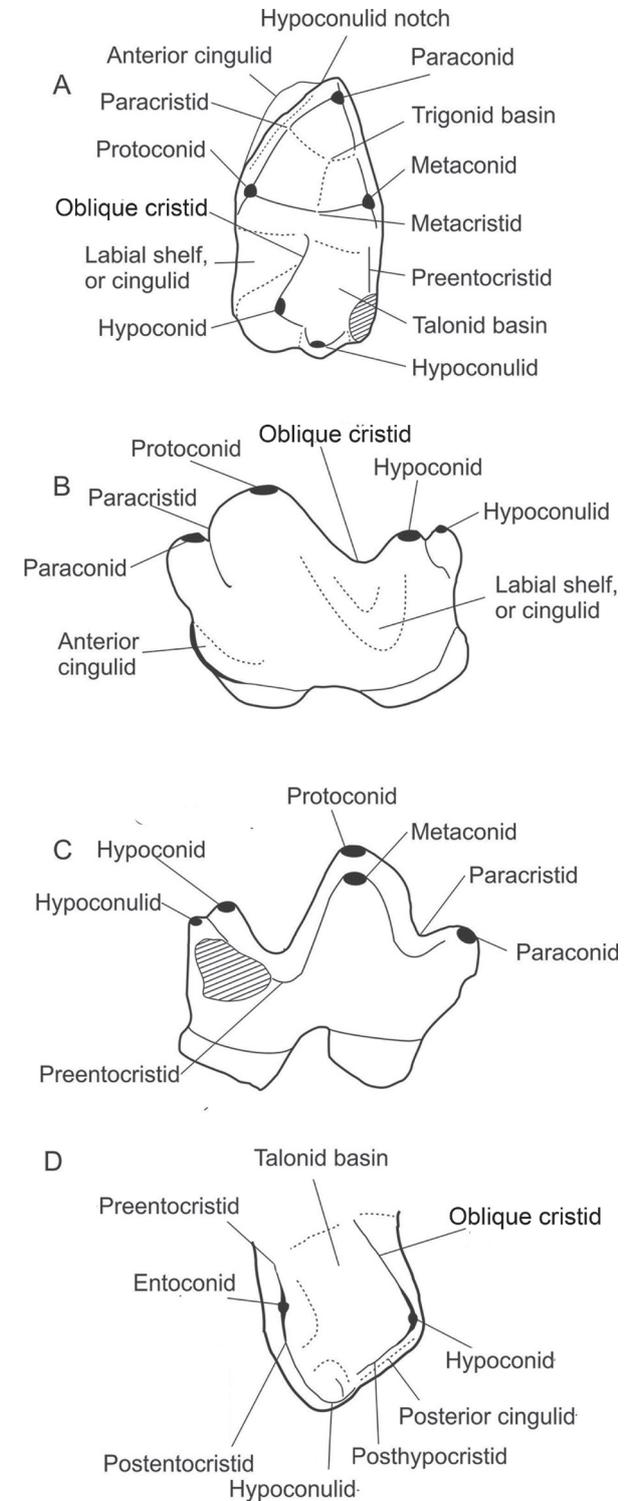


Figure 4. Schematic drawing of *Morotodon aenigmaticus* gen. et sp. nov. in occlusal (A), buccal (B), and lingual (C) views; talonid of the *Armintodelphys* (based on specimen IRSNB M2152 published by Smith and Smith (2013) (D).

anatoliadelphids, from the middle Eocene of Turkey), all other Cenozoic Afro-Eurasian metatherians (36 species) have been referred either to the Peradectidae (six species) or to the Herpetotheriidae (the remaining ones). It is obvious to us that *Morotodon aenigmaticus* is neither a deltatheroidan nor an anatoliadelphid. On the contrary, its molar pattern is much more similar to that of “opossum-like marsupials” such as herpetotheriid and peradectid marsupialiforms. Herpetotheriids differ from peradectids in several aspects of their respective molar structure. Regarding the lower ones, Crochet (1979, 1980) noted that the former (his “Didelphini”) have hypoconulids and entoconids of unequal height (the entoconid is higher in m1-3, but not in m4). On the contrary, peradectids (his “Peradectini”) have entoconids and hypoconulids of similar height in all lower molars, including the m4. Even though the entoconid is broken in the m4 of *Morotodon aenigmaticus*, it is clear that the hypoconulid was a larger cusp (see the lingual

