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Taxonomy and affinities of African cenozoic metatherians

Taxonomía y afinidades de los metaterios cenozoicos africanos

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Abstract: The record of extinct African metatherians (Mammalia, Theria) is scanty, restricted in time (Eocene–Miocene), and its taxonomy is still subject of debate. A review of all African metatherians, or alleged metatherians, known up to now, led us to the recognition of only three taxa referable to this group: (1) *Kasserinotherium tunisiense* (Peradectoidea?), from the early Eocene of Tunisia; (2) *Peratherium africanum* (Herpetotheriidae), from the early Oligocene of Egypt and Oman, and (3) an indeterminate Herpetotheriidae? from the early Miocene of Uganda. Herpetotheriids probably reached Afro-Arabia from Europe in one or more dispersal waves since the early Oligocene. *Kasserinotherium*, on the contrary, suggests an earlier (Paleocene) arrival from South America, judging from its alleged affinities with South American and Australian taxa. Such a migration event (probably, through a filter corridor such as the Rio Grande Rise-Walvis Ridge system in the South Atlantic) may also explain the enigmatic presence of polydolopimorphian metatherians in the Cenozoic of central Anatolia (Turkey). A more radical hypothesis is that all European (Eurasian?) Marsupialiformes have an ultimate origin in South America, from where they dispersed via Africa by the Paleocene–earliest Eocene.

Resumen: El registro de metaterios (Mammalia, Theria) africanos extintos es escaso, temporalmente restringido (Eoceno–Mioceno) y su taxonomía es aún objeto de debate. Una revisión de la totalidad de los metaterios, o supuestos metaterios de este continente nos llevó al reconocimiento de sólo tres taxones referibles a este grupo: (1) *Kasserinotherium tunisiense* (Peradectoidea?), del Eoceno temprano de Túnez; (2) *Peratherium africanum* (Herpetotheriidae), del Oligoceno de Egipto y Omán, y (3) un Herpetotheriidae? indeterminado del Mioceno temprano de Uganda. Los herpetotéridos probablemente llegaron a Afro-Arabia en una o más oleadas de dispersión a partir del Oligoceno temprano. *Kasserinotherium*, por el contrario, sugiere una llegada más temprana (Paleoceno) desde América del Sur, a juzgar por las afinidades sugeridas con formas de este último continente y de Australia. Un evento migratorio de este tipo (ocurrido, probablemente, a través de un corredor de filtro como el sistema Rio Grande-Cadena de Walvis en el Atlántico Sur) podría también explicar la enigmática presencia de metaterios polidolopimorfios en el Cenozoico de Anatolia central (Turquía). Una hipótesis más radical postula que todos los Marsupialiformes europeos (o, incluso, los de Eurasia en su conjunto) tuvieron un origen último en América del Sur, desde donde se dispersaron vía África hacia el Paleoceno–Eoceno más temprano.

INTRODUCTION

Living metatherians are widely distributed both in Australasia and in the Americas. During the last hundred million years, however, they occupied every single continent on Earth, even though their temporal ranges and diversity were strongly unequal. The earliest records of Metatheria come from the Early Cretaceous (Aptian–Albian) of North America, where they had a wide distribution, both temporal and geographical (Crochet, 1980; Gunnell, 2010; Williamson *et al*., 2014; Goin *et al*., 2016; Bi *et al*., 2018). Previously, *Sinodelphys* was included in Metatheria (Luo *et al*., 2003), but posterior analyses showed closer affinities with the Eutheria (Bi

et al., 2018). The discovery of *Juramaia* indicates that the dichotomy between Metatheria and Eutheria was a Late Jurassic event, probably prior to 160 Ma (Luo *et al*., 2011).

The mammalian record from the Paleogene of Africa is very scarce; around 40 localities have been found, mainly concentrated in the Maghreb, although the literature of this period is dominated by the site of Fayum (Pickford *et al*., 2008). By contrast, the Paleogene record of the African Southern Hemisphere is limited to a very few localities, and only one site in East Africa (Van Couvering & Delson, 2020). Of all these sites, only

three have yielded metatherian remains (excluding Moroto, which is from the Miocene), all of them being very scarce. Because of this, a great subordination of these taxa to eutherians can be observed, probably because the ecological niches of these new immigrants were already occupied by other taxa (see below). Nevertheless, large parts of Africa are still unknown and may reveal new information on the taxonomy, affinities and distribution of African metatherians. The Cenozoic record of metatherians in Europe is relatively abundant and ranges from the early Eocene to the middle Miocene (Crochet, 1980). However, in other Old World continents their record is much scarcer (Crochet et al., 2007; Gunnell, 2010). This is particularly the case for Africa (Fig. 1), whose metatherian record is uneven, quite fragmentary, and controversial. No Mesozoic metatherians are known from Africa (Averianov et al., 2003), leading to the assumption that they arrived there during Cenozoic times either from Europe, or from South America, or both (see below).

The Cenozoic record of metatherian mammals in Africa is still a subject of debate. Remains of African metatherians are scarcely found, are represented by isolated, often fragmentary specimens, and are restricted to its central and northernmost regions. In addition, there is an ongoing debate on the metatherian nature of several of these taxa (Gunnell, 2010).

Up to now, only three African taxa are unambiguously referable to the Metatheria: (1) *Peratherium africanum* Simons & Bown, 1984, from the early Oligocene of Egypt and Oman (Arabian Peninsula); (2) *Kasserinotherium tunisiense* Crochet, 1986, from the early Eocene of Tunisia, and (3) an indeterminate ?herpetotheriid taxon from the early Miocene of Uganda. Other alleged metatherian taxa from Africa have been disputed as probable eutherians or mammals of still unknown affinities: (4) an indeterminate mammal from the Late Cretaceous of Madagascar; (5) *Garatherium mahboubii* Crochet, 1984 from the early Eocene of Algeria; (6) *Ghamidtherium dimaiensis* Sánchez-Villagra et al., 2007 from the late Eocene of Egypt; and finally, (7) two upper molars also coming from the late Eocene of Egypt were described as enigmatic mammals of uncertain (and even possibly metatherian) affinities.

Here we provide a review of all African metatherians, or alleged metatherians, known up to now. Because of its geographic vicinity with Africa, we also consider one case of an alleged metatherian from Madagascar. We compare them with eutherian and other metatherian lineages, and discuss their possible affinities. We also argue on the possible dual origin of Cenozoic African metatherians, thus adding to the ongoing discussion on the origins and biogeographical significance of these still enigmatic mammals from the Afro-Arabian record.
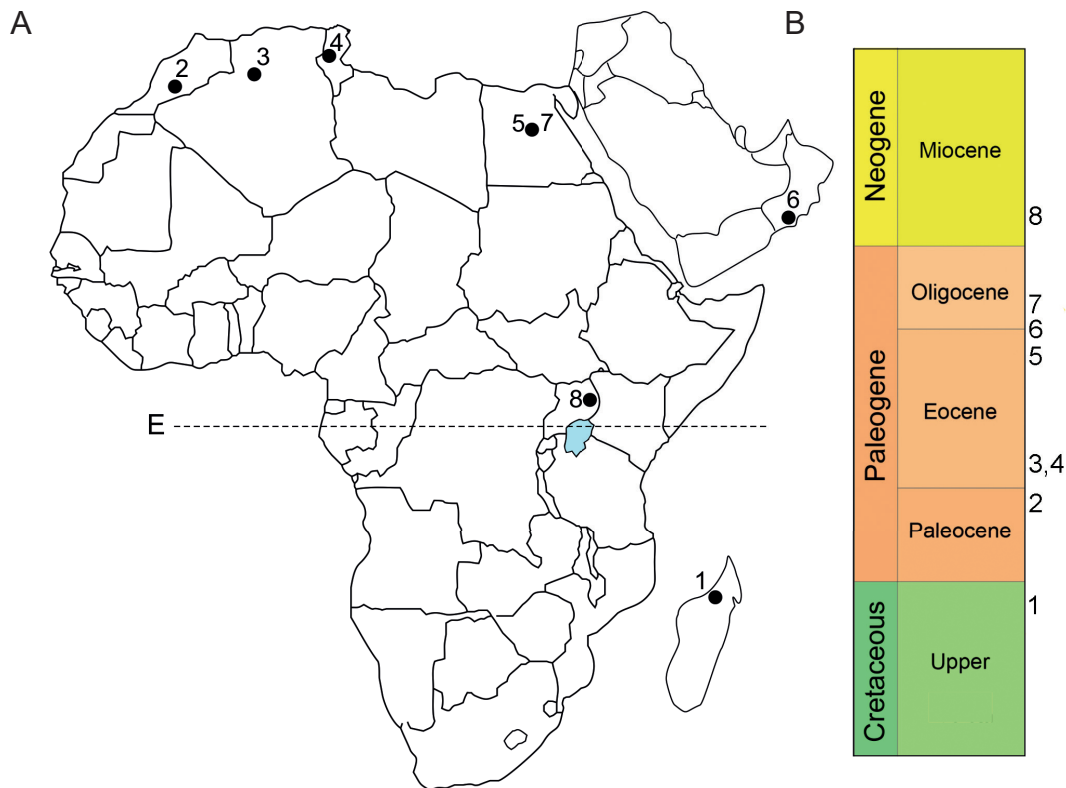

