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Early Tertiary mammals from North Africa reinforce the molecular Afrotheria clade

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The phylogenetic pattern and timing of the radiation of mammals, especially the geographical origins of major crown clades, are areas of controversy among molecular biologists, morphologists and palaeontologists. Molecular phylogeneticists have identified an Afrotheria clade, which includes several taxa as different as tenrecs (Tenrecidae), golden moles (Chrysochloridae), elephant-shrews (Macroscelididae), aardvarks (Tubulidentata) and paenungulates (elephants, sea cows and hyracoids). Molecular data also suggest a Cretaceous African origin for Afrotheria within Placentalia followed by a long period of endemic evolution on the Afro-Arabian continent after the mid-Cretaceous Gondwanan breakup (approx. 105–25 Myr ago). However, there was no morphological support for such a natural grouping so far. Here, we report new dental and postcranial evidence of Eocene stem hyrax and macroscelidid from North Africa that, for the first time, provides a congruent phylogenetic view with the molecular Afrotheria clade. These new fossils imply, however, substantial changes regarding the historical biogeography of afrotheres. Their long period of isolation in Africa, as assumed by molecular inferences, is now to be reconsidered inasmuch as Eocene paenungulates and elephant-shrews are here found to be related to some Early Tertiary Euramerican 'hyopsodontid condylarths' (archaic hoofed mammals). As a result, stem members of afrotherian clades are not strictly African but also include some Early Paleogene Holarctic mammals.

Keywords: molecules versus fossils; Afrotheria; Africa; Eocene; hyrax; elephant shrew

1. INTRODUCTION

Recent molecular analyses have proposed well-resolved higher level phylogenies for living eutherian mammals in recognizing four superordinal clades: Laurasiatheria (shrews, moles, hedgehogs, bats, cetaceans, even- and odd-toed ungulates, carnivorans and pangolins), Euarchontoglires (rodents, rabbits, primates, flying lemurs and tree shrews), Xenarthra (anteaters, sloths and armadillos) and Afrotheria, which includes tenrecs (Tenrecidae), golden moles (Chrysochloridae), elephant-shrews (Macroscelididae), aardvarks (Tubulidentata) and elephants, sea cows and hyraxes (Paenungulata; Murphy *et al.* 2001*a*,*b*; Springer *et al.* 2003, 2004). For Afrotheria, there is a broad molecular consensus for its monophyly deriving from various nuclear and mitochondrial genes as well as from rare genomic changes that constitute probable synapomorphies (Madsen *et al.* 2001). In contrast, morphological data have until now failed to provide strong support for Afrotheria (Shoshani & McKenna 1998; Archibald 2003; Robinson & Seiffert 2004; Zack *et al.* 2005). In the absence of a comprehensive fossil record for stem members of crown Afrotheria, most high-level phylogenetic analyses have been based primarily on the morphology of extant afrotheres (Asher *et al.* 2003). However, modern afrotheres seem inadequate for reconstructing morphological phylogenies because their long period of endemism in Africa favoured the emergence of morphological convergences with laurasiatherian mammals due to similar selection pressures. Stem members of Afrotheria are thus highly critical for resolution of this phylogenetic issue because they exhibit morphological patterns that have not been overwritten by subsequent evolution and further specializations.

Intensive palaeontological work in Early to Middle Eocene North African localities in Algeria (Gour Lazib) and Tunisia (Chambi) have led to the recovery of several new fossils of mammals. Based on biostratigraphic studies,