views of specimen UM MOR II 48'04 in Figs 2, 3). However, it is impossible to assign *Morotodon* to either family with certainty. Our observations on the relative height of both cuspids in the m4 of species of *Peradectes*, *Peratherium*, and *Amphiperatherium* indicate high variability in this feature. Among both herpetotheriid genera, all states can be observed: entoconid higher, hypoconulid higher, or both cusps being subequal. In Table 2 we have summarized our observations of several features of the m4 of *Morotodon aenigmaticus* and species of *Peradectes*, *Peratherium*, and *Amphiperatherium* figured in the literature. It can be seen that in most of the surveyed features there is variability enough among species, in such a way that it precludes any certain assignation of *Morotodon*. In general terms, however, as well as in at least one feature (see below and Table 2) we note that *Morotodon aenigmaticus* resembles species of Herpetotheriidae more closely than of any peradectid so far known.

Table 2. A comparison of dental features of the last lower molar in *Morotodon aenigmaticus* and in species of *Peradectes*, *Peratherium* and *Amphiperatherium*.

Features in m4	<i>Morotodon</i>	<i>Peradectes</i>	<i>Peratherium</i>	<i>Amphiperatherium</i>
1. Paracristid inclination	45°	45°, or less	45° or less	45°, less than 45°, more than 45°
2. Metaconid position relative to the protoconid	Slightly posterior	Posterior, or at the same level	Same level, or metaconid posterior	Same level, or metaconid posterior, or protoconid posterior
3. Hypoconulid position on the rear of the entoconid / proximity with the entoconid	Central	Almost central, or far lingual, or almost twinned to entoconid	Almost central, or far lingual, or almost twinned to entoconid	Almost central, or far lingual, or almost twinned to entoconid
4. Postcingulid (present /absent /variable)	Absent	Variable	Variable	Variable
5. Buccal cingulid (pres/abs/var)	Present	Variable	Variable	Variable
6. Relative heights, entoconid / hypoconulid	Hypoconulid higher	Hypoconulid higher, or equal	Hypoconulid higher, or equal, or entoconid higher	Hypoconulid higher, or equal, or entoconid higher
7. Width of the talonid at its anterior edge	Narrow	Less narrow, or wide	Narrow	Narrow, or less narrow
8. Mesiodistal compression of paraconid	Not compressed	Compressed, or not compressed	Compressed, or not compressed	Compressed, or not compressed
9. Entoconid position relative to hypoconid	Entoconid slightly anterior	Same level, or ent. Slightly anterior, or ent. Slightly posterior	Same level, or ent. slightly anterior	Same level, or ent. slightly anterior
10. Width of distal edge of the talonid	Wide	Wide, or reduced but wider than the anterior edge	Narrow, or almost as wide as the trigonid	Almost as wide as the trigonid, or narrow
11. Postentocristid linking entoconid with hypoconulid	Absent	Present	Absent	Absent
12. Metacristid slope (almost vertical, gently sloping)	Almost vertical	Almost vertical	Almost vertical	Almost vertical, one species gently sloping

Ladevéze et al. (2012) studied a large sample of dental materials (around 400 specimens) belonging to herpetotheriid metatherians from the earliest Eocene of Dormaal (Belgium). Previous reviews of the herpetotheriids from Dormaal led to the recognition of only two species: *Peratherium constans* Teilhard de Chardin, 1927 and *Amphiperatherium brabantense* Crochet, 1979. Ladevéze et al. (2012) concluded that, due to the dental variability shown by the dental materials, the two species are indistinguishable, therefore they referred both to *Peratherium constans*. Actually, they not only questioned the validity of the *Amphiperatherium* species but also the status of the genus *Amphiperatherium* itself. While we agree that

several features used to distinguish the two genera are subtle, and subject to variability (see above), we prefer to maintain the validity of *Amphiperatherium* until a thorough review of all Northern Hemisphere (North American and Eurasian) herpetotheriids is made.