Figure 1. A, Map of Africa and the Arabian Peninsula showing the fossil localities mentioned in this work. Included are localities of both metatherians and previously alleged metatherians; **B**, Stratigraphic column of the Cenozoic Era indicating the ages of the metatherian taxa, or alleged metatherians, mentioned in this work; **E**, Equator; **1**, Zhelestidae, gen. et sp. indet; **2,** ?*Garatherium todrae*; **3**, *Garatherium mahboubii*; **4,** *Kasserinotherium tunisiense*; **5**, *Ghamidtherium dimaiensis*; **6–7**, *Peratherium africanum*; **8,** Herpetotheriidae? gen. et sp. indet.

Institutional Abbreviations. CGM, Cairo Geological Museum, Cairo, Egypt; **DPC**, Duke University Primate Center, Durham, United States of America; **TQ**, Taqah collections, Université Montpellier II, Montpellier, France; **UM MOR II**, Moroto II locality collections, Uganda Museum, Kampala, Uganda; **EY**, Cartographic Service, National Mining Bureau, Tunisia; **UA**, University of Antananarivo, Madagascar.

Anatomical and other abbreviations. Ma, *Megannum*, one million years in the radioisotopic time scale; **P/p**, upper/lower premolars; **M/m**, upper/lower molars; terminology of molar structures follows Goin *et al*. (2016); **StA**, **StB**, **StC**, **StD**, stylar cusps in the upper molars.

SYSTEMATIC PALAEONTOLOGY

The material discussed here has been studied from the direct observation of their remains (*Kasserinotherium tunisiense* and *Garatherium mahboubii*) housed in l'Institut des Sciences de l'Evolution de Montpellier (Université de Montpellier, France), high quality photographs (Herpetotheriidae? genus and species indet.), and the rest from both their original publications and revisions. In addition, these taxa have been compared with reference collections of metatheria, both originals and casts, of European, South American, North American and Asian origin housed at Museo de La Plata (Universidad Nacional de La Plata, Argentina), l'Institut des Sciences de l'Evolution de Montpellier (Université de Montpellier, France), and Muséum national d'Histoire naturelle (Paris, France). We assume

Table 1. Measurements (in mm) of all upper and lower molars of the African metatherians mentioned in this work (from Simons & Bown, 1984; Crochet, 1986; Crochet *et al.*, 1992; Pickford & Mein, 2006; Hooker *et al.*, 2008). **L**, length; **W**, width; **Wtr**, width trigonid; **Wta**, width talonid; **Min**, minimum; **Max**, maximum.

Element	Collection	Measurement	n	Min	Mean	Max
		Peratherium africanum				
dp3	TQ	L	1		1.75	
		W	1		0.95	
p2	CGM	L	1		1.75	
		W	1		1.00	
p3	CGM	L	1		1.70	
		W	1		1.05	
m1	CGM/DPC	L	3	1.70	1.74	1.77
		Wtr	1		1.15	
		Wta	3	1.14	1.23	1.36
m2	CGM/DPC	L	4	1.85	1.98	2.20
		Wtr	3	1.00	1.12	1.21
		Wta	2	1.10	1.17	1.25
m3	CGM/DPC	L	4	1.95	2.09	2.20
		Wtr	3	1.25	1.28	1.30
		Wta	3	1.15	1.20	1.25
m4	CGM/DPC	L	1		2.15	
		Wta	1		0.98	
P2	DPC	L	1		1.60	
		W	1		0.71	
P3	DPC	L	1		2.01	
		W	1		1.08	
M2	DPC	L	1		1.94	
		W	1		2.54	
M3	DPC	L	1		2.14	
		W	1		2.87	
		Herpetotheriidae?				
m4	UM MORII	L	1		1.63	
		Wtr	1		0.93	
		Wta	1		0.94	
		Kasserinotherium tunisiense				
M1	EY	L	1		1.60	
		W	1		1.75	
M3	EY	L	1		1.42	
		W	1		1.55	

the conventional metatherian dental formula as I/i 5/4, C/c 1/1, P/p 3/3, M/m 4/4, although there are other hypotheses (*e.g.*, O'Leary *et al.*, 2013). Measurements (Tab. 1) are in mm.

Class MAMMALIA Linnaeus, 1758
Infraclass METATHERIA Huxley, 1880
Clade MARSUPIALIFORMES Vullo *et al.* 2009
Family HERPETOTHERIIDAE Trouessart, 1879

A recent phylogenetic analysis by Ladevèze *et al.* (2020) including dental, petrosal, and postcranial features led to the exclusion of herpetotheriids (and of peradectids) from the Didelphimorphia. Moreover, it led to the conclusion that the Herpetotheriidae as currently understood (*i.e.*, including at least *Herpetotherium*, *Copedelphys*, *Peratherium*, and *Amphiperatherium*) is not a natural group. The authors opted to maintain the Herpetotheriidae for historical reasons, and recognized the new Subfamily Peratheriinae, within the Herpetotheriidae, for the inclusion of *Peratherium* and *Amphiperatherium* (Ladevèze *et al.*, 2020). Here we use the family term Herpetotheriidae in its traditional concept and contents.

Genus *Peratherium* Aymard, 1846

Type-species. *Didelphis crassum* Aymard 1846. *Peratherium crassum* Aymard, in Gervais (1848, p. 134, 1859, p. 266). Early Oligocene; Egypt and Oman.

Peratherium africanum Simons & Bown, 1984
Figure 2A–2D

Type. Right dentary fragment with p2-m3, roots of c1 and p1 and alveoli for m4 (CGM 40236) from the upper Jebel Qatrani Formation, Rupelian, Oligocene, Quarry M, Fayum Province, Egypt.

Referred specimens. Left dentary with m2-3 and part of m4 (CGM40237); left edentulous dentary fragment (DPC 3120); right maxillary fragment with P2-M3, roots of P1 and parts of alveoli of C1 and M4 (DPC 16946); right dentary fragment with p3-m4, two empty alveoli anterior to p3 and part of the root of p1? (DPC 3820); right dentary fragment with eroded p3-m4 and partial roots of c1-p2 (DPC 8201); left dp3 (TQ94).

Occurrence. Jebel Qatrani Formation, Fayum Depression, northern Egypt) and Taqah (Sultanate of Oman).

Age. Early Oligocene.

Original diagnosis. Moderately small marsupial, approximately the size of *Peratherium cuvieri* (Fischer, 1829) (aprox. M2, length: 2.1, width: 2.4; m2, length 2, width: 1.4). Resembles *P. cuvieri* and *Peratherium perrierense* Crochet, 1979 in having the entoconid close against the trigonid on m1-2 and connected to it by a raised wall. It resembles *P. cuvieri* and

Peratherium antiquum (Blainville, 1840) in having short m1-3 talonids. Differs from these and other species in having essentially vertical m1-3 hypoconulids that are as large and as tall as the entoconids. The hypoflexids of m1-3 are very shallow as in *Peratherium perrierense* Crochet, 1979 and *P. antiquum* and in contrast to *P. cuvieri* and other species. m1 < m2 < m3 < m4, as in *Peratherium elegans* (Aymard, 1846), *P. perrierense*, *P. antiquum*, *Peratherium bretouense* Crochet, 1979, and *Peratherium lavergnense* Crochet, 1979, and in contrast to most other species. There is no diastema between p1-2, in contrast with all above forms excepting *P. lavergnense*; p2 has a distinct paraconid (anterior cusp) in contrast to all other known species of *Peratherium*.