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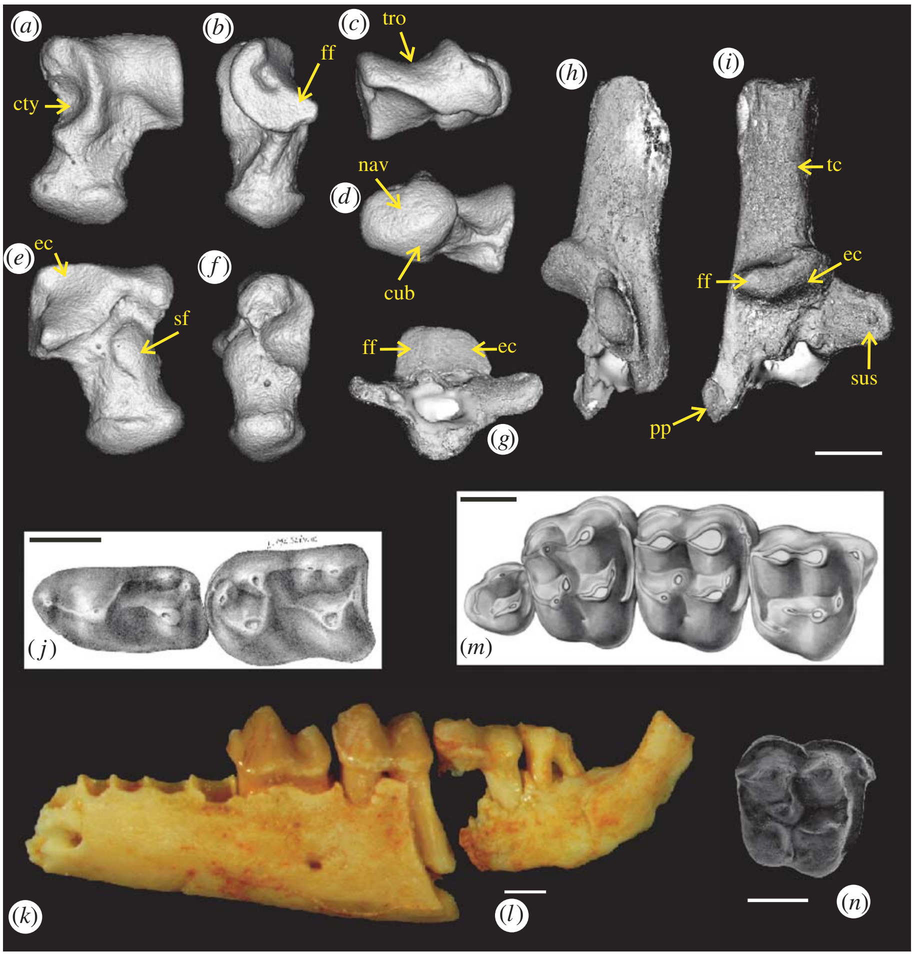

Figure 1. Stem macroscelid *Chambius kasserinensis*, early Eocene, Chambi, Tunisia. Left astragalus UM/CB77 in (*a*) dorsal, (*b*) lateral, (*c*) proximal, (*d*) distal, (*e*) plantar and (*f*) medial views; these three-dimensional renderings have been generated from microtomographic data obtained on the ID19 beamline of the European Synchrotron Radiation Facility (Grenoble, France). Right calcaneus UM/CB79 in (*g*) distal, (*h*) medial and (*i*) dorsal views. Left dentary UM/CB73 preserving premolar $(P)_4$–molar $(M)_1$ in (*j*) occlusal and (*k*) labial views. Left dentary UM/CB74 preserving M_2–M_3 in (*l*) labial view. Right upper maxillary holotype UM/CB6 preserving P^4–M^3 in (*m*) occlusal view. Right M2 UM/CB71 in (*n*) occlusal view. Scale bars, 1 mm. cty, cotylar fossa; cub, cuboid facet; ec, ectal facet; ff, fibular facet; nav, navicular facet; pp, peroneal process; sf, sustentacular facet; sus, sustentaculum; tc, tuber calcanei; tro, astragalar trochlea.

the Gour Lazib formation has been assigned either a late Ypresian or Early Lutetian age (Tabuce *et al.* 2004) and the Chambi locality an Ypresian age (Hartenberger *et al.* 2001). The newly discovered Algerian fossils document rodents, primates (particularly assigned to *Algeripithecus*, the oldest alleged anthropoid), creodonts, chiropterans, insectivores and hyraxes. For the last clade, we have recovered several fragmentary upper and lower jaws as well as tarsal bones of *Microhyrax lavocati* (Sudre 1979; Tabuce *et al.* 2001*a*), which considerably improves our knowledge of this basal hyrax. From Chambi, we collected additional remains (teeth and tarsal bones) of *Chambius kasserinensis* (Hartenberger 1986), the oldest known and most primitive elephant-shrew, whose postcranial anatomy was so far unknown. These fossils extend back the date of the oldest macroscelidean records with associated dental and postcranial remains by *ca* 30–40 Myr.

2. RESULTS

(a) *Description and comparisons*

Chambius is a small mammal with an estimated body weight of 13 g according to the equation of Legendre (1989). Its upper molars appear to be more primitive than those of more recent *Nementchatherium* (Tabuce *et al.* 2001*b*) and *Herodotius* (Simons *et al.* 1991) in having a robust metaconule, a more prominent parastyle and a comparatively more reduced hypocone (figure 1). On the basis of their tooth characters, basal elephant-shrews have been compared with 'hyopsodontid condylarths', notably with the North American *Haplomylus* and the European louisinine *Microhyus*, and these studies suggested 'condylarth' affinities for basal elephant-shrews. This hypothesis was recently strengthened on tarsal characters shared between *Haplomylus* (Zack *et al.* 2005), *Microhyus* (Tabuce *et al.* 2006) and extant elephant-shrews. *Chambius* tarsal bones reveal specializations for rapid running and/or jumping terrestrial locomotion. The pulley-shaped and the semi-circular crests of the astragalar trochlea are indicative of lateral stability and dynamic movements (Lewis 1989); the tibio-astragalar motion was certainly limited to flexion–extension. The calcaneus of *Chambius* is long both proximally and distally to subtarsal joints, a morphology also characteristic of cursorial and/or saltatorial mammals (Tabuce *et al.* 2006). The calcaneus bears an ectal facet oriented at nearly 90° to the long axis of the bone. This character, observed in both living elephant-shrews and *Haplomylus*, constitutes a derived condition within eutherians (Zack *et al.* 2005). *Microhyus* differs in having a