If molars in general are subject to some degree of variability, the case of m4 is more evident. Unlike several eutherians, metatherian molars invariably erupt successively, from front to back; the hypoconulid of the preceding molar serves as a guide for the alignment of the succeeding one. The hypoconulid of the former fits in the hypoconulid notch of the latter – a groove delimited lingually by the mesial end of the anterior cingulid, and buccally

by the paraconid. In such a way, the succeeding molar erupts in precise alignment in the molar row. In mammals with mostly orthal jaw movements, such as those with insectivorous, faunivorous or carnivorous feeding habits, it is understandable that selective pressures strongly favour stable morphologies among these structures – any malocclusion could lead to the breaking of teeth. Not having a succeeding molar behind, the m4 in metatherians, and especially the talonid, is subject to a larger degree of variability (see, e.g., Martin 2005 on the various talonid morphologies in the m4 of the living didelphid *Lestodelphys halli*). The position of the hypoconulid at the distal edge of the talonid, for instance, tends to be located much more buccally with respect to the entoconid than in the preceding molars (m1-3; see, e.g., Hooker et al. 2008).

Table 2 shows a dozen features of the m4 structure, most of them dealing with the talonid. All these features were used to compare *Morotodon aenigmaticus* with several species of *Peradectes* (Peradectidae), and *Peratherium* and *Amphiperatherium* (Herpetotheriidae). Many of them are subject to some, or much, variability. When all features are considered, however, *Morotodon* fits better in the herpetotheriid than in the peradectid general pattern.

Following Ladéveze et al. (2012), Smith and Smith (2013) stated that the presence of a postentocristid (Fig. 4) in the lower molars was a diagnostic feature of the Peradectidae, while in herpetotheriids there is a notch between the entoconid and the hypoconulid. *Morotodon aenigmaticus* lacks a postentocristid, thus suggesting affinities to the Herpetotheriidae.

Among herpetotheriids, *Morotodon* is more similar to some species of *Peratherium*, such as *P. sudrei*, *P. perrierense*, *P. constans* and *P. cayluxi*, but differs in the position of the hypoconulid, the size of the hypoconid and the length of the anterior cingulid. More remarkable is the similarity with *Amphiperatherium goethei*; among other features, the two taxa share a proportionally similar size and position of the hypoconulid. Among North American metatherians, we note a general similarity with *Golerdelphys stocki*, even though the materials referred to this species have not preserved the m4. However, judging from its preserved molars, similar morphologies can be observed: short and wide anterior cingulid, not mesiodistally compressed paraconid, proportionally large and vertical hypoconulid, laterally compressed entoconid, and, probably, presence of a buccal shelf (or cingulid; see fig. 4E in Williamson and Lofgren 2014). Summarizing, we find that *Morotodon aenigmaticus* shares more features with herpetotheriids than with any other group of Marsupialiformes. Not being able to establish this assignment with complete certainty, we opt to refer the African taxon to the ?Herpetotheriidae.

Origin of *Morotodon aenigmaticus* gen. et sp. nov.

Most of the similarities between the m4 of *Morotodon* and that of several herpetotheriids are based on features

which are generalized for the family: relatively large hypoconulid, non-reduced talonid, paraconid in a mesio-lingual location, not appressed to the metaconid. The already mentioned species of European genera that show these similarities are all from the Eocene except *P. cayluxi*, from the basal Oligocene (Crochet 1980). In turn, *Golerdelphys stocki* comes from the late Palaeocene Goler Formation in USA, North America (Williamson and Lofgren 2014). Summarizing, all metatherians showing similarities with *Morotodon aenigmaticus* come from Paleogene levels of the Northern Hemisphere. Its origin from some region of Eurasia, by the Eocene or Oligocene is, in consequence, the most probable hypothesis. Additional evidence supporting this hypothesis is the high abundance of Eocene metatherians in Europe (Crochet 1980) and previously recognized migrations between the two continents by several taxa: the occurrence of metatherians in the Eocene-Oligocene of northern Africa and Arabia (Gunnell 2010), the entrance into Africa of several lineages of rodents (zegdoumyids, anomaluroids and phiomyids), primates, and anthracotheres. Inversely, it should be noted the record of embrithopods and a probable proboscidean of African affinities in the Paleocene-Eocene of Europe and/or Asia (Sen 2013; and references therein).

