

The largest land mammal known, the rhinocerotid *Paraceratherium* (the ght and leg indicated in metres).

geology and on the evolution of African mammals (pp. 27 and 75). However, it must be appreciated that much remains to be discovered about the evolution of mammals, especially the timing and speed of their radiations. Very different concepts have been elaborated, and in keeping with the palaeontological/ geological background, the three principal models for mammalian evolution have acquired crumb-breaking names: the Explosive, the Short-fuse and the Long fuse model.

The Explosive model has become identified with the geological evidence for a late and sudden explosion of mammal types after the K-T asteroid impact of 65.5 mya (best known for being the event in which dinosaurs became extinct) (Alroy 1999, Banton 1999, Foose *et al.* 1999). The post K-T 'explosive' model is best exemplified by Wible *et al.* (2007). The Short-fuse model depends upon molecular clock interpretations of the primary diversification of placental mammals taking place during the Cretaceous (Dunbar & Hedges 1998, Bininda-Emonds *et al.* 2007). The Long-fuse model is an amalgam of the previous two in suggesting that the stem taxa for most of today's orders probably diverged during the Cretaceous but most of the elaborations we see in modern mammals are after the K-T event (Springer *et al.* 2003, Donnell & Donnell 2003, Meredith *et al.* 2011).

Inasmuch as we have tried to illustrate the most likely radiation of mammals, we have often referred to Bininda-Emonds *et al.* (2007). Detailed comparisons of the genotypes of all known orders of mammals, as pioneered by Bininda-Emonds and by other molecular biologists, have permitted the erection of entirely new superordinal taxa: superorders, cohorts and supercohorts. Their adoption has been far from universal and both the new taxonomic names and their existence are contested. However, their identification has been backed up by robust and authoritative arguments accompanied by molecular clocks that vary greatly in their calibration of divergence times. These phylogenetic trees have served to emphasize that the evolutionary branching of mammal orders, families and species has taken place in real time and in real continental or local settings. Many of these assessments will need revision, but we have included three tentative trees (see p. 141) as pioneering efforts to understand the mammalian radiations.

Under this phylogeny, Mammalia breaks down into four supercohorts, namely Afrotheria, Xenarthra, Supraprimates (also known as Euarchontoglires) and Laurasiatheria. These, in turn have been subdivided into cohorts and superorders, descending ultimately to the species, portrait profiles of which are our ultimate product and purpose. In the text that follows each supercohort merits a profile (excepting Xenarthra, which is exclusively American) and our opening texts and volume concern the Afrotheria: the one group that has best claim to be endemic to the African continent.

The primacy of maternal care and prolonged dependency has had particular emphasis in the definition of Mammalia: that emphasis is also evident in much of the behaviour of mammals, especially where it concerns their social lives. Unlike most reptile and bird mothers, a mammalian mother must care for her offspring: that is, after all, why she has a womb and mammary! To ensure that the young (and their lactating mothers) have access to the best resources that are available and at the optimal times of year, there has been selection for a wide range of very different types of social systems. In spread-out, often residential patterns of land-marks, several or single females enter or share the territories of single males. Competition among the latter tends to ensure that the best resources have been won by vigorous territory-builders. Where resources are more dispersed or seasonal, females can enjoy enhanced protection and access to food within groups that have enlarged male hierarchies. Yet another strategy has been either a sustained or a semi-permanent association with a male or males that actually help raise offspring (typically their own only). Long term pair bonding has developed in some species (notably wild dogs *Lycaon*, where the sexes are of similar size and appearance).

Male competition can have conspicuous consequences for male external appearance. Weapons, in the form of horns, tusks or antlers, accompanied by loud calls and/or pungent scents and emphatic displays of patterns or structures have been developed to defend territories or rank. Age-related gigantism has evolved in the males of hierarchical species, such as gorillas, fur-seals, giraffes and elands.