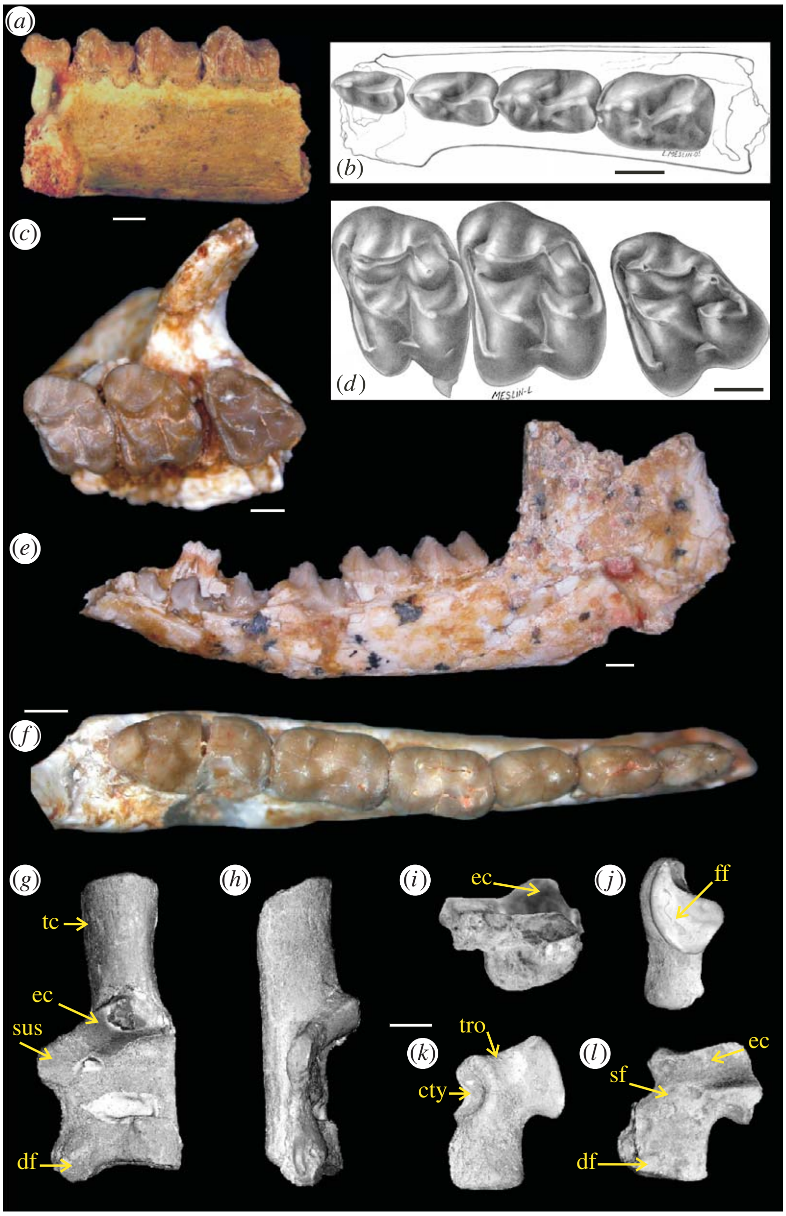

Figure 2. Stem hyrax *Microhyrax lavocati*, early to middle Eocene, Gour Lazib, Algeria. Right dentary UM/HGL04-11 preserving P$_1$–P$_4$ in (*a*) lingual and (*b*) occlusal views. Left upper maxillary UM/HGL50-101 preserving M^1–M^3 in occlusal views (*c* and *d*). Right dentary UM/HGL50-102 preserving P$_1$–M$_2$ and deciduous premolar (DP)$_2$ in (*e*) lingual view. Right dentary UM/HGL50-108 preserving P$_2$–M$_3$ in (*f*) occlusal view. Left calcaneus UM/HGL90-11 in (*g*) dorsal, (*h*) medial, and (*i*) distal views. Left astragalus UM/HGL50-103 in (*j*) lateral and (*k*) plantar views. Right astragalus UM/HGL51-11 in (*l*) distal view. Scale bars, 2 mm. cty, cotylar fossa; df, distal facet; ec, ectal facet; ff, fibular facet; sf, sustentacular facet; sus, sustentaculum; tc, tuber calcanei; tro, astragalar trochlea.