The hypothesis of an Eurasian origin of *Morotodon* is reinforced by the tectonic, climatic and eustatic events that happened by the latest Paleocene and earliest Eocene, which may have facilitated these faunal exchanges. Evidence of a land bridge at northwestern Iran and southeastern Turkey is yielded by the Gercüs Formation; these floodplain/lacustrine/lagoonal/coastal plain sediments were deposited during the first phases of the collision between Africa and Eurasia (Haq et al. 1987; Zachos et al. 2001; Sengör et al. 2008; Sen 2013).

Palaeoecology

The sediments of the southern layers of Moroto II were deposited in a shallow valley, similar to the present day Karamoja Plain (Pickford and Mein 2006), in the Moroto region. The composition of these sediments indicates a depositional environment dominated by shallow rivers, but with more or less permanent bodies of water in dry seasons. This is evident from the high number of aquatic or amphibious taxa, including invertebrates (e.g., crabs) and vertebrates such as fishes, frogs, crocodiles, aquatic turtles or amphibious mammals (e.g., anthracotheres; see Pickford and Mein 2006).

The plentiful presence of the terrestrial snail *Nothapalinus*, suggests the presence of grassy areas (Pickford 1995). However, the record of anomalurid rodents, galagids, cercopithecids, hominoids and folivorous proboscideans also suggests the nearby presence of thicker vegetation. In summary, the evidence at hand suggests that during the basal middle Miocene the Moroto landscapes were dominated by open woodland and bushland (see Suppl. material 3).

Following the palaeoecological analysis of some herpetotheriid species made by Kurz (2005), we infer similar ecological patterns in *Morotodon aenigmaticus*. Its molar pattern matches that of other insectivorous “opossum-like” marsupialiforms; in addition, the relatively well-developed paracristid also suggests some faunivorous habits. Briefly, it can be inferred that it had an insectivorous–faunivorous diet and, probably, cursorial locomotion. Species of *Amphiperatherium* were scansorial and more insectivorous than those of *Peratherium* (see Kurz 2005). The terrestrial character of the representatives of this family is confirmed by a study of a complete skeleton referable to *Herpetotherium*, found in North America (Horovitz et al. 2008); it differs from peradectids in that the latter were more arboreal and insectivorous to frugivorous in their feeding habits (Kurz 2005; Rose et al. 2012). The suggested habits of *Morotodon* are consistent with the inferred palaeoenvironment of Moroto II.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Supplementary material 1

3-D video of a digital reconstruction of *Morotodon aenigmaticus* gen. et sp. nov.

Authors: Vicente D. Crespo, Francisco J. Goin, Martin Pickford

Data type: 3-D video (avi file)

Explanation note: 3-D video of a digital reconstruction of *Morotodon aenigmaticus* gen. et sp. nov.

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Link: <https://doi.org/10.3897/fr.25.80706.suppl1>

Supplementary material 2

***Morotodon aenigmaticus* gen. et sp. nov. Stereoscopic pairs and schematic drawing of specimen UM MOR II, 48'04**

Authors: Vicente D. Crespo, Francisco J. Goin, Martin Pickford

Data type: Stereoscopic pairs and schematic drawing

Explanation note: A–E, *Morotodon aenigmaticus* gen. et sp. nov. Stereoscopic pairs and schematic drawing of specimen UM MOR II, 48'04 (an isolated left m4) in occlusal (A), labial (B), lingual (C), anterior (D), posterior (E), and basal views. Scale bar: 1 mm.

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Link: <https://doi.org/10.3897/fr.25.80706.suppl2>

Supplementary material 3

Reconstruction of the palaeoenvironment of Moroto II

Authors: Vicente D. Crespo, Francisco J. Goin, Martin Pickford

Data type: Images

Explanation note: Reconstruction of the palaeoenvironment of Moroto II. Left to right: the anthracothere *Brachyodus* sp.; the primate *Afropithecus turkanensis* Leakey & Leakey, 1986; the deinothere *Deinotherium hobleiyi* Andrews, 1911; the creodont *Hyainailouros sulzeri* Biedermann, 1863 and the metatherian *Morotodon aenigmaticus* gen. et sp. nov.

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