African mammals have provided much material for evolutionary theory. From Darwin, noting the abundance of spotted and striped felids to invoke just such an evolutionary ancestry to explain patterned lion cubs (Darwin 1859) to Richard Dawkins using gorillas and cheetahs to illustrate an evolutionary 'arms race' (Dawkins 1986). Jonny Jarvis has revealed fundamental connections between the colony and behaviour of *Mosquitofelis* (mole-rats) and the evolution of complex social structures (Jarvis *et al.* 1992, Jarvis 1993), Julia Crook and Robin Dunbar have explored many socio-biological aspects of evolution from their studies of African primates (Crook & Garlan 1966, Dunbar 1988) while Dorothy Cheney and Robert Seyfarth have begun to plumb the depths of primate communication with baboons and vervet monkeys (Seyfarth & Cheney 1984, Cheney & Seyfarth 1990, 2007). The list could run on and on.

The diversity of ways in which mammals have evolved ways of living, become social or communicated subtle information with one another are all areas of active ongoing research. We report on this explosion of interest in African mammals and on the multifaceted attempts to understand how the extraordinary variety of mammals has evolved. There are important strands of thought among the many that are discussed in the volume that follow.

Jonathan Kingdon

Supercohort AFROTHERIA

Afrotheria Stanhope, Waddell, Marston, de Jong, Hedges, Chevret, Kuo & Springer, 1993. Proc. Nat. Acad. Sci. (USA) 95: 9971

Modern placental mammals have not always inhabited Africa, and very recent fossil discoveries have raised, once again, the central question of just where the first placentals arose. At the centre of this controversy is the very new revelation, initially from molecular evidence, of a single and unexpectedly diverse evolutionary radiation of mammals that is unequivocally African. It has been named the Afrotheria ('African mammals'). This radiation includes three orders that have long been recognized as being related and of African origin, namely the elephants (order Proboscidea), manatees and dugongs (order Sirenia) and hyraxes (order Proboscidea). They have now been joined by four other groups: the aardvark (order Tupaiaformes), sengis or elephant-shrews (order Macroscelididae), golden-moles (family Chrysochloridae) and tenrecs and otter-shrews (family Tenrecidae), now grouped in the new order, Afrotheria (Stanhope *et al.* 1993). Some authors have argued that this new order should be called Tenrecidae or Afroscelididae, but both of these names present taxonomic difficulties (Dronner & Jenkins 2005).

Are these animals modern derivatives of the very earliest placental mammals or are they later products of the Afro-Arabian landmass's known physical isolation? We know now that Afro-Arabia became separated, sequentially, from Eurasia, Indo-Malagasy and then South America by plate tectonics that opened up the Tethys Sea and proto Atlantic in the later Mesozoic. Understanding the origins of placental and of the afrotherian radiation is inseparable from the geological history of continents. That mammals confined to a single continent should radiate into highly diverse forms is entirely consistent with a very lengthy isolation, but was the afrotherian common ancestor native or immigrant? This question can only be answered with absolute certainty by more fossils from appropriate periods, but in the interim the biogeographic significance of both placental and afrotherian origins continues to be a matter of debate.

Some scholars have argued that the presence of two Gondwanan branches (Afrotheria and the endemic South American order Xenarthra) favours a Gondwanan, and possibly even African, origin for placental mammals (Murphy, Eklark, O'Brien *et al.* 2001). Others cite the presence of much more primitive Late Cretaceous placentals and marsupials in Asia as evidence for a northern origin (Archibald 2003, Robinson & Seiffert 2004, Wible *et al.* 2007). If placental mammals did originate in Asia, as now seems most likely, then basal afrotherians must have dispersed to the Afro-Arabian landmass some time between the predicted origin of placentals (~108 mya) and the putative origin of afrotherians (~80 mya) (Springer *et al.* 2003).

A broad acceptance of Afrotheria has rendered traditional taxonomies obsolete, but it is interesting to trace some earlier insights and intuitions. The present work is one of the first to attempt to come to grips with some of the implications and intralocus roadblocks to the many new questions that these discoveries raise. As for traditional ideas about relationships, they had to be founded on whatever evidence was available at the time, which often did not amount to much. The evidence is still incomplete but the molecular revolution that has unearthed the reality of Afrotheria is but part of a global effort to construct genealogical trees for all biota.