proximodistally elongated crestentic ectal facet. *Microhyus* differs also from *Chambius*, *Haplomylus* and modern elephant-shrews in the lack of a fibular facet. *Chambius* and *Microhyus* share a large peroneal process. This plesiomorphic condition (Szalay & Decker 1974; Hooker 2001) sets apart *Chambius* from both modern macroscelids and *Haplomylus*. The astragalus of *Chambius* is, nevertheless, typically macroscelidid in showing a sustentacular facet shifted to the medioplantar side of the bone. This character occurs only in the living elephant-shrews *Petrodromus*, *Elephantulus*, *Rhynchocyon* (unknown in *Macroscelides*), as well as in Scandentia (Meng *et al.* 2003). *Chambius* presents a cuboid facet on the astragalus as in living elephant-shrews. In addition, as in modern macroscelids, the *Chambius* astragalus displays a large concave depression, called a cotylar fossa, for articulation with the medial malleolus of the tibia. This character also occurs in some 'condylarths', notably in the louisinine (Tabuce *et al.* 2006) and apheliscine (Zack *et al.* 2005) 'hyopsodontids'. Following these comparisons, it appears that *Chambius* tarsal bones represent a morphological intermediate between *Haplomylus* and living elephant-shrews, thus reinforcing the relationships between some archaic Euramerican 'ungulates' and members of Afrotheria.

Hyraxes have been classified among the 'ungulates' by morphologists since the end of the nineteenth century but recently assigned to Afrotheria by molecular biologists. They represented, during the Paleogene, the most diverse group of terrestrial 'ungulates' in Africa (Rasmussen 1989; Schwartz *et al.* 1995). *Microhyrax*, from the early-middle Eocene of Gour Lazib (Algeria), is one of the smallest known hyraxes with a body mass estimated around 3 kg (Schwartz *et al.* 1995). *Microhyrax* displays a mosaic of primitive and derived dental characters (Tabuce *et al.* 2001*a*; figure 2). On one hand, lower premolars are simple relative to other Paleogene hyraxes: the metaconid is small on premolar $(P)_{2-4}$, and the talonid is reduced bearing only a strong hypoconid and a salient cristid obliqua. On the other hand, lower molars are reminiscent to those of *Megalohyrax*, *Titanohyrax*, *Antilohyrax*, *Saghatherium*, *Thyrohyrax* and *Selenohyrax* from the Eocene/Oligocene of the Fayum (Egypt) in showing derived structures such as the interrupted protocristid and hypocristid (Rasmussen 1989). *Microhyrax* is, however, clearly distinct from these taxa in its simple premolars and the morphological pattern of upper molars. Molar $(M)^{1-3}$ display evident primitive characters such as small parastyle and mesostyle, weakly W-shaped ectoloph and paraconular swelling (Tabuce *et al.* 2001*a*). *Microhyrax* is also unique by the increasing reduction of the metacone from M^1 to M^3.

