Review

Afrotherian mammals: a review of current data

Rodolphe Tabuce[1],*, Robert J. Asher[2] and Thomas Lehmann[3]

[1] Institut des Sciences de l'Evolution, cc064,
Université Montpellier II, place Eugène Bataillon,
34095 Montpellier cedex 05, France,
e-mail: rtabuce@isem.univ-montp2.fr
[2] Department of Zoology, University of Cambridge,
Downing Street, Cambridge CB2 3EJ, UK
[3] Museum für Naturkunde der Humboldt-Universität zu
Berlin, Forschungsabteilung Invalidenstrasse 43,
10115 Berlin, Germany

*Corresponding author

Abstract

The supraordinal mammalian clade Afrotheria was first recognized in its entirety based on DNA analysis dating to the mid-1990s. Since then, this "African clade", which includes proboscideans, sirenians, hyracoids, tubulidentates, elephant-shrews, tenrecs and chrysochlorids, has been supported by numerous molecular and genomic studies. According to these molecular inferences, the origin of crown Afrotheria goes back into the Cretaceous, with estimates from over 100 to under 80 Mya. Morphological phylogenies have not completely recovered Afrotheria, although its paenungulate core (proboscideans, sirenians and hyracoids) was named in 1945 by the paleontologist George Simpson. Recent paleontological studies concur with molecular ones in evoking some affinities between paenungulates, aardvarks and elephant-shrews. Moreover, the position of tenrecs and golden moles within afrotherians is supported by some recent concatenations of morphological and molecular phylogenetic datasets. The phylogenetic position of Afrotheria relative to the other supraordinal placental clades has been debated, the most recent analyses of genomic and concatenated data support a basal position within Placentalia. Molecular data suggest an African origin for Afrotheria and a long period of endemism on that continent. When adding the paleontological data to this scenario, the paleobiogeographic history of Afrotheria becomes more complex. For instance, these data argue for the broad distribution of afrotherians during the Tertiary and do not exclude their Laurasian origin. In fact, some Laurasian taxa could be closely related to the earliest afrotherians (hyracoids, proboscideans and elephant-shrews) found in the early Eocene of North Africa. Other Afrotherian groups are known with certitude from East Africa since the beginning of the Miocene.

Keywords: fossil record; molecules; morphology; phylogeny.

Introduction

The resolution of the phylogenetic relationships among mammalian placental orders and the question of when and where the eutherian radiation took place is a controversial topic between morphologists (including paleontologists) and molecular biologists. Molecular analyses, based on large nuclear gene datasets strongly support the division of living placental lineages into four superordinal groups: Afrotheria, Xenarthra, Euarchontoglires and Laurasiatheria (Murphy et al. 2001a,b, Scally et al. 2001, Amrine-Madsen et al. 2003, Springer et al. 2004, Nikolaev et al. 2007, Nishihara et al. 2007, Springer and Murphy 2007, Wildman et al. 2007) (Figure 1). The clade Afrotheria includes six placental orders: Proboscidea (elephants), Sirenia (dugongs and manatees), Hyracoidea (hyracoids), Macroscelidea (elephant-shrews), Tubulidentata (aardvarks) and Tenrecoidea (tenrecs and golden moles, also known as "Afrosoricida"). According to these analyses, these taxa evolved and have been in Africa since the Cretaceous.

Compared to the overwhelming molecular and genomic support for Afrotheria (Redi et al. 2007, Springer and Murphy 2007), the available morphological data are equivocal concerning the validity of such a clade. The different Afrotherian orders have long been scattered among ungulates (proboscideans, sirenians, hyracoids and tubulidentates), lipotyphlan insectivores (tenrecids and chrysochlorids), or considered as the sister group of glires (macroscelids). One explanation for this disagreement between molecules and morphology is the supposed long endemic evolution of afrotherians that may have overwritten morphological afrotherian synapomorphies (Robinson and Seiffert 2004). According to the fossil record, afrotherians have indeed a long history on the Afro-Arabian continent. Likewise, their living representatives are mostly present in Afro-Arabia and Madagascar, except for the Asian elephant, West Indian and Amazonian manatees, and Australasian dugongs. The study of the earliest afrotherians, and eutherians in general, is thus important because they provide direct evidence of the order of acquisition of characters. These fossils present character combinations absent in modern taxa, and they allow the study of characters that have been "erased" by subsequent evolution within a clade (Benton 1995).

In that regard, the recent studies of such fossil eutherians on one hand (Zack et al. 2005, Tabuce et al. 2007, Wible et al. 2007), and the mapping of several morphological characters observed on living afrotherians on molecular phylogenies on the other hand (Werdelin and Nilsonne 1999, Whidden 2002, Cox 2006, Mess and Carter 2006, Sánchez-Villagra et al. 2007) have revealed
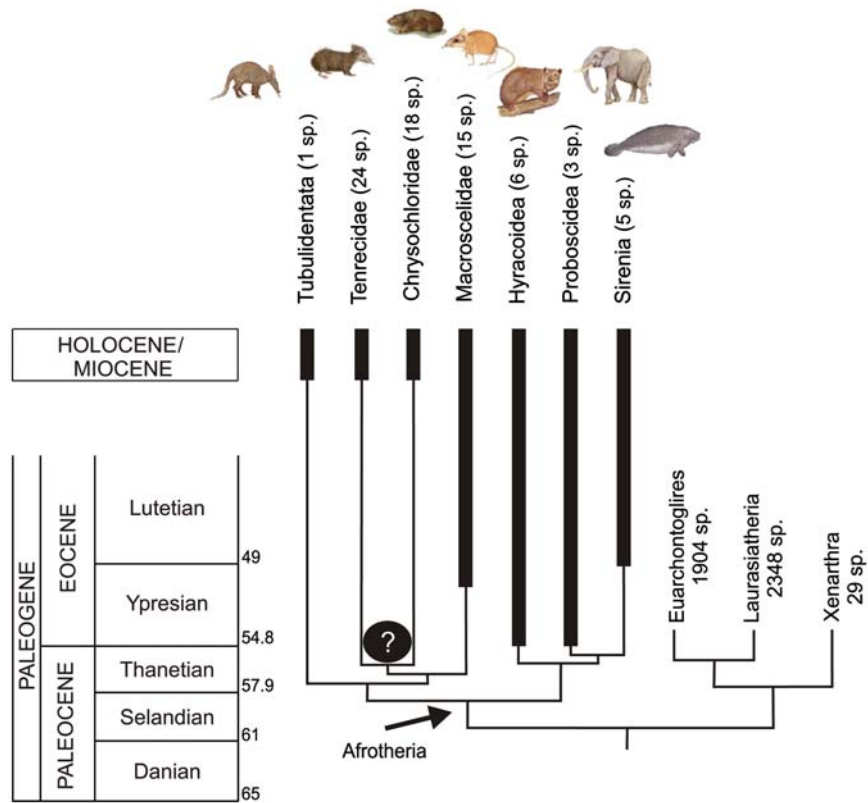
Figure 1 Phylogeny of Afrotheria defined by nuclear and mitochondrial DNA sequence data based on a consensus of recent phylogenetic analyses (Kjer and Honeycutt 2007, Springer and Murphy 2007). Known stratigraphic distribution of afrotherian orders are indicated by black bold lines. Question mark indicates the possible occurrence of stem and/or crown Afrosoricida (tenrecs plus golden moles) during the Paleogene (Seiffert et al. 2007).

some interesting characters proposed as afrotherian synapomorphies.

In this paper, we summarize the fossil record of early afrotherians, review the strong molecular signal for Afrotheria and synthesize the morphological data relative to afrotherian monophyly focusing on recent advances. We also consider the latest large morphological datasets and the combined molecular-morphological analyses that deal with interordinal mammalian relationships in order to discuss the group's African origin, their divergence times and their supposed long Afro-Arabian endemism.

Fossil record of early afrotherians

Proboscidea

The oldest and most primitive proboscidean is *Phosphatherium* from the earliest Eocene of Ouled Abdoun basin, Morocco (Gheerbrant et al. 1996, 1998, 2005a) (Figure 2). This fox-sized genus is known by several jaws and partial skulls. Although plesiomorphic in its anterior dentition and skull structure ("condylarth"-like), *Phosphatherium* is typically proboscidean by its true lophodonty and the orbit opening in the maxilla. *Daouitherium*, also from the Ypresian of Morocco, shares with *Phosphatherium* numerous dental traits (Gheerbrant et al. 2002). *Daouitherium* appears to be structurally intermediate between *Phosphatherium* and *Numidotherium*, a genus known from the early to middle Eocene of El Kohol, Algeria and

from the late Eocene of Dor el Talha, Libya (Mahboubi et al. 1986, Court 1995). Proboscidean features of *Numidotherium* are the pneumatized skull and the second incisors enlarged as tusks. Recently, O'Leary et al. (2006) reported an indeterminate proboscidean from the Eocene of Mali. Other Paleogene genera (*Moeritherium*, *Barytherium*, *Phiomia* and *Palaeomastodon*) are well documented in the rich beds of the late Eocene to early Oligocene layers of the Fayum, Egypt (Andrews 1906) and from other parts of Arabo-Africa (Shoshani et al. 1996). *Moeritherium* was long considered morphotypic for the order, but it is now considered as a peculiar early offshoot within proboscideans (Delmer et al. 2006). *Phiomia* and *Palaeomastodon* are considered more closely related to modern elephants (elephantoids) than other Paleogene taxa according to their columnar limbs, large tusks, external nasal opening shifted in front of the orbits, etc. (Tassy 1996). Recently, primitive deinotheres and gomphotheres have been discovered in the late Oligocene of Ethiopia, extending the fossil records of these more modern groups considerably back in time (Sanders et al. 2004). The first Asian elephantoid is known from the early Oligocene of Pakistan (Antoine et al. 2003).