Revised diagnosis by Crochet *et al.* (1992). Peradectidae of rather small size typified by the increasing length of the lower molars from m1 to m4. Distinguished from all other Holarctic Peradectidae by its molars with reduced talonid and with an oblique crest ending buccally against the trigonid. Presence of a diastema between p1 and p2. Molars with hypoconulid and entoconid of similar height and linked by high crests. Cusp tips of the molars worn by strong abrasion.

Revised diagnosis by Hooker *et al.* (2008). Medium-sized *Peratherium*, length of M3: 2.14 mm. M1-3 transversely elongate with deep ectoflexus, especially on M3 where it emarginates half the width of the stylar shelf; weakly dilambdodont with metacone much larger than paracone; large, mesially placed stylar cusp B confluent with cusp A; very small stylar cusp C on the distal flank of cusp B; paracingulum interrupted adjacent to paracone. Lower molars with short talonid and buccally located cristid obliqua; hypoconulid large, taller than the entoconid and close to its lingual margin; shallow distolingual area of talonid, after wear becoming a curved 'crest' linking hypoconulid to entoconid (hypoconulid-entoconid talonid fold).

Discussion. Bown and Simons (1984a) described the first marsupial remains from Africa on the basis of three fragmentary mandibles from the Jebel Qatrani Formation. Even though they did not formally describe them as belonging to a new taxon, they highlighted the similarities between the African materials with the genus *Peratherium*. A few months later Simons and Bown (1984) formally described the anterior material as the new species *P. africanum*. This material undoubtedly belongs to a metatherian in having three premolars and four molars. These authors followed Crochet (1977, 1980) in referring the species to *Peratherium*, as the protoconid increases in height from m1 through m4; the anterior face of the metaconid is generally subvertical in lingual view; the entoconids are conical, often tall; the width of m4 talonid is reduced, with the hypoconulid placed equally between the hypoconid and the entoconid; the molars tend to lengthen from m1 through m4; and the talonid of m4 is strongly reduced.

These authors highlighted that *P. africanum* shares all of these characters to a greater or lesser degree and discarded the genus *Herpetotherium* because *P. africanum* does not have its m2 and m3 of subequal length; the m4 is shorter than other molars; the m1-4 metaconids are nearly as tall as the protoconids, and the molar entoconids are strongly lengthened at their buccal bases. They emphasized the strong similarity of this species with *P. cuvieri*, *P. antiquum* and *P. perrierense*. The authors discussed on the European origin of this species, although Jaeger and Martin

(1984) argued on a vicariant origin of this taxon, and the possibility of it being a survivor of an ancestral marsupial stock common to South America and Africa before the opening of the South Atlantic. Bown and Simons (1984b) replied that there is no evidence to support this hypothesis involving the composition and dispersion of an unknown fauna.

A few years later Crochet *et al.* (1992) described a dp3 from Oman, and assigned it, in spite of its relative large size, to *P.* aff. *P. africanum* on the basis of the broadly structured cusps, high entocristid, very shallow
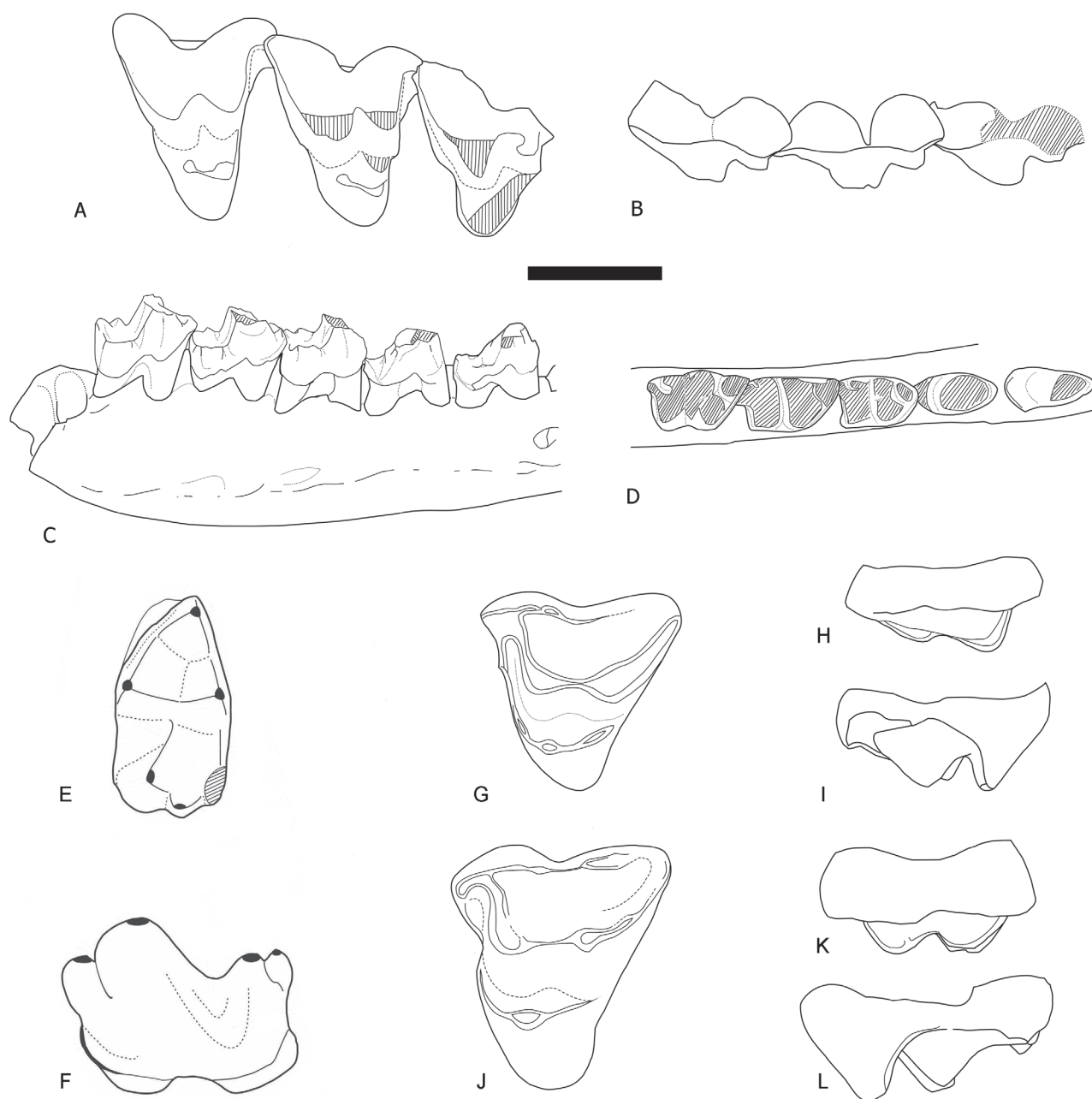

Figure 2. A–B, *Peratherium africanum*, DPC 16946, right maxilla with P2–M3 (M1-3 in this figure), after Hooker *et al.* (2008, fig. 1) in occlusal and buccal views; **C–D,** *Peratherium africanum* CGM4 0236 (holotype), right mandible showing p2-m3 in buccal and occlusal views; **E–F,** Herpetotheriidae? gen et sp. indet. UM MOR II 48'04, left m3 in occlusal and buccal views; **G–L,** *Kasserinotherium tunisiense*; **G–I,** EY 10, holotype, a left M3 in occlusal, buccal, and anterior views; **J–L,** EY 12, right M1 (inverted drawing) in occlusal, buccal, and anterior views, after Crochet (1986, figs. 1, 2); scale bar = 1 mm.

hypoflexid, the cristida obliqua ending buccally against the trigonid wall, the well-cuspate hypoconulid, the entoconid linked to the hypoconulid by a high crest, and the strongly abraded tip of the cusps. The authors noted that the assignment of this species to the genus *Peratherium* was very weak (mostly based on the increasing length of the lower molars); moreover, they argued that some features of the original diagnosis are typical of the Peradectidae: hypoconulid and entoconid of similar height, and occurrence of a high crest linking the entoconid. In consequence, they described *Qatranitherium* as a new genus of peradectid. With this new classification, these authors emphasized the ancient origin of the Afro-Arabian marsupials, independent of the more recent immigrations of the European taxa. Later McKenna and Bell (1997), following Simons and Bown (1984), regarded the genus as synonymous with the herpetotheriine *Peratherium*.