Functionally, the tarsal bones of *Microhyrax* show no cursorial adaptations given the short tuber calcanei and moderately grooved astragalar trochlea, which indicates little flexion–extension. But, as the living *Dendrohyrax*, *Microhyrax* might display some arboreal capacity according to its mobile midtarsal joint (Fischer 1986). Basal perissodactyls differ from *Microhyrax* in having a saddle-shaped navicular facet. The peculiar combination of all tarsal characters strongly supports a relationship between *Microhyrax* and tethytheres (proboscideans and sirenians). The head of the astragalus in *Microhyrax* is characterized by a navicular facet with no trace of cuboid facet. This serial arrangement, called taxeopody, differs from the diplarthral or alternating arrangement observed in perissodactyls. Taxeopody characterizes Proboscidea, Sirenia, Embrithopoda (putative tethytheres), more derived hyraxes (Rasmussen *et al.* 1990) and several 'condylarths' such as *Meniscotherium*, a North American phenacodont and European 'hyopsodontid' louisinines (*Microhyus* and *Paschatherium*; Godinot *et al.* 1996; Tabuce *et al.* 2006). The astragalus of *Microhyrax* is typically hyracoid by the combination of a spiral articulation for the fibular malleolus and a deep cotylar fossa (Rasmussen *et al.* 1990). This latter trait is thus a key astragalar character shared by basal hyraxes (*Microhyrax*) and elephant-shrews (*Chambius*). Moreover, it characterizes *Numidotherium koholense*, a basal proboscidean from the early Eocene of northwestern Africa (Mahboubi *et al.* 1984). The Eocene Asian tethythere 'anthracobunids' (Gingerich *et al.* 1990), the tubulidentates and their possible extinct relative *Plesiorycteropus* (MacPhee 1994), plus the louisinine (Tabuce *et al.* 2006) and apheliscine (Zack *et al.* 2005) 'condylarths', also display the cotylar fossa. Considering that this peculiar astragalar feature occurred among several groups having different modes of locomotion (hyraxes are terrestrial to scansorial or even cursorial; elephant-shrews, louisinines and apheliscines are cursorial to saltatorial; tubulidentates show fossorial capacities; and modern proboscideans are characterized by their graviportal stance), this character is seemingly not strictly functional and, therefore, it could be interpreted as the result of shared ancestry (see also Zack *et al.* 2005). Consequently, the cotylar fossa observed here in stem members of Hyracoidea, Proboscidea, Tubulidentata and Macroscelidea, represents a reliable afrotherian synapomorphy. However, living golden moles and tenrecs, both crown members of Afrotheria, do not show this tarsal evidence (Salton & Szalay 2004). The lack of paleontological data for stem tenrecs and golden moles is a critical issue for assessing if this astragalar feature has never been developed in both groups or if it has been subsequently lost. This character also needs to be checked on the Eocene quadrupedal sirenian *Pezosiren* (other sirenians have no hindlimbs) (Domning 2001). Anyway, the cotylar fossa could not be a strict afrotherian synapomorphy as it is also present in some other eutherian mammals: cercopithecoid primates (e.g. *Macaca*, *Colobus*; MacPhee 1994), 'condylarths' (e.g. *Meniscotherium*, *Ancodon*), creodonts (e.g. *Oxyaena*; Gunnell & Gingerich 1991) and archaic South American 'ungulates' (Cifelli 1983).

(b) *Phylogenetic analysis*

On the basis of a recent phylogenetic analysis, including the tarsal anatomy of modern hyraxes and elephant-shrews, the monophyly of Afrotheria was not supported (Zack *et al.* 2005). Zack *et al.* (2005) scored the operational taxonomic units (OTU) Macroscelidea as a chimera based on the tarsal characters of the living *Rhynchocyon* with the dental features of the Eocene *Chambius*. The OTU Hyracoidea was also established on a composite morphology based on several Eocene, Oligocene and modern hyraxes. We modified the analysis of Zack *et al.* (2005) in removing these taxonomic chimeras and in scoring the tarsal and dental morphology of *Microhyrax* (hyrax) and *Chambius* (macroscelidid) from new paleontological evidence of both taxa. Other macroscelidids are represented by *Rhynchocyon* (Pliocene to Holocene) and *Myohyrax* (Miocene; Butler 1995). In addition to hyracoids and macroscelidids, we supplemented the analysis by sampling the afrotherian orders known since the Eocene: proboscideans (*N. koholense*) and sirenians (*Protosiren*). The phylogenetic relationships within the paenungulate clade (see Gheerbrant *et al.* (2005*a*) for an overview of paenungulate classification and history) were assessed in coding *Anthracobune* ('Anthracobunidae' from the early-middle Eocene of Indo-Pakistan), *Arsinoitherium* (Embrithopoda from the late Eocene?, early Oligocene of Africa) and *Phenacolophus* (a putative archaic embrithopod from the late Palaeocene of China and Mongolia). Other representatives of modern 'ungulates' are *Diacodexis* (Cetartiodactyla) and *Hyracotherium* (Perissodactyla). As for archaic 'ungulates', the matrix includes at least one representative of each of the 'condylarth' families: two arctocyonids (*Molinodus* and *Chriacus*), a mesonychid (*Dissacus*), a periptychid (*Mithrandir*), a mioclaenid (*Claenodon*), a phenacodontid (*Ectocion*), five 'hyopsodontids' (*Hyopsodus*, *Apheliscus*, *Haplomylus*, *Paschatherium* and *Microhyus*) and *Protungulatum* ('condylarth' *incertae sedis*, specified as outgroup).