Sirenia

Sirenia is the only taxon of the clade Afrotheria to have fossils on most continents (except Antarctica) (Figure 3). The oldest and most primitive fossil record for Sirenia is *Prorastomus*, a member of the family "Prorastomidae",
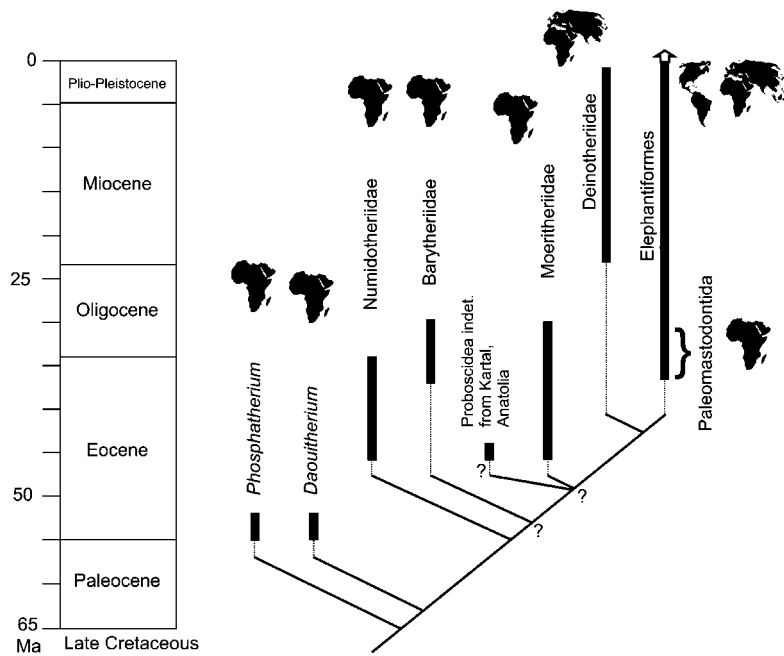
Figure 2   Phylogeny of early proboscidean taxa showing stratigraphic and geographic distributions. Question marks indicate uncertain phylogenetic relationships (modified from Gheerbrant et al. 2005b).

found in the early middle Eocene of Jamaica (Savage et al. 1994). This animal is only known by a skull, mandible and atlas. Therefore, the earliest ascertained fully quadrupedal sirenian is *Pezosiren*, a slightly younger taxon also found in Jamaica and included in the "Prorastomidae", but represented by abundant postcranial and cranial remains (Domning 2001). The prorastomids are amphibious quadrupeds that have similarities with early "condylarths", but have sirenian aquatic specializations, such as retracted nasal openings, absence of paranasal

air sinuses, and dense and swollen ribs (Gheerbrant et al. 2005b). From these taxa, Gheerbrant et al. (2005b, p. 88) extracted some basal sirenian traits: "premaxilla-frontal contact, enlarged premaxillary rostrum with slightly enlarged I1, long, deep, and narrow mandibular symphysis bearing parasagittally arranged incisor-canine toothrows, and the presence of five premolars." The next most primitive sirenian family is the middle Eocene Protosirenidae, represented by a single genus – *Protosiren* – widely distributed from North Africa (Egypt) to South Asia
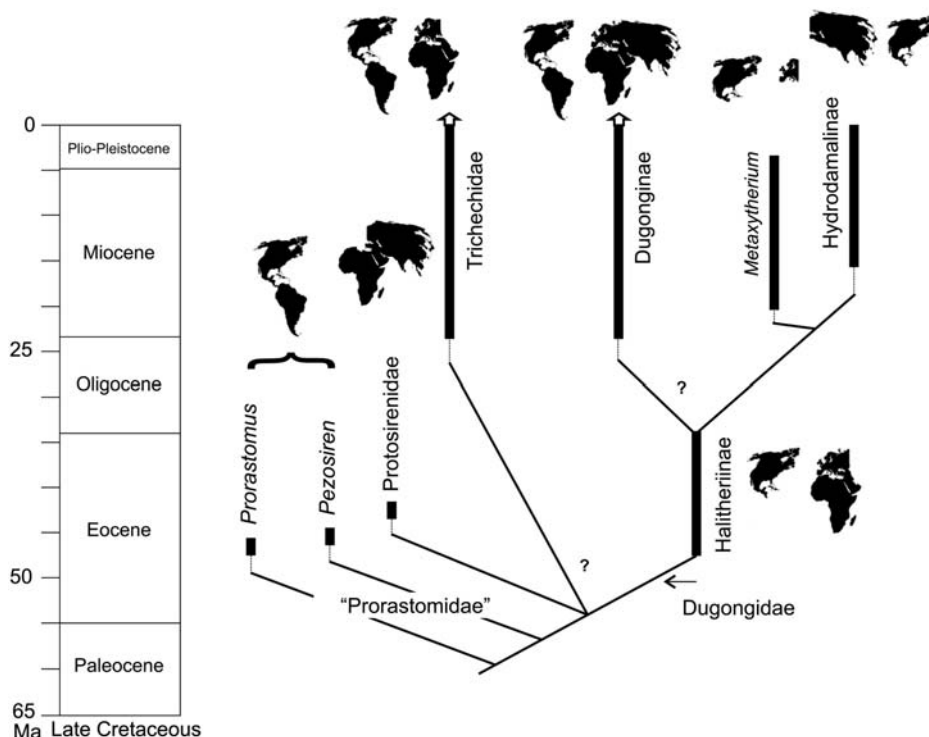

Figure 3   Phylogeny of early sirenian taxa showing stratigraphic and geographic distributions. Question marks indicate uncertain phylogenetic relationships (modified from Gheerbrant et al. 2005b).

(Indo-Pakistan) (Abel 1907, Domning and Gingerich 1994, Gingerich et al. 1994, 1995, Zalmout et al. 2003). Both prorastomids and protosirenids were extinct by the end of the Eocene. The extant Dugongidae [*Dugong* and *Hydrodamalis* (recently extinct)] are closely related to the Halitheriinae (e.g., *Eosiren*, *Eotheroides*, *Halitherium*, *Prototherium*), fully aquatic sirenians with only vestigial hind limbs that lived from middle and late Eocene to Pliocene in the Mediterranean [Europe, Egypt (Fayum)], the Caribbean, Florida, and California (Domning 1994, Gheerbrant et al. 2005b). The last family – Trichechidae – represented currently by the manatees (*Trichechus*) arose in the late Eocene or early Oligocene possibly from the Dugongidae (Domning 1994) or perhaps from the Protosirenidae (Sagne 2001). The earliest fossil record for that family is however from the middle Miocene of South America (Domning 1982, 1994).

Early extinct relatives of proboscideans and sirenians – and thus putative afrotherians – are the orders Embrithopoda and Desmostylia and several other taxa of debatable affinities (e.g., Anthracobunidae). The embrithopods were long identified only from the Fayum with the bizarre, large genus *Arsinoitherium* (Andrews 1906, Court 1992), but basal representatives were also found in Eastern Europe (Sen and Heintz 1979, Rădulescu and Sudre 1985, Maas et al. 1998). The order is supposed to be related to the late Paleocene Asian *Phenacolophus* and *Minchenella* (McKenna and Manning 1977), these genera could also be ancestors for anthracobunids and desmostylians. The anthracobunids are also Asian taxa known from the early-middle Eocene of Indo-Pakistan, they are characterized by common features, such as a complete dental formula (i.e., 3 incisors, 1 canine, 3–4 premolars and 3 molars) and an astragalar foramen. Desmostylians are an extinct order of marine taxa only known from the Oligocene to Miocene levels of the North Pacific area (Domning et al. 1996), they appear to be seashore herbivores and they share cranial derived characters with proboscideans.

Hyracoidea

With the exception of a possible Pakistani Oligocene hyrax (Pickford 1986a), all of the Paleogene fossil record of the order is restricted to the Afro-Arabian continent (Figure 4). Hyracoids were the most diverse herbivore "ungulates" of the African Paleogene. The most primitive genus is *Seggeurius* from the early Eocene of El Kohol, Algeria (Mahboubi et al. 1986, Court and Mahboubi 1993) and possibly from Morocco (Gheerbrant et al. 2003), it is characterized by bunodont molars and simplified premolars. *Titanohyrax tantulus* from the early Eocene of Chambi, Tunisia and from the early-middle Eocene of Gour Lazib, Algeria is more derived for its lopho-selenodonty (Court and Hartenberger 1992). From Gour Lazib at least seven species have been reported (Adaci et al. 2007), among them *Microhyrax lavocati* and *Titanohyrax mongereaui* (Sudre 1979, Tabuce et al. 2001a), these genera illustrate a variety of ecological adaptations and suggest that the origin of the order must be older than early Eocene. If earliest hyracoids are essentially known from dental remains, late Eocene and Oligocene species from the Fayum are documented by skull and complete
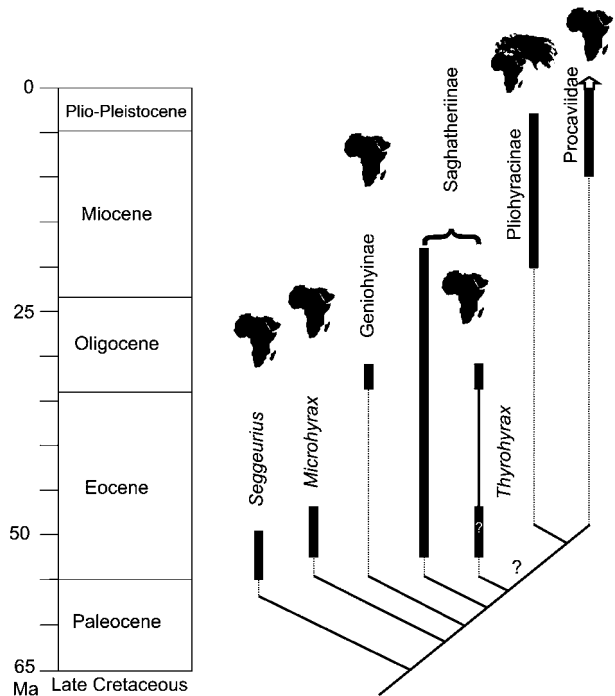

Figure 4 Phylogeny of early hyracoidean taxa showing stratigraphic and geographic distributions based on a consensus estimates from the literature (Meyer 1979, Rasmussen and Simons 2000, Tabuce et al. 2001a). Question marks indicate uncertain phylogenetic relationships.

jaws (Rasmussen and Simons 2000). Other late Eocene to Oligocene hyracoids have been discovered in several regions of Africa (Pickford 1986b, Tabuce et al. 2000, Kappelman et al. 2003). The genus *Thyrohyrax*, known from the Fayum and Oman, is characterized by a lophodonty that suggests possible relationships with modern hyracoids (Figure 4); moreover, Gheerbrant et al. (2007) described nearly complete skeletons belonging to *Saghatherium* from Jebel al Hasawnah, Libya that are clearly similar to living species.