Hooker *et al.* (2008) described new materials including a near complete maxilla from the type locality, and placed this species in the genus *Peratherium* on the basis of the following features: the morphology of the upper molars is clearly herpetotheriid by its dilambdodonty and enlarged metacone; the crest linking the lower molar hypoconulid to the entoconid is not the lingual branch of the postcristid as in *Peradectes*; the appearance of an entocristid is enhanced by the advanced wear state and the proximity of the entoconid to the metaconid (as it happens in several species of *Peratherium*); a buccally positioned cristid obliqua (typical of *Peradectes* and several species of *Peratherium*); and in that the hypoconulid is located near the lingual margin of the tooth, while it is more buccally placed in peradectids.

Family HERPETOTHERIIDAE?

Genus and species indet.
Figure 2E–2F

Material. UM MOR II 48'04, an ultimate lower left molar.

Occurrence. Moroto II locality, north of Nakiloro Village, Moroto District, northeastern Uganda. Kogole Beds (Miocene valley infillings east and south of Kogole Hill).

Age. Late early Miocene, upper Burdigalian.

Discussion. Pickford and Mein (2006) described UM MOR II 48'04 as an m1 or m2, and argued that the specimen belongs to a possible marsupial, rejecting the idea that it is referable to the Tenrecidae or Chrysochloridae on the basis of the number of the cuspids in the talonid. Taking that into account, besides the highly specialized Anatoliadelphyidae, until now only two families of marsupialiform metatherians are present in the Cenozoic of the Old World, Peradectidae and Herpetoteriidae. The first can be discarded because of the presence of a postentocristid in the lower molars (a diagnostic feature of the Peradectidae; Ladevèze

et al., 2012; Smith & Smith, 2013). On the contrary, in herpetotheriids there is a notch between the entoconid and the hypoconulid, as is the case of specimen UM MOR II 48'04. We also note that herpetotheriids have hypoconulids and entoconids of unequal height (the entoconid is higher in m1-3, but not in m4) while in peradectids entoconids and hypoconulids are of similar height in all lower molars, including the m4 (Crochet, 1979, 1980). Even though the entoconid is broken in the UM MOR II 48'04, it is clear that the hypoconulid was a larger cusp. In summary, the African specimen most probably belongs to the Herpetotheriidae, being impossible to refer it to any known taxon of this family.

Superfamily ?PERADECTOIDEA
Genus *Kasserinotherium* Crochet, 1986

Type-species. *Kasserinotherium tunisiense* Crochet, 1986. Early Eocene, Tunisia.

Kasserinotherium tunisiense Crochet, 1986
Figure 2G–2L

Type. EY 10, left M3.

Referred specimens. EY 12, right M1.

Occurrence. Kasserine locality area, Chambi Massif, central Tunisia. Basal levels of "Couches Rouges", Chambi Massif.

Age. Early Eocene.

Original diagnosis (after Crochet, 1986, translated from French). Small peradectine; upper molars have stylar cusps that are not very distinct; StA is supported by a spur clearly anterior to the rest of the crown and not separated from StB by a notch; the preparacrista meets the apex of StB; the centrocrista is not deeply indented between the paracone and the metacone; the protofossa is significantly lengthy; the lingual base of the protocone slightly tilted posteriorly; conules absent.

Discussion. Crochet (1986) described two upper molars from the early Eocene of Chambi as belonging to a new genus of peradectine metatherian. He regarded them as belonging to a marsupial because of the presence of a line of stylar cusps and a large stylar area, together with the absence of a hypocone and of a cingulum below the protocone, and by the presence of a rectilinear centrocrista with a predilambdodont morphology. Following previous definitions and concepts (*e.g.*, Crochet, 1980) he regarded the new taxon as belonging to Peradectinae (see also Crochet *et al.*, 2007), noting similarities between *Kasserinotherium* and *Peradectes*, *Mimoperadectes* and *Alphadon* (Crochet, 1986). A later phylogenetic analysis placed this genus as sister-taxon to the early Oligocene, Chinese peradectid *Junggaroperadectes* (Maga, 2008). Other authors doubted the metatherian nature of *Kasserinotherium*: without further arguments,

McKenna and Bell (1997, p. 49) regarded this genus as an indeterminate Theria, while Van Couvering and Delson (2020) included it within their "Placentalia indet." Finally, Gunnell (2010) noted that because of the primitive, simple nature of these materials (both upper molars), there is no convincing reason to believe that *Kasserinotherium* represents a marsupial (*i.e.*, a metatherian in the current concept of this marsupialiform group).

Contra Gunnell (2010) we regard the upper molar pattern of *Kasserinotherium* neither "primitive" nor "simple". On the contrary, it displays a unique mixture of generalized and derived features: straight centrocrista, wide stylar shelf, preprotocrista ending at the parastylar corner of the tooth, reduced protocone, lack of conules, relatively long postmetacristae, labiolingually compressed stylar cusps. This combination of features is suggestive of faunivorous feeding habits (see also Beck, 2013, and below).

On the basis of the available evidence we agree with Crochet's original thoughts on the metatherian nature of *Kasserinotherium.* We discard roughly similar placental mammals as primitive afrosoricids (after Seiffert, 2010a) because of the absence of metaconule, a relative narrow tooth, the more developed postero-buccal side of the tooth and the shorter pre- and postprotocrista. However, we doubt its peradectid (*s.s.*) affinities. When Crochet (1986) considered the affinities of *Kasserinotherium*, his only sources of comparisons among European marsupialiforms were the "Peradectini" (Peradectidae) and the "Didelphini" (actually, the Herpetotheriidae). As peradectids have a straight centrocrista, while herpetotheriids have a v-shaped one, he was confident on the peradectid nature of *Kasserinotherium*. However, there are a number of metatherian lineages that keep the plesiomorphic condition of a straight centrocrista: "alphadontids", stagodontids, pediomyids, etc. (see, *e.g.*, Kielan-Jaworowska *et al.*, 2004). Even among didelphimorphians, several taxa have straight centrocristae in part or all the upper molar series (Goin, 1997).

Goin and Candela (2004) suggested affinities between *Kasserinotherium* and *Wirunodon chanku* Goin & Candela, 2004 (Marsupialiformes, Order and Family indet.), from the Paleogene (late Eocene?) of Santa Rosa local fauna in the Peruvian Amazonia. Both taxa are strikingly similar in having a "*...very small size, straight centrocrista, conules absent, reduced protocone and trigon fossa, reduced and labiolingually compressed stylar cusps, wide stylar shelf, and well-developed postmetacrista…*" (Goin & Candela, 2004, p. 43). In turn, Beck (2013) noted similar dental features shared by *Kasserinotherium*, *Wirunodon*, and *Archaeonothos henkgodthelpi* Beck, 2013, from the early Eocene Tingamarra fauna of southern Queensland, Australia. He stated that the last species differs from *Kasserinotherium* and *Wirunodon* in having a larger size, a more mesial-posteriorly compressed protocone, a larger differential height between the

paracone and the metacone, larger StB, smaller StD, while the preparacrista ends at StB rather than StA. Both Goin and Candela (2004) as well as Beck (2013) noted several features suggestive that all these taxa could be referred *s.l.* to the Peradectidae; however, their distinctive combination of derived and generalized features was noticeable enough to not refer them to any known family of marsupialiform metatherians. Part of the problematic nature of this topic is the radically different geographical provenances of the involved taxa: *Kasserinotherium* comes from northwestern Africa, *Wirunodon* from western Amazonia in South America, and *Archaeonothos* from southern Queensland in eastern Australia. Any hypothesis linking these three taxa should give a convincing biogeographic response to such disparate provenances (see below). What seems clear to us is that, even though *Kasserinotherium* (and *Wirunodon* and *Archaeonothos* as well) does not belong to the Peradectidae *s.s.*, they may be part of an early (Paleocene?; see below) peradectoid off shoot exclusive to the southern continents.

Infraclass EUTHERIA Huxley, 1880
Family ZHELESTIDAE Nesov, 1985

Gen. et sp. indet.
Figure 3A–3B

Specimen. An isolated, fragmentary lower molar (UA 8699).

Occurrence. Locality MAD93-35, Mahajanga Basin, Northwestern Madagascar. Anembalemba Member of the Maevarano Formation.

Age. Latest Cretaceous (Maastrichtian).