People familiar with wild animals, especially hunters and herders, in Africa and elsewhere, have often recognized that similar species or similar attributes imply ancestry. Thus fishermen, finding ivory tusks in elephant-like Dugong skulls sometimes called them 'elephants of the sea'. Scientific comparisons of the anatomy of elephants and hyraxes with dugongs and manatees, living and fossil, led to the recognition that these superficially very different animals shared a common ancestry (Simpson 1945). This conclusion had been greatly facilitated by the recovery of numerous fossils of these large mammals, primarily from the late Eocene beds of the Fayum Depression in Egypt (Andrews 1906). Following Simpson (1915), this taxonomic clustering is now referred to as the Proboscidea, and has subsequently come to be strongly supported by a vast array of genetic data (Springer *et al.* 1999, Murphy *et al.* 2001a, Amrine-Madsen *et al.* 2003, Murata *et al.* 2003, Nishida *et al.* 2004, Nishida *et al.* 2005, Meredith *et al.* 2011).

Determining the similarities of the aardvark, sengis, otter-shrews and golden-moles has long been much more difficult because their early fossil record is either scarce or non-existent. The aardvark shares a number of morphological features with similarly myrmecophagous pangolins (order Pholidota) and xenarthrans, and as such was historically aligned with these taxa, although more recently there has been suggestions that it might be more closely related to 'ungulates' – perissodactyls and/or artiodactyls (Nowak 1986, 1992, Sheehan 1986).

While the oldest possible fossil of Macroscelididae is from the early Eocene, about 50 mya (Hartenberger 1986, Talmos *et al.* 2011), and that of primitive tenrec and/or golden-mole relatives may be Palaeocene or Eocene (Seiffert 2010, Goswami *et al.* 2011), aardvarks do not appear in the fossil record until the early Miocene, about 20–18 mya (Madsen 1986, Patterson 1975). From the time of their initial discovery, these groups have always puzzled biologists, and have been very unsatisfactorily allocated to various other mammalian higher taxa, never with any confidence. Apart from the rarity of their fossils, a major reason for much of this confusion has been the combination of apparently primitive features and extreme specializations (or 'autapomorphies'), and their resulting transformation into swimming, digging and leaping 'insect-eaters'.

Insectivora has long served as a taxonomic waste paper basket into which all small, apparently primitive, lower-brain-containing mammals were thrown. Thus, sengis, golden-moles and tenrecs once joined solenodons, shrews, moles, hedgehogs (and, early in the history of taxonomy, even tree shrews and flying lemurs) in the Insectivora (Wagner 1855). The monotyphal insectivores (i.e. those with caeca – the flying lemur, tree shrews and sengis) were subsequently elevated to their own order (Gill 1872, Butler 1956), leaving behind the remaining insectivores, which were also placed in their own order, Lipotyphla (Butler 1972). However, the lipotyphlan assemblage has long been an unstable one. Following their exclusion from the insectivores, some came to be aligned either with the rabbits, hares and pikas (order Lagomorpha) (McKenna 1975, Szalay 1977) or with lagomorphs and rodents together (Gillespie 1986). Only with the recovery of early fossil macroscelidians

(Hartenberger 1986, Simons *et al.* 1991) was it recognized that their origins might lie with some 'ungulate' group.

Fortunately, technological advances have allowed scientists to rapidly sequence and compare large amounts of DNA, and a much more accurate, objective and less biased analysis of the affinities of all biota has become possible. As noted, these data have confirmed the paenungulate clustering of elephants, hyraxes, and dugongs and manatees, but, much more importantly, have also revealed that paenungulates are the larger representatives of an extremely important and very ancient endemic African radiation that includes many very small mammals as well. A close relationship between aardvarks and paenungulates was first suggested by an analysis of eye lens crystallins (de Jong *et al.* 1984) that would also later provide the first biochemical evidence for the sengis' close relationship with paenungulates (de Jong *et al.* 1993). Analyses of mitochondrial and nuclear gene sequences subsequently expanded this group to include the golden-moles (Lavergne *et al.* 1996, Springer *et al.* 1997) and tenrecs (Stanhope *et al.* 1998). An ancient, single origin for this assemblage is now supported by numerous protein and nucleotide sequences (Amrine-Madsen *et al.* 2003, Meredith *et al.* 2011) as well as rare genomic changes such as protein sequence signatures (Van Dijk *et al.* 2001), unique deletions (Madsen *et al.* 2001, Scally *et al.* 2001), short interspersed nuclear elements or 'jumping genes' (SINs, Nikaido *et al.* 2003, Nishihara *et al.* 2005) and chromosomal rearrangements (Robinson *et al.* 2004).