Tubulidentata

The Tubulidentata are unique among mammals for being the only order represented by a single living species: *Orycteropus afer*. The fossil record, however, shows
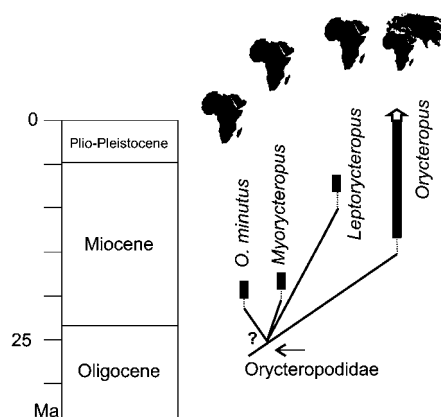

Figure 5 Phylogeny of tubulidentates showing stratigraphic and geographic distributions. Question mark indicates uncertain phylogenetic relationships.

much more biodiversity (Lehmann 2006, 2007) (Figure 5). Some Eo-Oligocene fossils from Quercy, France (*Archaeorycteropus*, *Leptomanis*, *Palaeorycteropus*) and Wyoming, USA (*Tubulodon*) have been suggested as the earliest known tubulidentates, but have been reassigned to different taxa upon closer examination (Gazin 1952, Patterson 1975, MacPhee 1994). The evolutionary history of the aardvarks is therefore only documented for the last 20 Ma. The oldest ascertained fossil Tubulidentata come from the early Miocene of East Africa (Koru, Napak and Songhor sites) and consist of very fragmentary remains (MacInnes 1956, Pickford 1975, Pickford and Andrews 1981). The aardvark from Songhor has been assigned to *Orycteropus minutus* by Pickford (1975), but this species should be "queried until more diagnostic, associated materials become available" (Patterson 1978, p. 273). The earliest best-known fossil aardvark is therefore *Myorycteropus* from the early Miocene of Kenya (MacInnes 1956, Pickford 1975). It is a small aardvark species showing typical tubulidentate tooth structure. It was a very efficient digger, even more specialized than the extant *O. afer*. This taxon is thus unlikely to be the stem group of the other tubulidentates, but is rather a sister taxon as suggested by MacInnes (1956) and Patterson (1975). *Orycteropus* is the only genus so far to be known from Africa, Europe and Asia (Lehmann et al. 2005). The relationships among the three known genera (*Leptorycteropus* from the late Miocene of Kenya, *Myorycteropus* and *Orycteropus*) are debated, but recent discoveries in Central Africa might shed some light (Lehmann et al. 2004, 2005, 2006).

Macroscelidea

Since the Eocene, the order is exclusively African in distribution (Figure 6). The earliest and most primitive genus, *Chambius* from the early Eocene of Chambi, Tunisia is documented by dental and postcranial remains (Hartenberger 1986, Tabuce et al. 2007). This genus is also possibly known from the Gour Lazib, Algeria (Adaci et al. 2007). *Chambius* belongs to the Herodotiines, a subfamily that also embraces *Herodotius* and *Nementcatherium* from the late Eocene of the Fayum and Bir El Ater, respectively (Simons et al. 1991, Tabuce et al. 2001b). These forms are primitive for their bunodont and low-crowned molars, but evoke modern elephant-shrews by their submolariform fourth premolars and reduced third molars. *Metoldobotes* from the early Oligocene of the Fayum appears more derived, but remains of uncertain affinities (Butler 1995). The Mio-Pliocene of East and South Africa has also yielded specialized forms, such as *Myohyrax* (hyrax-like) and *Mylomygale* (rodent-like) (see Butler 1995). The first representatives of the living subfamilies (rhynchocyonines and macroscelidines) are known from the Miocene of Kenya (Butler 1984).

Chrysochloridae

There have been four fossil chrysochlorid species named in the literature, all of which are based on material from the Miocene to Pleistocene from Kenya, Namibia and South Africa. *Prochrysochloris miocaenicus* is known from cranial fragments found in the Kenyan Miocene (Butler 1984). Jaw fragments of the genus *Prochryso-*
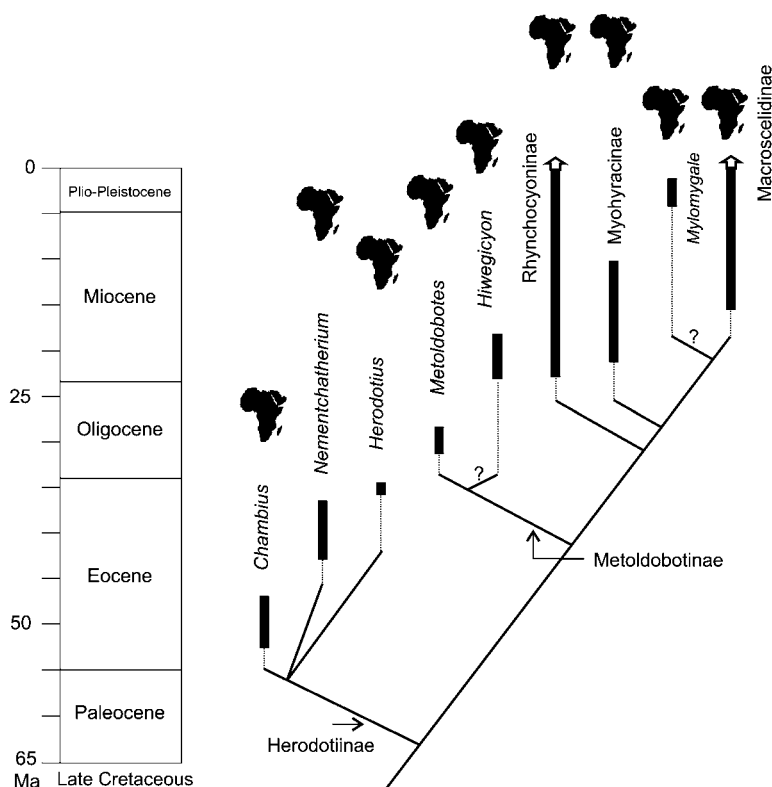

Figure 6 Phylogeny of early macroscelidean taxa showing stratigraphic and geographic distributions based on consensus estimates from the literature (Butler 1995, Tabuce et al. 2001b). Question marks indicate uncertain phylogenetic relationships.

chloris have also been recovered from the Miocene of southern Namibia (Mein and Pickford 2003). The Plio-Pleistocene of South Africa has yielded two fossil chrysochlorid species, both of which were described by Broom (1941): *Chlorotalpa spelea* from Sterkfontein and *Proamblysomus antiquus* from "one of the small caves at Mr. Bolt's workings at Sterkfontein" (Broom 1941, p. 215). "*Chrysotricha*" *hamiltoni* (De Graaff 1957) was considered by Butler (1978) to be part of the genus *Amblysomus*, and consists of a skull from Makapansgat, "found amongst the sorted material from the dumps" (De Graaff 1957, p. 21). Broom (1948, p. 11) also referred to a golden mole skull from Kromdraai, with "a number of teeth well preserved" and which "possibly belongs to the species *Proamblysomus antiquus*". Frustratingly, this specimen now appears to be lost. Several of the currently extant golden mole species also possess a fossil record in the Plio-Pleistocene of South Africa (Avery 2000, 2001).

Tenrecidae

Extinct tenrecid species are also known from the Miocene of Kenya and Namibia: *Protenrec tricuspis*, *Erythrozootes chamerpes* (Protenrecinae), and *Parageogale aletris* (Geogalinae) are known from early Miocene localities in southwest Kenya (Butler 1984). *Protenrec butleri* has recently been named from the Miocene of southern Namibia from the same locality that produced *Prochrysochloris* sp. (Mein and Pickford 2003). In contrast to golden moles, no definitive fossil tenrecs have yet been reported from South Africa. Nor does the limited material of fossil tenrecs in Madagascar exceed the living taxonomic diversity on the island (Goodman et al. 2003). Grandidier (1928) described "*Cryptogale australis*" based on subfossil cranial remains from Andrahomana cave, near Fort Dauphin (Taolanaro) in the southeast. However, following Heim de Balsac (1972), this specimen is currently regarded as an individual of the extant *Geogale aurita*. Interestingly, Butler and Hopwood (1958) had originally placed the Miocene tenrec *Parageogale aletris* in the same genus as the extant, Malagasy *Geogale aurita*. Butler (1984) subsequently referred it to a new genus, but his original hypothesis of a close relationship with the modern (and non-mainland) tenrec *Geogale* has been substantiated by phylogenetic analysis (Asher and Hofreiter 2006).

Afrotherian monophyly

Molecular evidence for Afrotheria

Initial support for elements of the "African clade" (proboscideans, sirenians, hyracoids, tubulidentates and elephant-shrews) was established by de Jong et al. (1981, 1993) in their study of the αA-lens crystallin protein sequence of several placental species. Since then, and after its formal designation by Stanhope et al. (1998), Afrotheria was supported by independent analyses that concatenated DNA sequences from many different nuclear genes (Madsen et al. 2001, Murphy et al. 2001a,b, Scally et al. 2001, Waddel et al. 2001, Delsuc

et al. 2002, Amrine-Madsen et al. 2003, Waddell and Shelley 2003, and see Springer and Murphy 2007 for references). These concatenations have since been dwarfed by several genomic analyses published in 2007, which sampled thousands of genes and provide unequivocal support for Afrotheria (Nikolaev et al. 2007, Nishihara et al. 2007, Wildman et al. 2007). Analyses of mitochondrial sequences have also corroborated the validity of Afrotheria (Murata et al. 2003, Reyes et al. 2004, Kjer and Honeycutt 2007). Moreover, some rare genomic changes have been identified in support of this clade, including SINEs (Nikaido et al. 2003, Nishihara et al. 2005) and LINE transposition (Waters et al. 2007), the 9-bp deletion of the BRCA1 gene (Madsen et al. 2001), the 5′ and 3′ deletions present in apolipoprotein B gene (Amrine-Madsen et al. 2003) and the protein sequence signatures revealed by van Dijk et al. (2001). More recently, chromosomal syntenies (Yang et al. 2003, Robinson et al. 2004, Gilbert et al. 2006, Kellogg et al. 2007) and genome size of placentals (Redi et al. 2007) also greatly support Afrotheria.