Discussion. Krause (2001; see also Case & Krause, 2002) referred specimen UA 8699 to the Metatheria because of several features: presence of a prominent distobuccal cingulid extending from the base of the hypoconid towards the hypoconulid apex; the hypoconulid is lingually placed, well away from the hypoconid; the talonid is at least as broad as the trigonid; the trigonid is low; finally, wear is mostly horizontal. Averianov *et al.* (2003) argued that these same features also appear among zhelestid eutherians, and highlighted the similarities between specimen UA 8699 and lower molars of the spanish zhelestid *Lainodon orueetxebarriai*. An indirect clue of the possible affinities of UA 8699 and *Lainodon* is that both sites have faunistic similarities including snakes, dinosaurs and turtles, although the origin of the Madagascar fauna is largely discussed (see Rage, 2003 and references therein). Later, Krause (2013) maintained his arguments on the metatherian nature of this specimen, while Archibald and Averianov (2012) kept on regarding it as a Zhelestidae indet. The fact that the only specimen at hand from the Late Cretaceous of Madagascar is a lower, worn, broken molar, does not

help in clarifying its taxonomy. Our own observations on the figured materials and original descriptions led us to tentatively agree with Averianov *et al.* (2003) suggestion that it most probably belongs to a zhelestid eutherian mammal.

Clade EUARCHONTA Waddell *et al.*,1999
Family ADAPISORICULIDAE Van Valen, 1967
Genus *Garatherium* Crochet, 1984

Type-species. *Garatherium mahboubii* Crochet, 1984. Early Eocene, Algeria.

Garatherium mahboubii Crochet, 1984
Figure 3C–3F

Type. Uncatalogued specimen, originally referred to a right M3 (our interpretation: a right M2).

Referred specimens. The type only.

Occurrence. Brézina region, South Oran, El Kohol (Locus B), Algeria; "…*membre marno-calcaire de la formation d'El Kohol…*" (Crochet, 1984, p. 277).

Age. Late early Eocene (Ypresian).

Original diagnosis (translated from French). Peradectine of very small size with an enhanced, didelphid-like dilambdodonty in the upper molars; StB only slightly lower than the paracone and much larger than StA; StC placed on the buccal edge of the molar
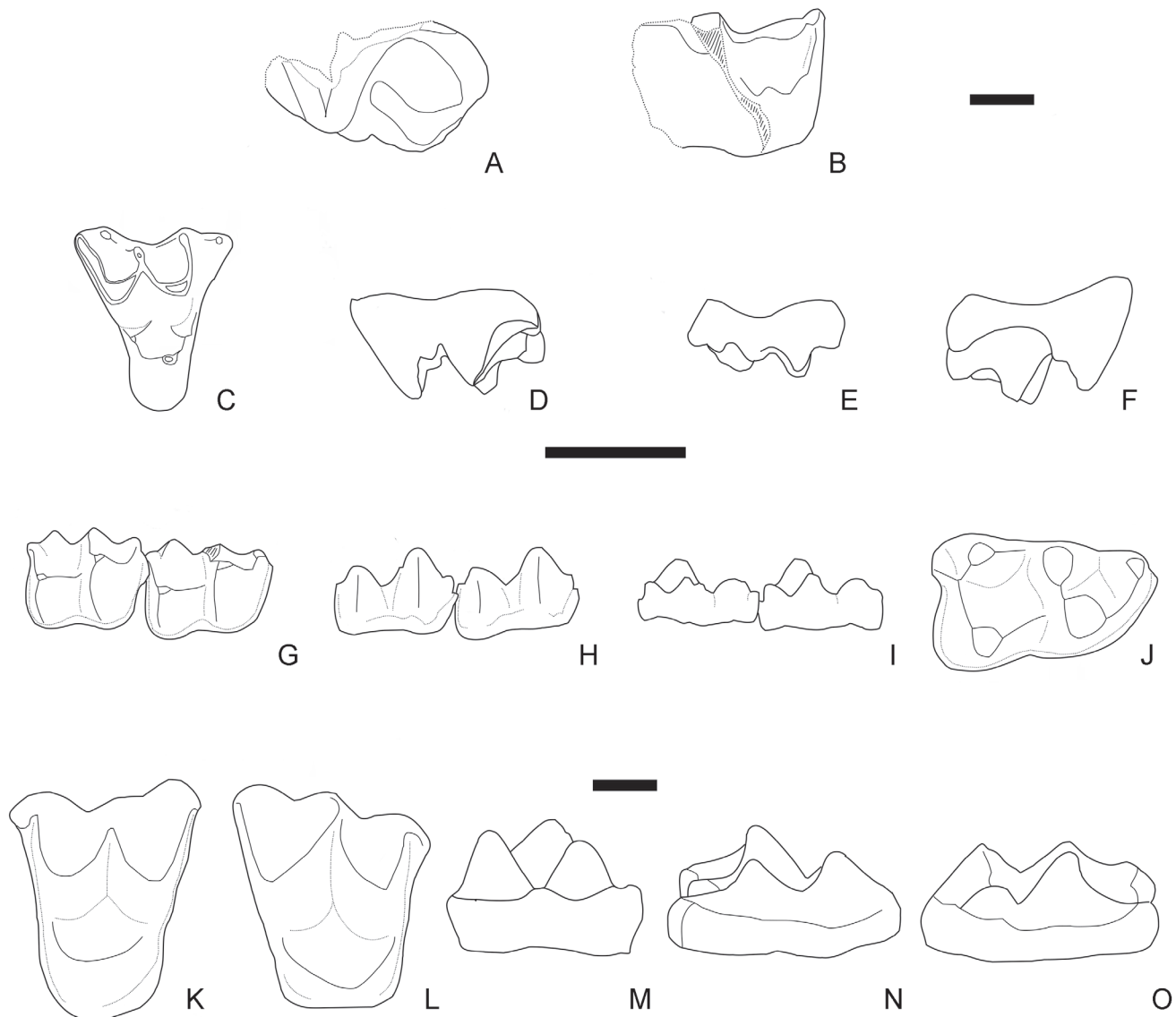
Figure 3. **A–B,** Zhelestidae gen. et sp. indet., UA 8699, fragment of lower molar in occlusal and buccal views, after Krause (2001, fig. 1A and 1E); **C–F,** *Garatherium mahboubii*, right M2 in occlusal, anterior, buccal, and posterior views, after Crochet (1984, fig. 1); **G–I,** *Ghamidtherium dimaiensis*, CGM 83699, right m1-2 in occlusal, buccal and lingual views, after Sánchez-Villagra *et al.* (2007, fig. 1B-D); **J,** Chiroptera indet., DPC 21498B, right m?1 in occlusal view, after Sánchez-Villagra *et al.* (2007, fig. 1E); **K–O,** ?*Khonsunycteris* or ?*Phasmatonycteris* or new genus and species; **K,** DPC 21372A, left M1 in occlusal view; **L–O,** DPC 21372B, M2 in occlusal, buccal, anterior, and posterior views, after Sánchez-Villagra *et al.* (2007, fig. 4); scale bar = 1 mm.

crown; concave preparacrista, with its lower portion placed at a mid-distance from the paracone and the StB; well-developed conules on the lingual slopes of paracone and metacone; protocone high; protofossa deep and narrow (Crochet, 1984, p. 279).

Discussion. Crochet (1984) described *Garatherium mahboubii* on the basis of a single upper molar from El Kohol (Algeria, lower Eocene), which had previously been referenced by Mahboubi *et al.* (1983). He referred it to a metatherian on the basis of the following combination of features: five distinct stylar cusps located buccally in the stylar shelf, lack of hypocone and of pre- and postcingula, wide stylar shelf, and presence of a "*dilambdodontie didelphidienne*" (Crochet, 1984, p. 282). In spite of its v-shaped, invasive centrocrista, he argued in favour of peradectid affinities on the basis of eight features (*e.g.*, size of stylar cusps, length of parastylar edge, similar height of paracone and metacone, conular size, etc.). He emphasized the similarities between *Garatherium* and *Alphadon* (the latter was then regarded as a Peradectinae).
After its original description, the taxonomic history of *Garatherium* has been quite controversial. Mahboubi *et al.* (1986) maintained the considerations by Crochet (1984). Kappelman *et al.* (1996) regarded *Garatherium* as a possible marsupial, while McKenna and Bell (1997) classified it within the Herpetotheriinae. More recently Métais *et al.* (2018) compared *G. mahboubii* with a *Galatiadelphys minor* Métais *et al.*, 2018, regarding the former as a purported metatherian. Gheerbrant (1991, 1995) reclassified *Garatherium* as an adapisoriculid eutherian. Gheerbrant *et al.* (1998) described another possible species of the genus *Garatherium* (?*Garatherium todrae* Gheerbrant *et al.*, 1998). The genus was also regarded as part of the Adapisoriculidae by Seiffert (2010a, 2010b), who discussed the possible intermediate condition between the (older) dilambdomorphs and tenrecoids, and the possibility that this genus actually represents an early stem tenrecoid. De Bast *et al.* (2012) also regarded *Garatherium* as an adapisoriculid and considered that it probably represents a second dispersal event between Europe and Africa during the late Palaeocene. Finally, Eldridge *et al.* (2019) followed the same arguments of Seiffert (2010a, 2010b). Taking in account all arguments at hand, we regard *Garatherium* as a probable adapisoriculid eutherian.