In order to minimize homoplasy, the taxonomic dataset exemplifies only groups that existed in the time period corresponding to the early palaeontological record of 'ungulates' and afrotheres. Despite their incomplete fossil record, early 'ungulates' and afrotheres present a major phylogenetic advantage as they are expected to provide morphological patterns that have not been overwritten by subsequent evolution (our primary assumption). Except for *Numidotherium* and *Protosiren*, for which cranial remains are documented, most selected afrotheres, especially *Chambius* and *Microhyrax*, are only known by dental and tarsal remains. In this context, we have limited

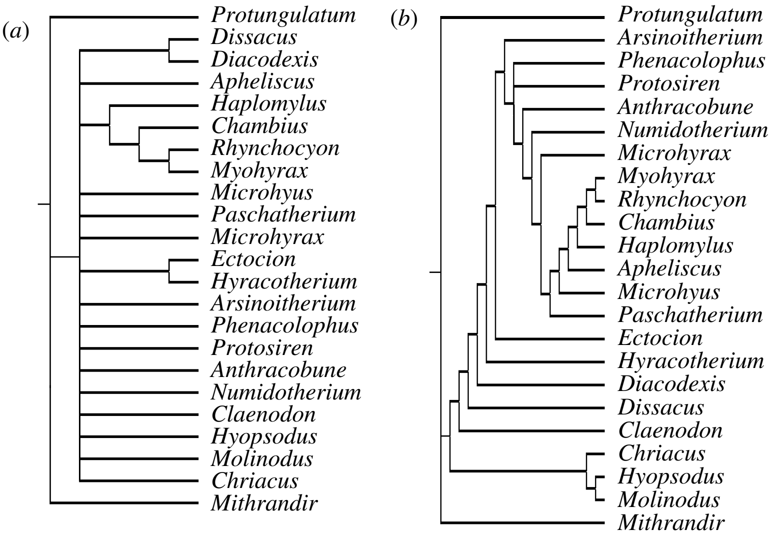

Figure 3. (*a*) Strict consensus tree of 105 equally parsimonious trees recovered from a parsimony analysis of 52 morphological characters, all characters are unordered. Tree length = 225 steps, consistency index = 0.33, retention index = 0.54. (*b*) Strict consensus tree of 3 equally parsimonious trees recovered after an *a posteriori* reweighting of the characters according to their rescaled consistency index, consistency index = 0.43, retention index = 0.67.

the analysis to dental and tarsal features as a means of minimizing the effect of missing data.

The data matrix contains 52 characters and 23 taxa (electronic supplementary material). We analysed the matrix using heuristic search option in PAUP v. 4.0b10 software (Swofford 2003) with the tree-bisection-reconnection branch-swapping algorithm, a random addition sequence and 1000 replications. An initial analysis of the dataset generated 105 equally most parsimonious trees of 225 steps each. The strict consensus tree is unresolved (figure 3*a*). A successive approximations reweighting by the method of Farris (1969) was performed, reweighting characters according to their rescaled consistency index, as a means of reducing the misleading effect of homoplasious characters. This analysis yielded three equally most parsimonious trees. The strict consensus presented in figure 3*b* shows the monophyly of an Afrotheria clade. In that topology, paenungulates, louisinines, aspheliscines and macroscelidids appear to be pectinately arranged. Among the paraphyletic paenungulates, *Arsinoitherium* occupies a basal position. Since its original description, the systematics and phylogenetic position of *Arsinoitherium* is disputed: Andrews (1906) related this genus to hyraxes, while, more recently, Court (1992*a*) and Gheerbrant *et al.* (2005*b*) considered *Arsinoitherium* as the sister group of proboscideans or tethytheres, respectively. *Arsinoitherium* exhibits an autapomorphic dental morphology. As such, it differs substantially from basal tethytheres in showing an unusual case of hypsodonty and in having a very peculiar bilophodonty of its cheek teeth. Court (1992*b*) hypothesized that this morphological dental pattern could derive from a hyperspecialized dilambdodonty. It seems to us that the homology of selected dental characters scored in *Arsinoitherium* with respect to the other ingroup taxa is not attested, thereby we excluded that genus from the phylogenetic analysis.

In that new phylogenetic framework, heuristic searches generated four equally most parsimonious trees of 214 steps each. The strict consensus presented in figure 4*a* is much more resolved than the previous analysis. The paenungulate, tethythere and macroscelid clades appear monophyletic, while louisinines and aspheliscines are polyphyletic. These results (figure 4*a*) are particularly interesting since they are consistent with current molecular phylogenies on high-level relationships within Afrotheria (figure 4*b*). For the first time, morpho-paleontological analyses recover undemonstrated relationships between some stem afrotheres: paenungulates are allied with macroscelids and far from the clade including Perissodactyla (here *Hyracotherium*) and Cetartiodactyla (here *Diacodexis*; figure 4*c*). The paenungulate clade is composed of hyraxes plus tethytheres: proboscideans, 'anthracobunids', *Phenacolophus* and sirenians. In addition, European louisinines are related to paenungulates, and the North American apheliscine *Haplomylus* appears as the sister group of macroscelids (figure 4*a*).