Within Afrotheria, Kjer and Honeycutt (2007) proposed to unite chrysochlorids with tubulidentates. The concatenated analysis by Waddell and Shelley (2003, Figure 10) places tenrecs with tubulidentates. In contrast, most other analyses place tenrecids and chrysochlorids in their own clade. With macroscelidids as their sister taxon, this group is known as Afroinsectivora, the latter plus aardvarks are known as Afroinsectiphillia (Springer and Murphy 2007). An interesting alternative hypothesis of intra-afrotherian phylogeny, with major implications for reconstructions of the placental common ancestor, is one of the combined morphology-DNA topologies presented by Seiffert (2007, Figure 1), which places tenrecs and golden moles at the base of Afrotheria. The Paenungulata clade (Proboscidea, Sirenia and Hyracoidea) is always recognized and, in most recent phylogenies except for Seiffert (2007), constitutes the sister group of Afroinsectiphilia. Tethytheria (Proboscidea and Sirenia) is accepted (Asher 2007, Kjer and Honeycutt 2007, Seiffert 2007) or rejected in favor of a Hyracoidea-Sirenia clade (Matthee et al. 2007, Springer and Murphy 2007) or a Hyracoidea-Proboscides clade (Amrine-Madsen et al. 2003).

Homoplasy among placental mammal clades

Paenungulata and Tethytheria were first recognized by Gregory (1910) and named by Simpson (1945) and McKenna (1975), respectively. Along with several other orders (perissodactyls, artiodactyls, cetaceans), paenungulates and tubulidentates were until recently regarded as "ungulates". Similarly, tenrecids and chrysochlorids were classified in Lipotyphla, along with other insectivoran-grade groups, such as moles, shrews and hedgehogs (McKenna and Bell 1997). Hence, one of the most important results of the molecular analyses was the demonstration of the polyphyly of ungulates and lipotyphlans. In parallel, DNA sequences have helped uncover constellations of morphologically homoplastic taxa that have evolved independently in separate geographic areas, again demonstrating how morphological convergence can result from similar selection pressures in analogous environments (Madsen et al. 2001).

For instance, among afrotherians, both hyracoids and proboscideans would be the ecomorphological equivalents of perissodactyls and artiodactyls (comprising the ungulate morphological grade), elephant-shrews present adaptation for jumping as lagomorphs (hence their previous association with Glires), and golden moles and some tenrecs resemble true moles (Talpidae) and hedgehogs (Erinaceidae), respectively.

Classic examples of mammalian convergence have been recognized for 200 years, particularly between marsupials and placentals, such as thylacines vs. canids, the borhyaenid *Thylacosmilus* vs. *Smilodon*, the diprotodont *Thylacoleo* vs. felids, and another kangaroo-relative, *Diprotodon*, vs. graviportal placental "ungulates", such as *Rhinoceros*. In each of these cases, the morphological signature of being a marsupial (e.g., dental replacement, jaw angle, for diprotodonts syndactyly, and – primitively – epipubic bones) has not been erased, despite the fantastic convergence of other skeletodental features among these mammals. In contrast, it appears that more (but not all) of the morphological "signature" of being an afrotherian has indeed been made difficult to recognize. As the cases of homoplasy between marsupials and placentals demonstrate, such extensive "erasure" does not always accompany parallelism, but it does appear to have happened to a relatively high degree among afrotherians.

Recent advances in morphological phylogeny

Among extant taxa, testicondy (i.e., the retention of testes in the abdominal cavity, just caudal to the kidneys) (Werdelin and Nilsonne 1999) has been viewed as an afrotherian synapomorphy. In addition, the occurrence of a long, tactile snout was informally regarded as another potential afrotherian character by Hedges (2001). Indeed, a "mobile proboscis" has also been viewed as a likely unifying feature of the competing hypothesis of "Lipotyphla", including tenrecs and golden moles with other "insectivorans", such as hedgehogs and shrews (Butler 1988). Closer anatomical investigation shows that "mobile proboscis" is not a robust synapomorphy for Afrotheria (Whidden 2002). Mess and Carter (2006) identified two potential afrotherian traits in a novel examination of placentation characters. Such features are intriguing, but cannot be observed in fossils. Cox (2006) noted also that characters of the orbital region (or eye socket) do not seem to favor the afrotherian clade. More recently, Sánchez-Villagra et al. (2007) (see also Narita and Kuratani 2005) proposed a high number of thoracolumbar vertebrae in Afrotheria as the first unambiguous skeletal synapomorphy of the clade. This trait shows some homoplasy, as perissodactyls, primates and xenarthrans also deviate from what appears to be a conserved formula across therian mammals. However, variable vertebral number may prove to be a fruitful source of further study to investigate the morphological integrity of Afrotheria. Finally, osteological features of the ankle (Seiffert 2007, Tabuce et al. 2007) as well as a peculiar pattern of dental eruption (Asher and Lehmann, Submitted) appear also to morphologically unite the otherwise disparate members of the afrotherian clade.

Considering that Afrotheria is an assemblage of both ungulate-like and insectivore-like mammals, paleontologists have reassessed some early Tertiary groups with adequate morphology to identify putative stem afrotherians. Seiffert et al. (2007) proposed that several "insectivore" mammals from the late Paleocene of Morocco and the Eocene to Oligocene of Egypt share some dental similarities with modern tenrecs and golden moles. In the same way, the discovery of the first Eocene elephant-shrews has led to the hypothesis of their relationships with some hyopsodontid "condylarths" (Hartenberger 1986, Simons et al. 1991, Tabuce et al. 2001b). This hypothesis – initially based on dental remains – was supported by the tarsal morphology of both the European louisinine and North American apheliscine "condylarths" (Zack et al. 2005, Tabuce et al. 2006a), which present macroscelidid features. Louisinines and apheliscines could represent in fact stem afrotherians as they share with basal elephant-shrews, proboscideans, sirenians and hyracoids some similarities including the occurrence of a cotylar fossa on the astragalus (Tabuce et al. 2007).

Studying primitive proboscideans, Gheerbrant et al. (2005a) favored the monophyly of the Paenungulata (proboscideans, sirenians and hyracoids); they proposed large upper incisors to be a synapomorphy for the group. Moreover, amastoidy (lack of exposure of the petrosal on the ventrolateral surface of the skull, Novacek and Wyss 1986) and taxeopody (serial alignment of tarsal and carpal bones, Rasmussen et al. 1990) are often considered to be putative derived traits for paenungulates. Therefore, following molecular studies, recent paleontological works support the paenungulate clade and suggest that Macroscelidea could be related to this group, as explained above. Likewise, the living Tethytheria (proboscideans, sirenians) is well supported by morphological data (e.g., molars with transverse lophs, occurrence of a submaxillary fossa) (Gheerbrant et al. 2005a). However, the hypothesis that some extinct taxa (desmostylians, embrithopods and anthracobunids) are included in tethytheres is less supported, because the characters used to include them within tethytheres are homoplastic and/or of ambiguous distribution: e.g., anterior orbits, robust zygomatic process of the squamosal, infraorbital foramen located close to the orbit, and presence of the postentoconule and the postentoconulid (Gheerbrant et al. 2005a). A study of the dental enamel microstructures of some tethytheres (Tabuce et al. 2006b) showed also that the relationships between extant tethytheres, embrithopods and anthracobunids are difficult to establish considering the current data. Thewissen et al. (2000) reported an undescribed anthracobunid skull from Pakistan that may appear crucial to help resolve extant and putative fossil tethythere relationships.

As for the Tubulidentata, another ungulate-grade afrotherian order, there is no strong consensus from morphological phylogenies on its position within Eutheria. Notably, Le Gros Clark and Sonntag (1926) foreshadowed the Afrotheria with their proposal that aardvarks were closely related to "Hyracoidea and Proboscidea". Recent studies all suggest an ancient divergence and the presence of a ghost lineage to at least the Palaeogene (Holroyd and Mussel 2005). Aardvarks have long been

considered to resemble "condylarths", similar to *Phena-codus* and *Ectoconus* (Le Gros Clark and Sonntag 1926, Colbert 1941). Many authors now consider that the mosaic of "condylarthran" and "ungulate" features observed in tubulidentates represents mostly symplesiomorphic characters (Thewissen 1985, Holroyd and Mussel 2005). In his study of the Malagasy sub-fossil *Plesiorycteropus*, MacPhee (1994) was able to place Tubulidentata in different positions among Eutheria depending on the assumption sets and selected deletions in his character matrix, highlighting the problems in assessing tubulidentate affinities. Likewise, the affinities of *Plesiorycteropus*, once classed among Tubulidentata, could not be resolved by MacPhee (1994) who created a new order, Bibymalagasia, for it. More recently, Cote et al. (2007) brought up to date the hypothesis of Simons and Gingerich (1974) that tubulidentates might be related to the Ptolemaiida, an enigmatic order only known from the Oligocene of Egypt and the early Miocene of Kenya. The main similarities between ptolemaiids and tubulidentates include hypsodont molars with a flat, worn occlusal surface, long and shallow mandible with elongated symphyseal region, lateral constriction between trigonids and talonids, and possibly V-shaped morphology of the anterior end of the nasals as observed in *Kelba* (Cote et al. 2007). In a recent combined analysis (Seiffert 2007), *Kelba* is placed as stem member of Tubulidentata lending support to this hypothesis.

Although competing hypotheses on the phylogeny of individual afrotherian taxa have been hotly debated in previous decades (e.g., the hyrax-perissodactyl clade, see Fischer and Tassy 1993), at least some elements of Afrotheria have been variably recognized by morphologists since the monograph on *Orycteropus* by Le Gros Clark and Sonntag (1926). The clade as a whole has, however, never been recognized using only anatomical data (Novacek and Wyss 1986, Asher 1999, Whidden 2002, Asher et al. 2003). Most recently, Wible et al. (2007), using a morphological dataset, recovered paenungulates, *Orycteropus* and a macroscelidid in the same clade. In addition, they also recovered clades largely consistent with the major placental radiations emphasized in most recent molecular studies (including Laurasiatheria and Archontoglires). An important exception to this was their reconstruction of the one sampled African insectivoran (the tenrecid *Potamogale*) near northern insectivorans, outside of Afrotheria.

There is little doubt that DNA sequence data are essential for obtaining a well-resolved mammalian phylogenetic tree. It should come as no surprise that an analysis of a subset of phylogenetic data [e.g., the ca. 400 morphological characters of Wible et al. (2007)] is not fully congruent with, e.g., recent genomic studies (Wildman et al. 2007) of placental mammal phylogeny. The hypotheses proposing a Cretaceous ancestry for specific placental clades (i.e., Glires and "ungulates") that were explicitly tested by Wible et al. (2007) were significantly rejected, and the tests of Wible et al. (2007) may be rightfully regarded as the most rigorous undertaken to date that address the paleontological case for Cretaceous (crown) Placentalia. However, we do not regard all aspects of the placental topology presented by Wible et al. (2007) as optimal, as there are analyses based on considerably more data relevant to modern placental mammal interordinal relations that differ, e.g., in supporting the inclusion of African insectivorans, such as tenrecs, in the Afrotheria (as summarized in Springer and Murphy 2007).