Order ?EULIPOTYPHLA Waddell *et al.*, 1999
Genus *Ghamidtherium* Sánchez-Villagra *et al.*, 2007

Type-species. *Ghamidtherium dimaiensis* Sánchez-Villagra *et al.*, 2007. Late Eocene, Egypt.

Ghamidtherium dimaiensis Sánchez-Villagra *et al.*, 2007
Figure 3G–3I

Material. In the original publication: CGM 83699, a right dentary fragment including m?2-3, and alveoli for m?4 and a partial first lower molar (m?1), preserving the trigonid and about half of the talonid (DPC 22442D). Our interpretation of the mandible: a right dentary fragment including m1-2 and the alveoli of p4 and m3.

Occurrence. BQ-2 Quarry, Fayum Depression, Egypt.

Age. Late Eocene (Priabonian).

Original diagnosis. *Ghamidtherium* differs from other Paleogene Afro-Arabian mammals in combining the following features: molar trigonids relatively open and uncompressed, with a large angle between the proto and paracristids that decreases distally; molar metaconids low relative to protoconids, slightly taller than paraconids; lingually situated hypoconulid relatively small, connected to hypoconid (nyctalodont); weak buccal cingulids that are restricted to hypoflexids; well-developed precingulids; tooth mesial to the m?2 relatively large (about 90% the length of the m?2, based on spacing of alveoli), with mesial alveolus not offset buccally with respect to the distal alveolus.

Discussion. On the basis of a mandible with two molars and an isolated lower molar (probably belonging to the same species) from Fayum (Quarry BQ-2, Egypt, earliest late Eocene), Sánchez-Villagra *et al.* (2007) recognized the species *Ghamidtherium dimaiensis*; in the same publication they also described two upper molars regarded as Mammalia indet. and discussed their probable belonging to Marsupialia or Chiroptera. We discuss all these specimens in the following sections.
Sánchez-Villagra *et al.* (2007) argued that the lower molars have marsupial-like features, as the large size of the tooth mesial to m?2, and that the alveoli before the m?2 belongs to an elongated tooth, probably one molar, because both features do not appear (to them) in Paleogene bats. They highlighted the twinning of the hypoconulid and entoconid as typical of marsupials, though they are present in many bats (nyctalodonty) and in several Eulipotyphla, as the soricids. They stressed that the Paleogene bats from Afro-Arabia are myotodont, an exception being the oldest philisid *Dizzya*, which is nyctalodont. Regarding the upper molars, they emphasised that they could be referred to, but not diagnosed as, Marsupialia because of the absence of a hypocone, presence of StC, a relatively low paracone, and the moderately slender lingual portion of the upper molars. Simmons *et al.* (2016) questioned the whether these materials pertain to a marsupial. Subsequently, Eldridge *et al.* (2019) argued that *Ghamidtherium dimaiensis* could actually be a bat.
Our interpretation of the mandible and the lower tooth is that they belong to two different species: they have quite different, distinct postcristids, one high and

straight ending in a small hypoconulid near to the entoconid, while in the isolated tooth there is a v-shaped postcristid in lateral view; in turn, the hypoconulid is well-developed and attached to the postcristid near the middle portion of the tooth. Other small differences (also highlighted by Sánchez-Villagra *et al.*, 2007) are the more developed protoconid (and less developed metaconid and paraconid) and the small entoconid in the mandibular teeth. The interpretation of the mandible and the two molars as m?2 and m?3 by Sánchez-Villagra *et al.* (2007) was based in the supposed absence of an elongated p4 among Paleogene chiropterans. However, some Palaeochiropterygidae as *Anatolianycteris insularis* from the middle Eocene of Turkey actually have an elongated p4 (Jones *et al.*, 2019), as it also happens in the Archaeonycteridae *Archaeonycteris*? *storchi* Smith *et al.*, 2007 from the early Eocene of India (Smith *et al.*, 2007). In addition, the morphology of the mandible is not characteristic of bats: in this group, the lower jaw may be either long in primitive forms (see, *e.g.*, Novacek, 1987; Gunnell & Simmons, 2005) or short in more advanced taxa, but

the basal section is always straight; on the contrary, in *Ghamidtherium* is curved as in the Eulipotyphla or the Afrotheria, even though the morphology of the teeth is more similar to that of the former. Summarizing, taking in account all evidence at hand, we suggest that specimen CGM 83699 may represent an indetermined Eulipotyphla.

Order CHIROPTERA Blumenbach, 1779

Chiroptera indet.
Figure 3J

Material. In the original publication (Sánchez-Villagra *et al.*, 2007): one tooth anterior to m?1 (DPC 21498B).

Occurrence. BQ-2 Quarry, Fayum Depression, Egypt.

Age. Earliest late Eocene (Priabonian).

Discussion. Sánchez-Villagra *et al.* (2007) described an isolated lower molar from Fayum (Quarry BQ-2, Egypt, earliest late Eocene) possibly belonging to the
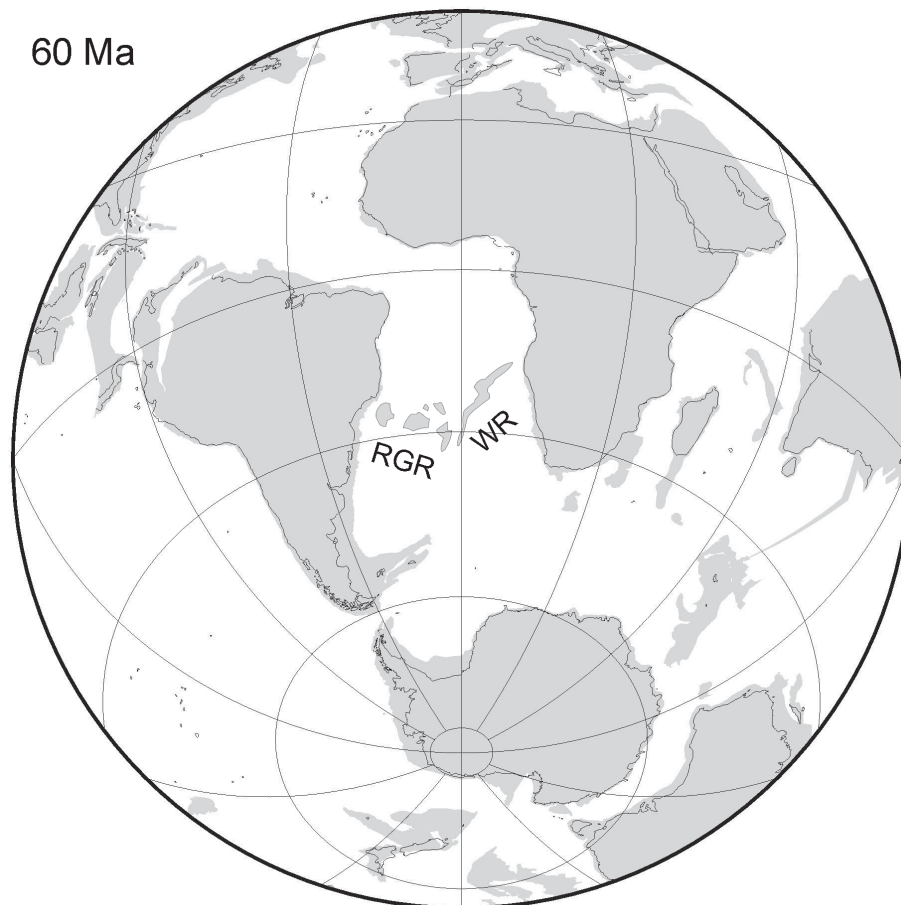