3. PALEOBIOGEOGRAPHIC IMPLICATIONS

In view of our results, and considering the strong molecular evidence for the monophyly of Afrotheria, the early biogeography history of this super-order must be amended since stem afrotheres are not only restricted to Africa but also include some Euramerican 'hyopsodontids' and Asian tethytheres. The occurrence in Asia of afrotheres during the Early Paleogene was already suspected in as much as 'anthracobunids' from the Indian subcontinent and *Phenacolophus* from central Asia were described as Tethytheria (see Gheerbrant *et al.* (2005*a*) for a summary). Therefore, stem afrotherians appeared both in Africa and in Holarctic area, which substantially changes the paleobiogeographic scenario derived from molecular inferences. Molecular phylogenies argue for an unusual case of endemism in Africa of Afrotheria from the Cretaceous to the Miocene (approx. 105–20 Myr ago; Madsen *et al.* 2001; Springer *et al.* 2003), while our results suggest the existence of dispersal events between Africa, Euramerica and Asia. According to the fossil record (figure 5), such events might have occurred around the Palaeocene/Eocene (P/E) boundary during which numerous intercontinental mammalian dispersals occurred (Bowen *et al.* 2002; Tabuce &

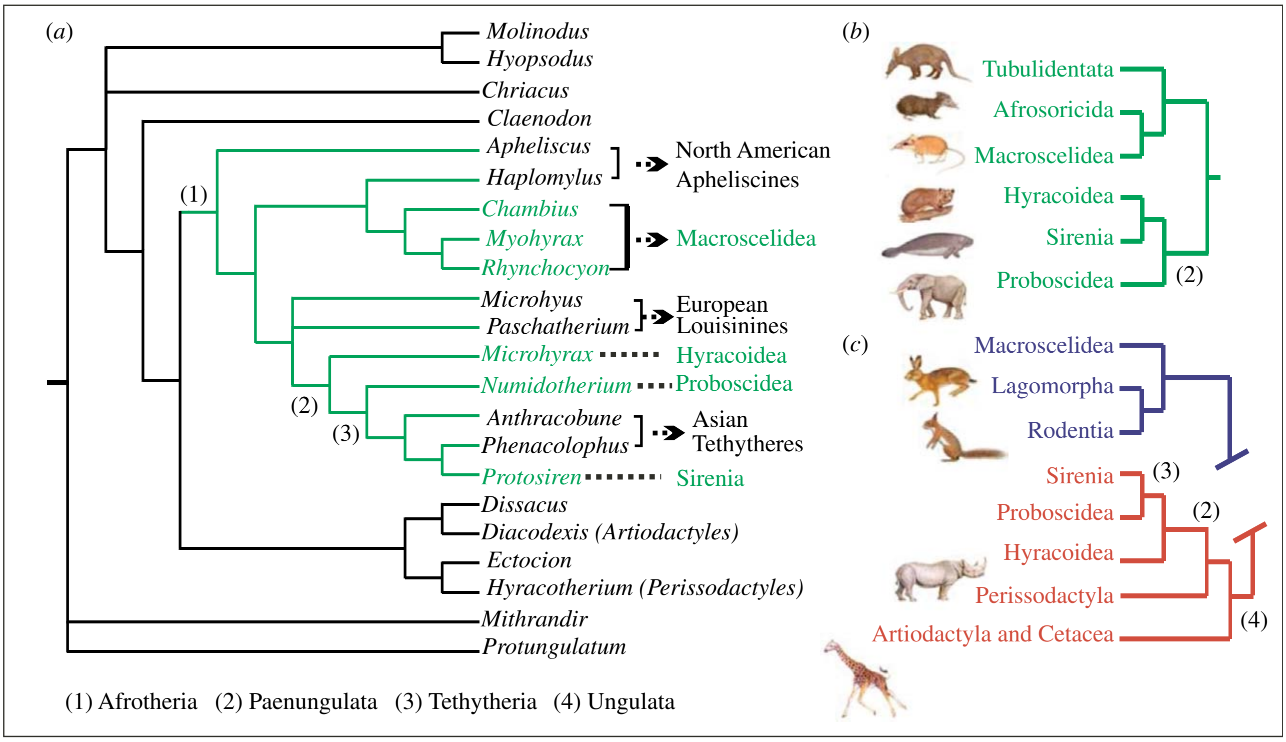

Figure 4. (*a*) Strict consensus of 4 equally parsimonious trees recovered from a parsimony analysis of 52 morphological characters, all characters are unordered. Tree length = 214 steps, consistency index = 0.35, retention index = 0.55. (*b*) molecular phylogeny of afrotheres resulting from Springer *et al.* (2004). (*c*) morphological phylogenetic position of selected afrotheres resulting from Shoshani & McKenna (1998); the majority of morphological studies consider Afrotheria to be polyphyletic: Macroscelidea are allied with Glires (Lagomorpha and Rodentia) among Anagalida; and Paenungulata (hyraxes, sirenians and proboscideans) are included in the super-order Ungulata. Green colour indicates, in (*a*) and (*b*), members of living afrotherian orders; in (*c*), blue colour indicates Anagalida, and red colour indicates Ungulata.