Combining morphological and molecular data

Morphological and DNA sequence data are often perceived as "different" and "conflicting" based more on the fact that the investigators who collect these data are typically trained differently, the former as geologists or anatomists and the latter as molecular biologists. These categories do not have an intrinsic, biological value, rather, they arise from the (highly complex) sociology of organizing academic disciplines. "DNA" and "morphology" ultimately represent different points on a developmental continuum or a "continuity of information" (van Valen 1982), and there is no fundamental reason why these categories of phylogenetic data should be treated differently than other such categories (indels, behaviors, rare genomic events, karyotypes, etc.). There are certainly a variety of reasons why an investigator might wish to evaluate a phylogenetic signal from a given data partition prior to combining it with another such partition (Phillips et al. 2006). However, the mere status of a character as either "morphological" or "molecular" should not, by itself, be one of these reasons.

There are many concatenations of phylogenetic data that address the position of afrotherians, both among themselves and relative to other mammals. Relatively few of these combine morphological and molecular data (Asher et al. 2003, Asher and Hofreiter 2006, Asher 2007, Seiffert 2007). As previously summarized, these studies generally support the position of golden moles and tenrecs in a clade together. One of the most interesting results is that of Seiffert (2003, 2007), who reconstructs tenrecs and golden moles as basal-most within Afrotheria in most of his assumption sets (Seiffert 2003, Figure 3.8). This result highlights the possibility that the ancestral afrotherian may have been insectivoran-like, rather than the ungulate-like hypothetical ancestor optimized on other topologies (Murphy et al. 2001b).

Divergence times and African 'endemism' of Afrotheria

Some molecular inferences propose a deep origin for Afrotheria near the root of the placental tree, but the early history of Afrotheria is still inconclusively resolved. For instance, some claims place the divergence of Afrotheria well into the Cretaceous, over 90 Mya (Kumar and Hedges 1998, Bininda-Emonds et al. 2007), whereas Springer and Murphy (2007) and Hallström et al. (2007) propose a younger estimate of ca. 80 Mya. Kitazoe et al. (2007) and Douzery et al. (2003) proposed even younger divergence dates for placental mammals, well under 80 Mya. Likewise for the relationships of afrotherians: some molecular analyses join Xenarthra and Afrotheria in the clade named Atlantogenata (Hallström et al. 2007, Murphy et al. 2007, Wildman et al. 2007), whereas other studies (Kriegs et al. 2006) place Afrotheria as sister taxon to Boreoeutheria (Euarchontoglires plus Laurasiatheria), with Xenarthra at

the placental base, in the so-called Epitheria clade (McKenna 1975). A third hypothesis proposes a basal placement for Afrotheria, near the placental root, as the sister taxon of all other placental mammals (Murphy et al. 2001b, Nishihara et al. 2007). Finally, a non-basal position of Afrotheria within Placentalia has also appeared in the literature (Arnason et al. 2002, Asher et al. 2003, Wible et al. 2007).

Two questions must be resolved to answer the early biogeography of Afrotheria: 1) are afrotherians basal within Placentalia, and 2) do eutherian mammal divergence dates greatly exceed paleontological estimates, with the origin of Eutheria deep in the Jurassic and the emergence of Afrotheria (with or without xenarthrans) at or near 100 Ma?

A positive answer to both would support the hypothesis that, as most recently formulated by Wildman et al. (2007), eutherians originated on the supercontinent of Pangaea and were subdivided in two lineages when the Tethyan seaway separated Gondwana from Laurasia during the Cretaceous. This process isolated the clade Boreoeutheria in the north and the Atlantogenata in the south. Later in the Cretaceous, the opening of the southern Atlantic Ocean between the African and South American landmasses led to the divergence of Xenarthra and Afrotheria by vicariance (Waddell et al. 1999, Wildman et al. 2007). Note that according to this hypothesis, Xenarthra and Afrotheria (Atlantogenata) form the basal-most placental clade. A variant on this vicariant theme also centers on the tectonic split of Africa from South America at ca. 100 Ma, corresponding to the hypothesized phylogenetic split of Afrotheria (as the basal most placental clade) from Xenarthra plus Boreoeutheria (Murphy et al. 2001b). In contrast to the former concept, this hypothesis places Afrotheria at the placental base, followed by Xenarthra as the sister taxon to all other placental clades.

With the exception of the Indian subcontinent, which separated from Madagascar ca. 85–90 Ma (Krause 2003), other Gondwanan continents had reached near-modern positions until the latest Cretaceous or early Paleogene. Hence, molecular clock reconstructions that estimate a common ancestor for placentals younger than 80 Ma (Douzery et al. 2003, Kitazoe et al. 2007) do not support the aforementioned vicariance hypotheses centering on Gondwana. In addition, if the tectonic separation between Africa and South America at 100 Ma played a causative role in placental mammal diversification, we would expect to find some crown representatives of Placentalia in Cretaceous rocks of one of these continents, or indeed from other continents shortly thereafter. Instead, none of the proposed Cretaceous-crown group relations (zalambdalestids-Glires, zhelestids-"ungulates") has stood up to close phylogenetic scrutiny (Asher et al. 2005, Wible et al. 2007). The Cretaceous and Palaeocene mammalian record in Africa is admittedly poor. However, data for this time and place do exist, documenting, e.g., the absence of eutherians in the "middle" Cretaceous of Morocco (Sigogneau-Russell et al. 1988). In contrast, the Moroccan sites yielded some forms that evoke typical Mesozoic American and European taxa. Mammalian endemism in Africa at this time is therefore overstated.

In the same way, the long supposed African endemism of the Afrotheria from Cretaceous to Paleogene can be criticized, as several faunal exchanges are well documented between Northern continents and Africa during this broad stretch of time (Gheerbrant and Rage 2006), possibly including Eocene anthracobunids and embrithopods from Eurasia (Beard 1998), which may in fact be afrotherians. Additionally, the occurrence of several stem putative afrotherians (louisinine and apheliscine "condylarths") in the Paleocene of northern continents could suggest a Laurasian origin for the group (Zack et al. 2005, Tabuce et al. 2007).

Fieldwork in the Cretaceous and Paleogene of Africa (Krause 2003, Seiffert 2007, Tabuce et al. 2007) and South America (Reguero et al. 2002, Goin et al. 2006) continues. All it will take is a single, ancient and diagnostic fragment of (for example) an aardvark tooth, an armadillo ankle or a proboscidean rostrum to fundamentally change the paleontological view that these taxa did not exist in otherwise diverse pre-Paleocene mammalian communities. Such a fragment has yet to be found.

Conclusions

Broad agreement exists on the validity of the paenungulate clade, as well as on the union of elephant-shrews and aardvarks in Afrotheria. Although the position of both tenrecs and chrysclorids has been historically far removed from Afrotheria, concatenations of relevant phylogenetic data also support this topology.

Nowadays, afrotherian orders are generally uncommon and poorly diversified. According to the IUCN Red List of the threatened mammalian species (IUCN 2006), at least 30 species of afrotherians are considered at risk. In terms of mammalian systematics, this places just under one-half of one of the four major placental radiations at risk of becoming extinct within the lifetime of the authors of this article.

Due to the depauperate nature of most living afrotherian clades, the 72 known living species of afrotherians represent less than 2% of the global placental specific diversity (Wilson and Reeder 2005). Consequently, molecular inferences on Afrotheria will be rapidly asymptotic, as the number of sampled taxa will rapidly reach its limit. In contrast, the fossil record reveals that 1) afrotherians were more diversified in the past, and 2) the paleobiogeography of Afrotheria is more complex than suggested by the various molecular scenarios. The study of late Cretaceous and Paleogene mammals from Afro-Arabia (and certainly Laurasia) is therefore of primary importance to reveal the long history of Afrotheria. The development of new sources of phylogenetic characters, both from living and extinct mammals (e.g., enamel microstructures, patterns of dental eruption, placentation, brain anatomy, etc.), and the exploration of new methods for coding, analyzing, and combining molecular and morphological characters are also crucial to shed light on the Afrotheria.

References

Abel, O. 1907. Die Stammesgeschichte der Meeressäugetiere. Meereskunde 11: 1–36.

Adaci, M., R. Tabuce, F. Mebrouk, M. Bensalah, P.-H. Fabre, L. Hautier, et al. 2007. Nouveaux sites à vertébrés paléogènes dans la région des Gour Lazib (Sahara nord-occidental, Algérie). C.R. Palevol. doi:10.1016/j.crpv.2007.09.001.

Amrine-Madsen, H., K.-P. Koepfli, R.K. Wayne and M.S. Springer. 2003. A new phylogenetic marker, apolipoprotein B, provides compelling evidence for eutherian relationships. Mol. Phylogenet. Evol. 28: 225–240.

Andrews, C.W. 1906. Catalogue of the tertiary vertebrates of the Fayum, Egypt. Br. Mus. (Nat. Hist.), Lond. 324 pp.

Antoine, P.-O., J.-L. Welcomme, L. Marivaux, I. Baloch, M. Benammi and P. Tassy. 2003. First record of Paleogene Elephantoidea (Mammalia, Proboscidea) from the Bugti Hills of Pakistan. J. Vertebr. Paleontol. 23: 977–980.

Arnason, U., J.A. Adegoke, K. Bodin, E.W. Born, Y.B. Esa, A. Gullberg, et al. 2002. Mammalian mitogenomic relationships and the root of the Eutherian tree. Proc. Natl. Acad. Sci. USA 99: 8151–8156.

Asher, R.J. 1999. A morphological basis for assessing the phylogeny of the "Tenrecoidea" (Mammalia, Lipotyphla). Cladistics 15: 231–252.

Asher, R.J. 2007. A web-database of mammalian morphology and a reanalysis of placental phylogeny. BMC Evol. Biol. 7: 108.

Asher, R.J. and M. Hofreiter. 2006. Tenrec phylogeny and the non-invasive extraction of nuclear DNA. Syst. Biol. 55: 181–194.

Asher, R.J., M.J. Novacek and J.H. Geisler. 2003. Relationships of endemic African mammals and their fossil relatives based on morphological and molecular evidence. J. Mammal. Evol. 10: 131–194.

Asher, R.J., J. Meng, J.R. Wible, M.C. McKenna, G.W. Rougier, D. Dashzeveg, et al. 2005. Stem Lagomorpha and the antiquity of Glires. Science 307: 1091–1094.