Figure 4. Position of the southern continents at 60 Ma. The palaeogeographic reconstruction was performed with the palaeomap maker of **ODSN** (Ocean Drilling Stratigraphic Network) Plate Tectonic Reconstruction Service (Research Center for Marine Geosciences / Kiel and the Geological Institute of the University Bremen; https://www.odsn.de/odsn/services/paleomap/paleomap.html). Projection: Lambert Azimuthal. Present day shorelines are in black. To the resulting palaeomap we added the contours of the Rio Grande Rise (**RGR**) and Walvis Ridge (**WR**) in the South Atlantic.

species *Ghamidtherium dimaiensis*, and discussed the possibility of it belonging to the Marsupialia or Chiroptera. We argued before that this tooth belongs to a different taxon (see above). Actually, the isolated tooth DPC 21498B may belong to a chiropteran, as it closely resembles the morphology described for the lower molars (necromantodonty *sensu* Maitre, 2014). Such a talonid morphology is present until the earliest Eocene (Maitre, 2014). The size of the tooth is relatively large for a bat; notwithstanding, similar sizes are found in Eocene philisids as *Witwatia* (Gunnell *et al.*, 2008; Ravel *et al.*, 2012).

Family VESPERTILIONIDAE Gray, 1821 or MYZOPODIDAE Thomas, 1904

?*Khonsunycteris* or ?*Phasmatonycteris* or new genus and species
Figure 3K–3O

Material. In the original publication, Mammalia indet. described by Sánchez-Villagra *et al.* (2007), DPC 21372A (fig. 4A), an isolated left upper molar (M?2) and DPC 21372B (fig. 4B, 4C), an isolated right upper molar (M?3). Our interpretation: DPC21372A is a M2 and DPC 21372B is a M1.

Occurrence. BQ-2 Quarry, Fayum Depression, Egypt.

Age. Late Eocene (Priabonian).

Discussion. After recognizing *Ghamidtherium dimaiensis* from Fayum (Quarry BQ-2, Egypt, earliest late Eocene), Sánchez-Villagra *et al.* (2007) described two upper molars and regarded them as Mammalia indet.; they discussed the possibility that they could belong either to the Marsupialia or to the Chiroptera. They emphasised that the upper molars can be referred to, but not diagnosed as, Marsupialia, because of the absence of a hypocone, presence of a stylar cusp C, the relatively low paracone, and the moderately slender lingual portion of the upper molars. Simmons *et al.* (2016) questioned the belonging of these materials to a marsupial.
In the same quarry where *Ghamidtherium* was found, four species of Chiroptera were recognized later: *Witwatia schlosseri* Gunnell *et al.*, 2008, *Witwatia eremicus* Gunnell *et al.*, 2008, *Qarunycteris moerisae* Gunnell *et al.*, 2008 and *Phasmatonycteris butleri* Gunnell *et al.*, 2014 (Gunnell *et al.*, 2008, 2014). The materials described by Sánchez-Villagra *et al.* (2007) either differ from these species or are not comparable because they were recognized on the basis of lower molars.
To us, the upper molars described in Sánchez-Villagra *et al.* (2007) have several features that characterize chiropteran species of the Vespertilionidae and Myzopodidae, as *Myotis*, *Pipistrellus* or *Miostrellus*, in the former, or *Myzopoda* in the second. These features include the shape of the protocone, absence of talon,

well-developed mesial and posterior cinguli, M2 having a small hypocone, among other features (Gunnell *et al.*, 2014; Crespo *et al.*, 2018, 2020). Notwithstanding, these materials also have unique features, as the connection of the preprotocrista with the paracone, which is disconnected to the paracingulum. While the M1 has a small hypocone that disconnects the postptotocrista to the metacone, in the M2 this appears connected to the metacone, similar to *Miostrellus* aff. *petersbuchensis* Rosina & Rummel, 2012 described by Crespo *et al.* (2020). This combination of features does not appear in other vespertilionid or myzopodid bats from the Eocene. Furthermore, Gunnell *et al.* (2008) described a new vespertilionid genus and species (*Khonsunycteris aegypticus* Gunnell *et al.*, 2008) from the Quarry L-41 from a nearly complete mandible. The age of this quarry is latest Eocene, while the quarry where *Ghamidtherium* was found (BQ-2) has been dated as early late Eocene. Judging from the sizes of the teeth, the upper molars are slightly larger, but could be included within the variability of *Khonsunycteris aegypticus*. Until upper molars of *Khonsunycteris* are found, we do not discard that the upper molars found in BQ-2 belong to the genus *Khonsunycteris*. More recently Gunnell *et al.* (2014) described from the same quarry of *Ghamidtherium* the myzopodid bat *Phasmatonycteris phiomensis* on the basis of a lower jaw. We question the taxonomic assignment of this species because it is quite smaller than the material described by Sánchez-Villagra *et al.* (2007); however, it shouldn't be discarded a referral to the same genus, or even family, until upper molars of *Phasmatonycteris* are found.

DISCUSSION

Hooker *et al.* (2008) stated that only two genera were uncontested African metatherians: the herpetotheriid *Peratherium africanum* and the ?peradectoid *Kasserinotherium tunisiense*. Here we reach the same conclusions, with the addition of a still undescribed ?herpetotheriid from the Miocene of Uganda, previously unknown. All other alleged metatherians described up to now are, to us, more probably eutherian mammals.
To Hooker *et al.* (2008) *Peratherium africanum* is closer to *P. lavergnense* than to any other species of the genus. Both species share a mesiobucally directed M3 parastyle in the upper molars, while in the lower ones the hypoconulid is lingually placed and have a hypoconulid-entoconid talonid fold. The next closer species are *P. cuvieri*, *P. elegans* and *P. antiquum*; in all these species the metacone is more than twice as tall as the paracone, there is a crest that links StA and StB, a weak StC and, in the lower molars, the talonids are shorter than the trigonids. All these species are strictly European in their distribution. In turn, *Kasserinotherium tunisiense* is closer to *Wirunodon chanku* (?late Eocene of South America) and *Archaeonothos henkgodthelpi* (earliest Eocene of Australia) than to any other

peradectoid marsupialiform so far known (see above for a detail of shared characters). The biogeographic implications of the implied affinities of both African metatherians are discussed below.

A first impression of this review is that metatherians were extremely scarce throughout the Cenozoic in Afro-Arabia, especially taking in account their success in other southern continents, as South America and Australia. It could be argued that there still exists a sampling bias, both geographically (findings of metatherian specimens are mostly restricted to the north of Afro-Arabia) as well as in specimen numbers. However, it should be mentioned that the (still scarce) evidence at hand contradicts this argument. The rich mammalian assemblages recovered from Lutetian levels in Sperrgebiet, Namibia, in southern Africa, led Pickford *et al.* (2008) to recognise 15 species, all of them eutherians. Moreover, they concluded that the Sperrgebiet mammals show close affinities with north African lineages, which argues against major biogeographic differences among Paleogene African mammals. On another line of reasoning, Cifelli and Davis (2003) discussed the Late Cretaceous, strikingly different patterns of diversification between eutherians and metatherians in North America and Eurasia. Eutherians dominated the mammalian assemblages in Eurasia throughout the Late Cretaceous, while in North America they were absent during most of this period. "*Clearly, the relative successes of the two groups differed widely on the two continents. Yet, the early representatives of both groups seem to have been highly similar ecologically—most were small, insectivorous, and probably nocturnal. This puzzle remains to be resolved.*" (Cifelli & Davis, 2003, p. 1900). We suggest that Cenozoic Afro-Arabian metatherians may have faced a similar situation than that of Eurasia during Late Cretaceous times: their arrival happened in a continent with a well-established diversity of eutherians filling similar ecological niches.

Dual origin of african metatherians?

As argued below, most probably metatherians did not originate in Africa, but instead dispersed to it at some time in the Late Cretaceous–early Paleogene. A thorough review of African paleogeographic, biogeographic and biotic relationships was given by Gheerbrant and Rage (2006). These authors conclude that, even though a former Gondwanan continent, after the separation of Africa and South America by mid-Cretaceous times, most biotic interchanges of the former continent were with Laurasian ones. "*Isolation was broken intermittently by the establishment of discontinuous, filter routes that linked Africa to other continents. These filters permitted rare interchanges between Africa and some other Gondwanan continents (Madagascar, South America, and perhaps India), but mainly between Africa and Laurasian areas.*" (Gheerbrant & Rage, 2006, p. 241).