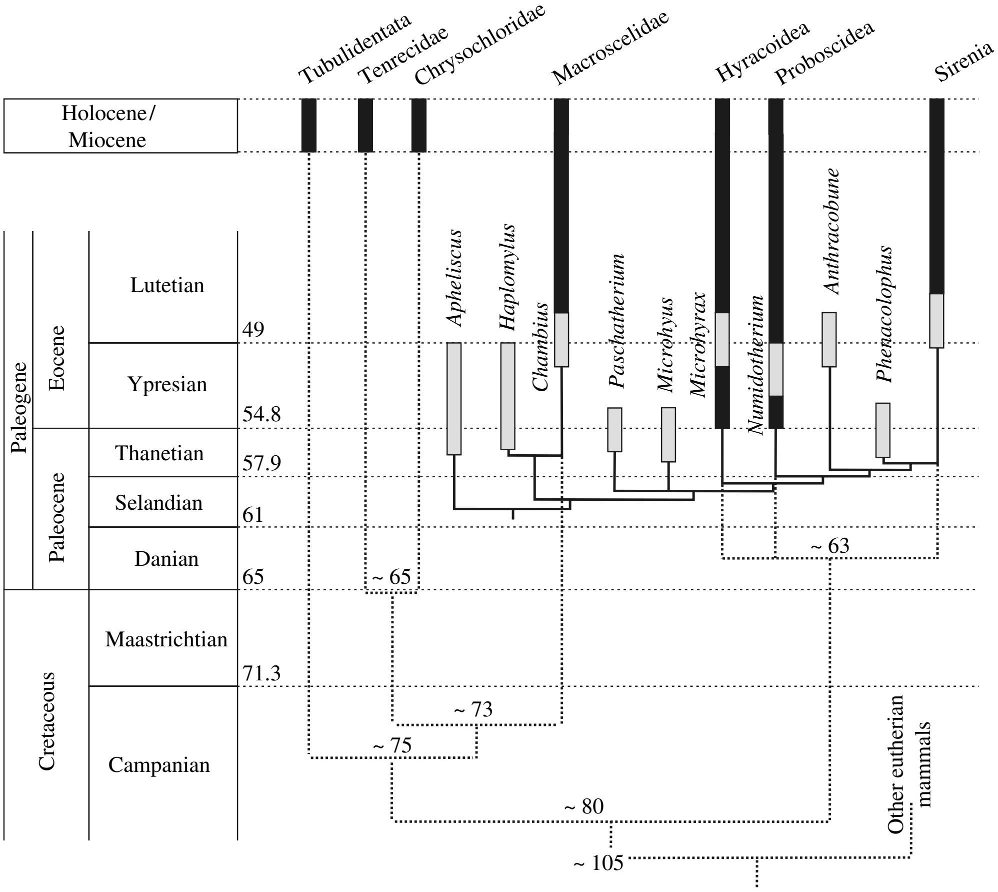

Figure 5. (*Caption opposite.*)

Figure 5. (*Opposite*.) Phylogeny, fossil record and molecular inferences for Afrotheria. Solid lines show phylogenetic relationships of afrotheres resulting from a parsimony analysis of 52 morphological characters (figure 4). Geological ranges of the selected early Paleogene afrotheres are indicated by grey bold lines. Known stratigraphic distribution of modern afrotherian orders are indicated by black bold lines. Dashed lines represent the molecular phylogeny and divergence times for afrotheres estimated by Springer *et al.* (2003).

Marivaux 2005; Gingerich 2006; Gheerbrant & Rage 2006). A question then arises about the direction of these afrotherian migrations, which depend on the geographical location considered wherein afrotherians were likely to have originated. Two scenarios are conceivable. The first one suggests Palaeocene Laurasian origins for Afrotheria, as expected by both our phylogenetic and current biostratigraphic datasets. Nevertheless, this scenario fails if we consider a Cretaceous origin for afrotheres as molecular studies suggest (figure 5). If these molecular estimates are valid, the second scenario implies a Cretaceous African origin for Afrotheria, followed by dispersal to Euramerica (apheliscines and louisinines) and Asia ('anthracobunids' and *Phenacolophus*) before the P/E boundary. However, the Cretaceous and Palaeocene fossil record of African mammals is too poorly documented to test this scenario and Late Cretaceous fossil mammals are urgently needed. Therefore, only a more complete African fossil record will allow a relevant morphological versus molecular debate regarding the origin, evolution and subsequent migrations of afrotherians.

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