Avery, D.M. 2000. Micromammals. In: (T.C. Partridge and R.R. Maud, eds). The Cenozoic of Southern Africa. Oxford monographs on geology and geophysics 40. Oxford University Press, New York. pp. 305–338.

Avery, D.M. 2001. The Plio-Pleistocene vegetation and climate of Sterkfontein and Swartkrans, South Africa, based on micromammals. J. Hum. Evol. 41: 113–132.

Beard, K.C. 1998. East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. B. Carnegie Mus. Nat. Hist. 34: 5–39.

Benton, M.J. 1995. Testing the time axis of phylogenies. Phil. Trans. R. Soc. Lond. 349: 5–10.

Bininda-Emonds, O.R.P., M. Cardillo, K.E. Jones, R.D.E. MacPhee, D.M.D. Beck, F. Grenyer, et al. 2007. The delayed rise of present-day mammals. Nature 446: 507–512.

Broom, R. 1941. On two Pleistocene golden moles. Ann. Transvaal Mus. 20: 215–216.

Broom, R. 1948. Some South African Pliocene and Pleistocene mammals. Ann. Transvaal Mus. 21: 1–38.

Butler, P.C. 1978. Insectivora and Chiroptera. In: (V.J. Maglio and H.B.S. Cooke, eds) Evolution of African Mammals. Harvard University Press, Cambridge, MA. pp. 56–68.

Butler, P.M. 1984. Maroscelidae, Insectivora, and Chiroptera from the Miocene of East Africa. Palaeovertebrata 14: 117–200.

Butler, P.M. 1988. Phylogeny of the insectivores. In: (M.J. Benton, ed) The phylogeny and classification of the tetrapods. Vol. 2. Clarendon Press, Oxford. pp. 117–141.

Butler, P.M. 1995. Fossil Macroscelidae. Mamm. Rev. 25: 3–14.

Butler, P.M. and A.T. Hopwood. 1958. Insectivora and chiroptera from the Miocene rocks of Kenya colony. Br. Mus. (Natu. Hist.), Lond.: Fossil Mamm. Africa 13: 1–35.

Colbert, E.H. 1941. A study of Orycteropus gaudryi from the island of Samos. Bull. Am. Mus. Nat. Hist. 78: 305–351.

Cote, S., L. Werdelin, E.R. Seiffert and J.C. Barry. 2007. Additional material of the enigmatic early Miocene mammal Kelba and its relationship to the order Ptolemaiida. Proc. Natl. Acad. Sci. USA 104: 5510–5515.

Court, N. 1992. The skull of Arsinoitherium (Mammalia, Embrithopoda) and the higher order interrelationships of ungulates. Palaeovertebrata 22: 1–43.

Court, N. 1995. A new species of Numidotherium (Mammalia: Proboscidea) from the Eocene of Lybia and the early phylogeny of the Proboscidea. J. Vertebr. Paleontol. 15: 650–671.

Court, N. and J.L. Hartenberger. 1992. A new species of the hyracoid mammal Titanohyrax from the Eocene of Tunisia. Palaeontology 35: 309–317.

Court, N. and M. Mahboubi. 1993. Reassessment of the lower Eocene Seggeurius amourensis: aspects of primitive dental morphology in mammalian order Hyracoidea. J. Paleontol. 67: 889–893.

Cox, P.G. 2006. Character evolution in the orbital region of the Afrotheria. J. Zool. 269: 514–526.

De Graaff, G. 1957. A new chrysochlorid from Makapansgat. Palaeontol. Afr. 5: 21–27.

Delmer, C., M. Mahboubi, R. Tabuce and P. Tassy. 2006. A new species of Moeritherium (Proboscidea, Mammalia) from the Eocene of Algeria: new perspectives on the ancestral morphotype of the genus. Palaeontology 49: 421–434.

Delsuc, F., M. Scally, O. Madsen, M.J. Stanhope, W.W. de Jong, F.M. Catzeflis, et al. 2002. Molecular phylogeny of living xenarthrans and the impact of taxon sampling on the placental tree rooting. Mol. Biol. Evol. 19: 1656–1671.

Domning, D.P. 1982. Evolution of manatees: a speculative history. J. Paleontol. 56: 599–619.

Domning, D.P. 1994. A phylogenetic analysis of the Sirenia. Proc. San Diego Soc. Nat. Hist. 29: 177–189.

Domning, D.P. 2001. The earliest known fully quadrupedal sirenian. Nature 413: 625–627.

Domning, D.P. and P.D. Gingerich. 1994. Protosiren smithae, new species (Mammalia, Sirenia), from the late middle Eocene of Wadi Hitan, Egypt. Contrib. Mus. Paleontol., Univ. Michigan 29: 69–87.

Domning, D.P., C.E. Ray and M. McKenna. 1996. Two new Oligocene Desmostylians and a discussion of Tethytherian systematics. Smithsonian Contrib. Paleobiol. 59: 1–56.

Douzery, E.J.P., F. Delsuc, M.J. Stanhope and D. Huchon. 2003. Local molecular clocks in three nuclear genes: divergence times for rodents and other mammals and incompatibility among fossil calibration. J. Mol. Evol. 57: 201–213.

Fischer, M.S. and P. Tassy. 1993. The interrelation between Proboscidea, Sirenia, Hyracoidea, and Mesaxonia: the morphological evidence. In: (F.S. Szalay, M.J. Novacek and M.C. McKenna, eds) Mammal phylogeny: placentals. Springer-Verlag, New York. pp. 217–234.

Gazin, C.L. 1952. The lower Eocene knight formation of western Wyoming and its mammalian faunas. Smithsonian Inst., Misc. Coll. Washington, DC. 117 (18): 1–82.

Gheerbrant, E. and J.C. Rage. 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? Palaeogeogr. Palaeoclimatol. Palaeoecol. 241: 224–246.

Gheerbrant, E., J. Sudre and H. Cappetta. 1996. A Palaeocene proboscidean from Morocco. Nature 383: 68–70.

Gheerbrant, E., J. Sudre, H. Cappetta and G. Bignot. 1998. Phosphatherium escuilliei du Thanétien du bassin des Ouled Abdoun (Maroc), plus ancien proboscidien (Mammalia) d'Afrique. Geobios-Lyon 30: 247–269.

Gheerbrant, E., J. Sudre, H. Cappetta, M. Iarochène, M. Amaghzaz and B. Bouya. 2002. A new large mammal from the Ypresian of Morocco: evidence of surprising diversity of early proboscideans. Acta Palaeontol. Pol. 47: 493–506.

Gheerbrant, E., J. Sudre, H. Cappetta, C. Mourer-Chauviré, E. Bourdon, M. Iarochène, et al. 2003. Les localités à mammifères des carrières de Grand Daoui, bassin des Ouled Abdoun, Maroc, Yprésien: premier état des lieux. Bull. Soc. Geol. Fr. 174: 279–293.

Gheerbrant, E., J. Sudre, P. Tassy, M. Amaghzaz, B. Bouya and M. Iarochène. 2005a. Nouvelles données sur *Phosphatherium escuilliei* (Mammalia, Proboscidea) de l'Éocène inférieur du Maroc, apports à la phylogénie des Proboscidea et des ongulés lophodontes. Geodiversitas 27: 239–333.

Gheerbrant, E., D.P. Domming and P. Tassy. 2005b. Paenungulata (Sirenia, Proboscidea, Hyracoidea, and relatives). In: (K.D. Rose and J.D. Archibald, eds) Placental mammals: origins and relationships of the major clades. Johns Hopkins University Press, Baltimore, MD. pp. 84–105.

Gheerbrant, E., S. Peigné and E. Thomas. 2007. Première description du squelette d'un mammifère hyracoïde paléogène: *Saghatherium antiquum* de l'Oligocène inférieur de Jebel al Hasawnah, Libye. Palaeontographica, A 279: 93–145.

Gilbert, C., P.C. O'Brien, G. Bronner, F. Yang, A. Hassanin, M.A. Ferguson-Smith, et al. 2006. Chromosome painting and molecular dating indicate a low rate of chromosomal evolution in golden moles (Mammalia, Chrysochloridae). Chromosome Res. 14: 793–803.

Gingerich, P.D., D.P. Domming, C.E. Blane and M.D. Uhen. 1994. Cranial morphology of *Protosiren fraasi* (Mammalia, Sirenia) from the middle Eocene of Egypt: a new study using computed tomography. Contrib. Mus. Paleontol., Univ. Michigan 29: 41–67.

Gingerich, P.D., M. Arif, M.A. Bhatti, H.A. Raza and S.M. Raza. 1995. *Protosiren* and *Babiacetus* (Mammalia, Sirenia and Cetacea) from the middle Eocene Drazinda Formation, Sulaiman Range, Punjab (Pakistan). Contrib. Mus. Paleontol., Univ. Michigan 29: 331–357.

Goin, F.J., R. Pascual, M.F. Tejedor, J.N. Gelfo, M.O. Woodburne, J.A. Case, et al. 2006. The earliest Tertiary therian mammal from South America. J. Vertebr. Paleontol. 26: 505–510.

Goodman, S.M., J.U. Ganzhorn and D. Rakotondravony. 2003. Introduction to the mammals. In: (S.M. Goodman and J.P. Benstead, eds) The natural history of Madagascar. Chicago University Press, Chicago, IL. pp. 1159–1186.

Grandidier, G. 1928. Un nouveau type de mammifère insectivore de Madagascar. Bull. Acad. Malgache 11: 85–90.

Gregory, W.K. 1910. The orders of mammals. Bull. Am. Mus. Nat. Hist. 27: 1–554.

Hallström, B., M. Kullberg, M. Nilsson and A. Janke. 2007. Phylogenetic data analyses provide evidence that Xenarthra and Afrotheria are sister groups. Mol. Biol. Evol. 24: 2059–2068.

Hartenberger, J.-L. 1986. Hypothèse paléontologique sur l'origine des Macroscelidae (Mammalia). C.R. Acad. Sci. Paris. Sér. II 302: 247–249.

Hedges, S.B. 2001. Afrotheria: plate tectonics meets genomics. Proc. Natl. Acad. Sci. USA 98: 1–2.

Heim de Balsac, H. 1972. Insectivores. In: (R. Battistini and G. Richard-Vindard, eds) Biogeography and ecology in Madagascar. W. Junk, The Hague. pp. 629–660.