Discussing the geographic origins of *Peratherium africanum* Simons and Bown (1984, p. 546) suggested five possibilities: "*…(1) they were indigenous to Africa; (2) they arrived in Africa via the sweepstakes route from South America; (3) they reached Africa from North America by way of Europe; (4) they made their way by land bridge or a sweepstakes path directly from Europe; or (5) by land bridge and/or sweepstakes route(s) from Asia or Europe via Asia*". On the same topic, Jaeger and Martin (1984, p. 379) suggested that a vicariant origin for the African marsupials should not be excluded, implying "*…the survival of an ancestral stock common to South America and Africa before the opening of the South Atlantic*". However, taking in account the timing of the opening of the South Atlantic, as well as the evolution of Cretaceous Marsupialiformes, it is clear than neither a *Peratherium* or a *Kasserinotherium* lineage were even remotely present by mid-Cretaceous times (see, *e.g.*, Williamson *et al.*, 2014). More recently Hooker *et al.* (2008) expressed few doubts on the European origins of *Peratherium*. In an attempt to date its arrival into Afro-Arabia, they (Hooker *et al.*, 2008, p. 644) suggested that "*…The most likely time for dispersal would have been during the low sea level at the time of the Oi-1 glaciation (c. 33.7–33 Ma)*"; *i.e.*, by the early Oligocene. The presence of *Kasserinotherium tunisiense* in the early Eocene of northern Africa casts one additional question on the ultimate origins of Afro-Arabian metatherians: did all of them arrive from the same continent(s)? The fact is that *Kasserinotherium*, even though belonging to a ?peradectoid stock, is distinct enough from any European peradectid in such a way that it suggests that there may be equally reasonable alternatives to that of a European (or even Holarctic) origin. In the following paragraphs we discuss each alternative considered by Simons and Bown (1984), both for *Kasserinotherium* and for *Peratherium*.

The idea that metatherians are indigenous to Africa is unsustainable on the basis of the known fossil record. There are no Mesozoic or Paleocene remains of a single metatherian from the whole continent. It is probable that more sampling efforts may give new evidences on the early Paleogene distribution of these mammals in Africa, but the possibility of a Mesozoic record is, to say the least, remote.

One hypothesis that deserves attention is a North American origin of African metatherians via Europe. The discovery of the herpetotheriid *Maastrichtidelphys meurismeti* Martin *et al.*, 2005 in the latest Cretaceous of the Netherlands led Martin *et al.* (2005) to postulate a trans-Atlantic, high-latitude dispersal route from North America to Europe by the end of the Mesozoic. A further speculation would be that metatherians arrived to Africa from Europe by early Paleogene times, *e.g.*, during the Paleocene. It should be noted, however, that *Maastrichtidelphys* shows closer affinities to North American herpetotheriids (*Nortedelphys*; Martin *et al.*, 2005) than to any European one. This means that North

American immigrant lineages of Marsupialiformes probably disappeared during the K–Pg mass extinction. On the other hand, except for a few records from the latest Paleocene (PETM; see, *e.g.*, Hooker, 2018) there is no Paleocene record of Metatherians in Europe, and from the early Eocene onwards all European marsupialiforms are distinct enough from their North American counterparts that Ladevèze *et al.* (2020) recognized the Subfamily Peratheriinae for their inclusion. Taking into account that Europe is a quite well-sampled continent for micromammals, it does not sound reasonable to suppose an endogenous (strictly European), Paleocene evolution of herpetotheriids whose record is still to be found. This same argument also goes against other alternatives postulated by Bown and Simons (1984b), *i.e.*, that metatherians arrived in Africa from Europe by land bridge or a sweepstakes path.

As mentioned, a fourth alternative is the arrival of metatherians to Africa by land bridge and/or sweepstakes route(s) from Asia or Europe via Asia. Against this hypothesis is the fact that the diversity of both herpetotheriids and peradectids in all the Cretaceous–Cenozoic record of Asia is extremely scarce. It sounds more logical to infer dispersals between Africa and Europe than with Asia.

A final alternative is that (at least some) metatherians arrived in Africa via a filter route from South America. Taking in account the probable affinities of *Kasserinotherium tunisiense*, we think that this possibility is the most reasonable at hand. Several filter corridors (island chains) between Africa and South America have been recognized, mainly in the South Atlantic, the most prominent ones being the Rio Grande Rise (east of Brazil) and the Walvis Ridge (west of southern Africa) system (see, *e.g.*, Oliveira *et al.*, 2009 and literature cited). These filter corridors would have been active during the Late Cretaceous–Paleogene span (Fig. 4). The Walvis Ridge (East of Namibia in Africa) and the Rio Grande Rise (East of Brazil in South America) are "*... the two most prominent bathymetric features in the South Atlantic Basin (...) [They form] a V-shaped pair of volcanic lineaments whose axis of symmetry is the South Atlantic spreading center*" (O'Connor & Duncan, 1990, p. 145). To Oliveira *et al.* (2009) these paleogeographic features (now underwater) may have constituted a continuous land bridge between both continents previous to 50 Ma; even after 50 Ma they conformed a series of islands that considerably shortened the distance between them. For this reason, they argued that the Walvis Ridge-Rio Grande Rise was the disperal route of plathyrrine primates and caviomorph rodents from Africa to South America. Among vertebrates, other examples of Late Cretaceous migrations between both continents include cichlid fishes, ratite birds, parrots, and geckos (see Oliveira *et al.*, 2009 and literature cited). Some lineages of vertebrates from the Eocene of Europe that have South America affinities

also seem to have dispersed through a trans-African route: ceratophryid anurans, boine and tropidolophiid snakes, and non-flying birds as Phororhacidae and Idiornithidae (see Rage & Rocek, 2007 and literature cited). A Paleocene dispersal of metatherians from South America to Africa could not only account for the inferred affinities of *Kasserinotherium* but also for the presence of anatoliadelphyid polydolopimorphians (*Anatoliadelphys*, *Orhaniyeia*) in the middle Eocene of Central Anatolia (Turkey). Interestingly, Métais *et al.* (2018) found phylogenetic affinities between anatoliadelphyids and South American and Australian bunodont polydolopimorphian metatherians such as *Palangania*, *Chulpasia* and *Thylacotinga*. "*We hypothesize that basal polydolopimorphians were actually present in Africa during the early and/ or middle Eocene, whence they rafted northward across Neotethys to colonize the Pontide terrane.*" (Métais *et al.*, 2018, p. 15). The obvious source of the Polydolopimorphia in Africa (not yet found) is South America. A recent phylogenetic analysis by Carneiro (2019) found, in turn, affinities between *Anatoliadelphys* and protodidelphid didelphimorphians, a clade of endemic South American didelphimorphians very abundant in the early Eocene (Itaboraian Age). In either of both alternatives, the most parsimonious hypothesis is that of South American ancestors dispersing to Africa (we suggest, by Paleocene times) before arriving into the Pontide terrane.

A more radical hypothesis is that all European (or even Eurasian) Cenozoic Marsupialiformes have an ultimate origin in South America, from where they dispersed via Africa by the Paleocene–earliest Eocene. That is, not only the African *Kasserinotherium* and the Anatolian polydolopimorphians, but also the African and European (Eurasian?) Herpetotheriidae. Regarding the later, it is worth mentioning that this was already suggested previously: discussing on the origins of European herpetotheriids (their "Didelphini") Crochet and Sigé (1983) tentatively argued on a South American origin of this lineage and a trans-African dispersal to Europe (but see, *e.g.*, Rose, 2012). Even though the known record favours a European origin of African herpetotheriids, a proper test of this hypothesis would be a phylogenetic analysis of all herpetotheriid, or purpoted herpetotheriids, so far known. On one hand, several claims have been made on the existence of South American herpetotheriids (Goin & Candela, 2004; Oliveira & Goin, 2012). On the other, a recent phylogenetic analysis found fundamental differences between North American and European herpetotheriids. Actually, as already mentioned, to Ladevèze *et al.* (2020) the Herpetotheriidae (including North American and European taxa) is not a natural group, being the European ones (*Peratherium*, *Amphiperatherium*) a clade of its own. An inclusive phylogenetic analysis would test again not only the monophyly of the group, but also the North American or South American affinities of the Peratheriinae.

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