Holroyd, P.A. and J.C. Mussel. 2005. Macroscelidea and Tubulidentata. In: (K.D. Rose and J.D. Archibald, eds) Placental mammals: origins and relationships of the major clades. Johns Hopkins University Press, Baltimore, MD. pp. 71–83.

IUCN. 2006. 2006 IUCN red list of threatened species. Available online: www.iucnredlist.org.

de Jong, W.W., A. Zweers and M. Goodman. 1981. Relationship of aardvark to elephants, hyraxes and sea cows from alpha-crystallin sequences. Nature 292: 538–540.

de Jong, W.W., J.A.M. Leunissen and G.J. Wistow. 1993. Eye lens crystallins and the phylogeny of placental orders: evidence for a macroscelid-paenungulate clade? In: (F.S. Szalay, M.J. Novacek and M.C. McKenna, eds) Mammal phylogeny: placentals. Springer Verlag, New York. pp. 5–12.

Kappelman, J., D.T. Rasmussen, W.J. Sanders, M. Feseha, T. Brown, P. Copeland, et al. 2003. Oligocene mammals from Ethiopia and faunal exchange between Afro-Arabia and Eurasia. Nature 426: 549–552.

Kellogg, M.E., S. Burkett, T.R. Dennis, G. Stone, B.A. Gray, P.M. McGuire, et al. 2007. Chromosome painting in the manatee supports Afrotheria and Paenungulata. BMC Evol. Biol. 7: 6.

Kitazoe, Y., H. Kishino, P.J. Waddell, N. Nakjima, T. Okabayashi, T. Watabe, et al. 2007. Robust time estimation reconciles views of the antiquity of placental mammals. PLoS ONE 2: e384.

Kjer, K.M. and R.L. Honeycutt. 2007. Site specific rates of mitochondrial genomes and the phylogeny of Eutheria. BMC Evol. Biol. 7: 8.

Krause, D.W. 2003. Late Cretaceous vertebrates of Madagascar: a window into Gondwanan biogeography at the end of the age of dinosaurs. In: (S.M. Goodman and J.P. Benstead, eds) The natural history of Madagascar. University of Chicago Press, Chicago, IL. pp. 40–47.

Kriegs, J.O., G. Churakov, M. Kiefmann, U. Jordan, J. Brosius and J. Schmitz. 2006. Retroposed elements as archives for the evolutionary history of placental mammals. PLoS Biol. 4: 537–544.

Kumar, S. and S.B. Hedges. 1998. A molecular timescale for vertebrate evolution. Nature 392: 917–920.

Le Gros Clark, W.E. and C.F. Sonntag. 1926. A monograph of *Orycteropus afer*. – III. The skull. The skeleton of the trunk and limbs. Proc. Zool. Soc. London. 30: 445–485.

Lehmann, T. 2006. The biodiversity of the Tubulidentata over Geological time. Afrotherian Conserv. 4: 6–11.

Lehmann, T. 2007. Amended taxonomy of the order Tubulidentata (Mammalia, Eutheria). Ann. Transvaal Mus. 44: 179–196.

Lehmann, T., P. Vignaud, H.T. Mackaye and M. Brunet. 2004. A fossil aardvark (Mammalia, Tubulidentata) from the lower Pliocene of Chad. J. Afr. Earth Sci. 40: 201–217.

Lehmann, T., P. Vignaud, A. Likius and M. Brunet. 2005. A new Orycteropodidae (Mammalia, Tubulidentata) in the Mio-Pliocene of northern Chad. Zool. J. Linn. Soc. Lond. 143: 109–131.

Lehmann, T., A. Likius, H.T. Mackaye, P. Vignaud and M. Brunet. 2006. A sub-complete fossil aardvark from the Upper Miocene of Chad. C.R. Palevol. 5: 693–703.

Maas, M.C., J.G.M. Thewissen and J. Kappelman. 1998. *Hypsamasia seni* (Mammalia, Embrithopoda) and other mammals from the Eocene Kartal formation of Turkey. Bull. Carnegie Mus. Nat. Hist. 34: 286–297.

MacInnes, D.G. 1956. Fossil Tubulidentata from East Africa. Br. Mus. (Nat. Hist.), Lond.: Fossil Mamm. Africa. 10: 1–38.

MacPhee, R.D.E. 1994. Morphology, adaptations, and relationships of *Plesiorycteropus*, and a diagnosis of a new order of eutherian mammals. Bull. Am. Mus. Nat. Hist. 220: 1–214.

Madsen, O.M., M. Scally, C.J. Douady, D.J. Kao, R.W. DeBry, R. Adkins, et al. 2001. Parallel adaptive radiations in two major clades of placental mammals. Nature 409: 610–614.

Mahboubi, M.R., R. Ameur, J.-Y. Crochet and J.-J. Jaeger. 1986. El Kohol (Saharan Atlas, Algeria), a new Eocene mammal locality in north-western Africa. Palaeontogr. Abt. A. 192: 15–49.

Matthee, C.A., G. Eick, S. Willow-Munro, C. Montgelard, A. Pardini and T.J. Robinson. 2007. Indel evolution of mammalian introns and the utility of non-coding nuclear markers in eutherian phylogenetics. Mol. Phylogenet. Evol. 42: 827–837.

McKenna, M.C. 1975. Toward a phylogenetic classification of the Mammalia. In: (W.P. Luckett and F.S. Szalay, eds) Phylogeny of the primates. Plenum Press, New York. pp. 21–46.

McKenna, M. and E. Manning. 1977. Affinities and palaeobiogeographic significance of the Mongolian Paleogene genus *Phenacolophus*. Geobios-Lyon, Mémoire Spécial 1: 61–85.

McKenna, M.C. and S.K. Bell. 1997. Classification of mammals above the species level. Columbia University Press, New York. pp. 631.

Mein, P. and M. Pickford. 2003. Insectivora from Arrisdrift, a basal Middle Miocene locality in Southern Namibia. In: (B. Senut and M. Pickford, coord) Faunas from the southern Namibia. Mem. Geol. Surv. Namibia 19: 143–146.

Mess, A. and A.M. Carter. 2006. Evolutionary transformations of fetal membrane characters in Eutheria with special reference to Afrotheria. J. Exp. Zool. (Mol. Dev. Evol.) 306B: 140–163.

Meyer, G.E. 1978. Hyracoidea. In: (V.J. Maglio and H.B.S. Cooke, eds.) Evolution of African Mammals. Harvard University Press, Cambridge. pp. 284–314.

Murata, Y., M. Nikaido, T. Sasaki, Y. Cao, Y. Fukumoto, M. Hasegawa, et al. Okda. 2003. Afrotherian phylogeny as inferred from complete mitochondrial genomes. Mol. Phylogenet. Evol. 28: 253–260.

Murphy, W.J., E. Eizirik, W.E. Johnson, Y.P. Zhang, O.A. Ryder and S.J. O'Brien. 2001a. Molecular phylogenetics and the origin of placental mammals. Nature 409: 614–618.

Murphy, W.J., E. Eizirik, S.J. O'Brien, O. Madsen, M. Scally, C.J. Douady, et al. 2001b. Resolution of the early placental mammal radiation using Bayesian phylogenetics. Science 294: 2348–2351.

Murphy, W.J., T.H. Pringle, T.A. Crider, M.S. Springer and W. Miller. 2007. Using genomic data to unravel the root of the placental phylogeny. Genome Res. 17: 413–421.

Narita, Y. and S. Kuratani. 2005. Evolution of the vertebral formulae in mammals: a perspective on developmental constraints. J. Exp. Zool. (Mol. Dev. Evol.) 304B: 91–106.

Nikaido, M., H. Nishihara, Y. Hukumoto and N. Okada. 2003. Ancient SINEs from African endemic mammals. Mol. Biol. Evol. 20: 522–527.

Nikolaev, S., J.I. Montoya-Burgos, E.H. Margulies, N.C.S. Program, J. Rougemont, B. Nyffeler, et al. 2007. Early history of mammals is elucidated with the ENCODE multiple species sequencing data. PloS Genet. 3: 1.

Nishihara, H., Y. Satta, M. Nikaido, J.G.M. Thewissen, M.J. Stanhope and N. Okada. 2005. A retroposon analysis of Afrotherian phylogeny. Mol. Biol. Evol. 22: 1823–1833.

Nishihara, H., N. Okada and M. Hasegawa. 2007. Rooting the Eutherian tree: the power and pitfalls of phylogenomics. Genome Biol. 8: R199.

Novacek, M.J. and A.R. Wyss. 1986. Higher level relationship of the recent Eutherian orders: morphological evidence. Cladistics 2: 257–287.

O'Leary, M.A., E.M. Roberts, M. Bouare, F. Sissoko and L. Tapanila. 2006. Malian Paenungulata (Mammalia: Placentalia): new African afrotheres from the early Eocene. J. Vertebr. Paleontol. 26: 981–988.

Patterson, B. 1975. The fossil aardvarks (Mammalia: Tubulidentata). Bull. Mus. Compar. Zool. Cambridge 147: 185–237.

Patterson, B. 1978. Pholidota and Tubulidentata. In: (V.J. Maglio and H.B.S. Cooke, eds) Evolution of African mammals. Harvard University Press, Cambridge, MA. pp. 268–278.

Phillips, M.J., P.A. McLenachan, C. Down, G.C. Gibb and D. Penny. 2006. Combined mitochondrial and nuclear DNA sequences resolve the interrelations of the major Australasian Marsupial radiations. Syst. Biol. 55: 122–137.

Pickford, M. 1975. New fossil Orycteropodidae (Mammalia, Tubulidentata) from East Africa. Neth. J. Zool. 25: 57–88.

Pickford, M. 1986a. Première découverte d'un Hyracoidea paléogène en Eurasie. C.R. Acad. Sci. Paris. Sér. II 303: 1251–1254.

Pickford, M. 1986b. Première découverte d'une faune mammalienne terrestre paléogène d'Afrique sub-saharienne. C.R. Acad. Sci. Paris. Sér. II 302: 1205–1210.

Pickford, M. and P. Andrews. 1981. The Tinderet Miocene sequence in Kenya. J. Hum. Evol. 10: I–33.

Rădulescu, C. and J. Sudre. 1985. Crivadiatherium iliescu n. sp., nouvel embrithopode (Mammalia) dans le Paléogène ancien de la Dépression de Hateg (Roumanie). Palaeovertebrata 15: 139–157.

Rasmussen, D.T. and E.L. Simons. 2000. Ecomorphological diversity among Paleogene hyracoids (Mammalia): a new cursorial browser from the Fayum, Egypt. J. Vertebr. Paleontol. 20: 167–176.

Rasmussen, D.T., M. Gagnon and E.L. Simons. 1990. Taxeopody in the carpus and tarsus of Oligocene Pliohyracidae (Mammalia: Hyracoidea) and the phyletic position of hyraxes. Proc. Natl. Acad. Sci. USA 87: 4688–4691.

Redi, C.A., S. Garagna, M. Zuccotti and E. Capanna. 2007. Genome size: a novel genomic signature in support of Afrotheria. J. Mol. Evol. 64: 484–487.

Reguero, M.A., A.M. Marenssi and S.N. Santillana. 2002. Antarctic Peninsula and South America (Patagonia) Paleogene terrestrial faunas and environments: biogeographic relationships. Palaeogeogr. Palaeoclimatol. Palaeoecol. 179: 189–210.

Reyes, A., C. Gissi, F. Catzeflis, E. Nevo, G. Pesole and C. Saccone. 2004. Congruent mammalian trees from mitochondrial and nuclear genes using Bayesian methods. Mol. Biol. Evol. 21: 397–403.

Robinson, T.J. and E.R. Seiffert. 2004. Afrotherian origins and interrelationships: new views and future prospects. Curr. Top. Dev. Biol. 63: 37–60.

Robinson, T.J., B. Fu, M.A. Ferguson-Smith and F. Yang. 2004. Cross-species chromosome painting in the golden mole and elephant shrew: support for the mammalian clades Afrotheria and Afroinsectiphillia but not Afroinsectivora. Proc. R. Soc. Lond. Biol. Sci. 271: 1477–1484.

Sagne, C. 2001. Halitherium taulannense, nouveau sirénien (Sirenia, Mammalia) de l'Éocène supérieur provenant du domaine Nord-Téthysien (Alpes-de-Haute-Provence, France). C.R. Acad. Sci. Paris 333: 471–476.

Sánchez-Villagra, M.R., Y. Narita and S. Kuratani. 2007. Thoracolumbar vertebral number: the first skeletal synapomorphy for afrotherian mammals. Syst. Biodivers. 5: 1–7.

Sanders, W.J., J. Kappelman and D.T. Rasmussen. 2004. New large-bodied mammals from the late Oligocene site of Chilga, Ethiopia. Acta Palaeontol. Pol. 49: 365–392.

Savage, R.J.G., D.P. Domning and J.G.M. Thewissen. 1994. Fossil Sirenia of the West Atlantic and Caribbean region. V. The most primitive known sirenian, Prorastomus sirenoides Owen, 1855. J. Vertebr. Paleontol. 14: 427–449.

Scally, M., O. Madsen, C.J. Douady, W.W. de Jong, M.J. Stanhope and M.S. Springer. 2001. Molecular evidence for the major clade of placental mammals. J. Mammal. Evol. 8: 239–277.

Seiffert, E.R. 2003. A Phylogenetic analysis of living and extinct afrotherian placentals. Ph.D. thesis, Duke University, Durham, NC. 239 pp.

Seiffert, E.R. 2007. A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. BMC Evol. Biol. 7: 224.

Seiffert, E.R., E.L. Simons, T.M. Ryan, T.M. Bown and Y. Attia. 2007. New remains of Eocene and Oligocene Afrosoricida (Afrotheria) from Egypt, with implications for the origin(s) of afrosoricid zalambdodonty. J. Vert. Paleontol. 24: 963–972.

Sen, S. and E. Heintz. 1979. Palaeoamasia kansui Ozansoy 1966, Embrithopode (Mammalia) d'Anatolie. Ann. Paleontol. (Vertebr.) Paris 65: 73–91.

Shoshani, J., R.M. West, N. Court, R.J.G. Savage and J.M. Harris. 1996. The earliest proboscideans: general plan, taxonomy, and palaeoecology. In: (J. Shoshani and P. Tassy, eds) The Proboscidea. Evolution and palaeoecology of elephants and their relatives. Oxford University Press, Oxford. pp. 57–75.

Sigogneau-Russell, D., M. Monbaron and D.E. Russell. 1988. Découverte de Mammifères dans le Mésozoique moyen d'Afrique. C.R. Acad. Sci. II 307: 1045–1050.

Simons, E.L. and P.D. Gingerich. 1974. New carnivorous mammals from the Oligocene of Egypt. Ann. Geol. Surv. Egypt 4: 157–166.

Simons, E.L., P.A. Holroyd and T.M. Brown. 1991. Early tertiary elephant shrews from Egypt and the origin of the Macroscelidae. Proc. Natl. Acad. Sci. USA 88: 9734–9737.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist. 85: 1–350.

Springer, M.S. and W.J. Murphy. 2007. Mammalian evolution and biomedicine: new views from phylogeny. Biol. Rev. 82: 375–392.

Springer, M.S., M.J. Stanhope, O. Madsen and W.W. de Jong. 2004. Molecules consolidate the placental mammal tree. Trends Ecol. Evol. 19: 430–438.

Stanhope, M.J., V.G. Waddel, O. Madsen, W.W. de Jong, S.B. Hedges, G.C. Cleven, et al. 1998. Molecular evidence for multiple origins of Insectivora and for a new order of endemic African insectivore mammals. Proc. Natl. Acad. Sci. USA 95: 9967–9972.

Sudre, J. 1979. Nouveaux mammifères éocènes du Sahara Occidental. Palaeovertabrata 9: 83–115.

Tabuce, R., B. Coiffait, P.-E. Coiffait, M. Mahboubi and J.-J. Jaeger. 2000. A new species of *Bunohyrax* (Hyracoidea, Mammalia) from the Eocene of Bir El Ater (Algeria). C.R. Acad. Sci. II 331: 1–26.

Tabuce, R., M. Mahboubi and J. Sudre. 2001a. Reassessment of the Algerian Eocene Hyracoid *Microhyrax*. The early diversity and basal phylogeny of the order Hyracoidea (Mammalia). Eclogae Geol. Helv. 94: 537–545.

Tabuce, R., B. Coiffait, P.-E. Coiffait, M. Mahboudi and J.-J. Jaeger. 2001b. A new genus of Macroscelidea (Mammalia) from the Eocene of Algeria: a possible origin of elephant shrews. J. Vertebr. Paleontol. 21: 535–546.

Tabuce, R., M.T. Antunes, R. Smith and T. Smith. 2006a. Dental and tarsal morphology of the European Paleocene/Eocene "condylarth" mammal *Microhyus*. Acta Palaeontol. Pol. 51: 37–52.

Tabuce, R., C. Delmer and E. Gheerbrant. 2006b. Evolution of the tooth enamel microstructure in the earliest proboscideans (Mammalia). Zool. J. Linn. Soc. 149: 611–628.

Tabuce, R., L. Marivaux, M. Adaci, M. Bensalah, J.-L. Hartenberger, M. Mahboubi, et al. 2007. Early tertiary mammals from North Africa reinforce the molecular Afrotheria clade. Proc. R. Soc. Lond. 274: 1159–1166.

Tassy, P. 1996. Who is who among the Proboscidea? In: (J. Shoshani and P. Tassy, eds) The Proboscidea. Evolution and palaeoecology of elephants and their relatives. Oxford University Press, Oxford. pp. 39–48.

Thewissen, J.G.M. 1985. Cephalic evidence for the affinities of Tubulidentata. Mammalia 49: 257–284.

Thewissen, J.G.M., E.M. Williams and S.T. Hussain. 2000. Anthracobunidae and the relationships among Desmostylia, Sirenia, and Proboscidea. J. Vertebr. Paleontol. 20: 73A.

van Dijk, M.A.M., O. Madsen, F. Catzeflis, M.J. Stanhope, W.W. de Jong and M. Pagel. 2001. Protein sequence signatures support the African clade of Mammals. Proc. Natl. Acad. Sci. USA 98: 188–194.

van Valen, L. 1982. Homology and causes. J. Morphol. 173: 305–312.

Waddell, P.J. and S. Shelley. 2003. Evaluating placental interordinal phylogenies with novel sequences including RAG1, γ-fibrinogen, ND6, and mt-tRNA, plus MCMC-driven nucleotide, amino acid, and codon models. Mol. Phylogenet. Evol. 28: 197–224.

Waddell, P.J., Y. Cao, M. Hasegawa and D.P. Mindell. 1999. Assessing the Cretaceous superordinal divergence times within birds and placental mammals using whole mitochondrial protein sequences and an extended statistical framework. Syst. Biol. 48: 119–137.

Waddel, P.J., H. Kishino and R. Ota. 2001. A phylogenetic foundation for comparative mammalian genomics. Genome Inform. 12: 141–154.

Waters, P.D., G. Dobigny, P.J. Waddell and T.J. Robinsons. 2007. Evolutionary history of LINE-1 in the major clades of placental mammals. PLoS ONE 2: e158.

Werdelin, L. and Å. Nilsonne. 1999. The evolution of the scrotum and testicular descent: a phylogenetic view. J. Theor. Biol. 196: 61–72.

Whidden, H.P. 2002. Extrinsic snout musculature in Afrotheria and Lipotyphla. J. Mammal. Evol. 9: 161–184.

Wible, J.R., G.W. Rougier, M.J. Novacek and R.J. Asher. 2007. Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. Nature 447: 1003–1006.

Wildman, D.E., M. Uddin, J.C. Opazo, G. Liu, V. Lefort, S. Guidon, et al. 2007. Genomics, biogeography, and the diversification of placental mammals. Proc. Natl. Acad. Sci. USA 104: 14395–14400.

Wilson, D.E. and D.M. Reeder (eds). 2005. Mammal species of the world: a taxonomic and geographic reference. Johns Hopkins University Press, Baltimore, MD. pp. 2142.

Yang, F., E.Z. Alkalaeva, P.L. Perelman, A.T. Pardini, W.R. Harrison, P.C.M. O'Brien, et al. 2003. Reciprocal chromosome painting among human, aardvark, and elephant (superorder Afrotheria) reveals the likely eutherian ancestral karyotype. Proc. Natl. Acad. Sci. USA 100: 1062–1066.

Zack, S.P., T.A. Penkrot, J.I. Bloch and K.D. Rose. 2005. Affinities of "hyopsodontids" to elephant shrews and a Holarctic origin of Afrotheria. Nature 434: 497–501.

Zalmout, I.S., M. Ul-Haq and P.D. Gingerich. 2003. New species of *Protosiren* (Mammalia, Sirenia) from the early middle Eocene of Baluchistan (Pakistan). Contrib. Mus. Paleontol., Univ. Michigan 31: 79–87.