Afrotheria has attracted a considerable amount of controversy or scepticism because its members share so little superficial anatomical similarity (Springer *et al.* 2005). Currently, about the only morphological characters uniting Afrotheria involve the reproductive tract, including undescended testicles (the testicond condition) in males (Werhlin & Nilsson 1999) and a four lobed allantois sac in females (Moss & Carter 2006), although some homoplasy exists in both traits. Sanchez-Villagra *et al.* (2007) have argued that afrotherians are specialised in having more thoracolumbar vertebrae than other placental mammals. There has also been intense speculation about the sequence and adaptive significance of phylogenetic branching within the supercohort (Seiffert 2002, 2007, Robinson & Seiffert 2004, Asher & Seiffert 2010). This interest stems primarily from the fact that living and extinct macroscelids share a number of apparently specialised craniodental and postcranial features with paenungulates that are not seen in tenrecs and golden-moles. The position of macroscelids relative to these taxa depends on whether molecular or anatomical data are considered. Phylogenetic analyses of afrotherians that use morphology suggest that sengis are more closely related to paenungulates than to the other afrotherian insectivores (Seiffert 2003, 2007), and imply that the lipotyphlan features of golden-moles and tenrecs were likely to have been present in the last common afrotherian ancestor. However, recent analyses of various types of genetic data (Amrine-Madsen *et al.* 2003, Workell & Stalley 2003, Robinson *et al.* 2004, Nishihara *et al.* 2005, Meredith *et al.* 2011) support a fundamentally different arrangement that aligns aardvarks and sengis with golden-moles and tenrecs in an assemblage that has been named 'Afroinsectiphilia' (Workell *et al.* 2001). If this latter result is correct, then it could be the case that the resemblances between sengis and paenungulates represent primitive features within Afrotheria and that the afrotherian common ancestor would have been more like a small paenungulate than a lipotyphlan.

The above possibility is attractive in that it implies morphological support for Afrotheria, but the ultimate answer is unlikely to be so clear cut, because at least some of the shared features of paenungulates and sengis are sure to be due to convergent evolution within the ancient afrotherian radiation. The best way to test these competing hypotheses will be to search for Late Cretaceous mammals in Africa from beds that span the time period since the living afrotherians are thought to have first appeared – about 80 mya (Springer *et al.* 2003, Meredith *et al.* 2011).

If Afro-Arabia had been sufficiently isolated from Eurasia throughout the Cretaceous, then the afrotherian common ancestor could have arrived on an African continent that was otherwise devoid of placental mammals and, presumably, of marsupials as well. Unfortunately, at present, we really do not know just how isolated Afro-Arabia was during this time period because very few vertebrate fossils (and no mammals – aside from a single railbone!) in Africa. Were the Afro-Arabian continent as decisively isolated as it is currently thought, its placental afrotherian colonists must have had some tolerance for exposure at sea. Whether this implies possession of semi-aquatic habits must remain conjecture.

However, the extraordinary morphological variation observable among past and present members of Afrotheria would appear to be consistent with an original, ancestral dispersal into a Late Cretaceous Afro-Arabia that had few, if any, eutherian mammal competitors. Estimates of divergence dates within Afrotheria indicate that the living orders radiated quickly (Springer *et al.* 2003), presumably invading vacant niches that would also come to be occupied by distantly related placental mammals on other continents. Several mammal lineages from outside Africa and members of the Afrotheria share many similar or convergent adaptations. These are listed and discussed further below, but they include myrmecophagy (various ant-eating mammals versus afrotherian aardvarks), fossoriality (various mole-like animals versus afrotherian golden-moles), the valvulodont pattern of molar cusps (solenodonts versus afrotherian tenrecs and golden-moles), large scale aquatic habits (whale and hippo-like mammals versus afrotherian sirenians), small scale semi-aquatic familiarity (several placental and one marsupial versus afrotherian potamogalates), cursoriality (at small body size) (a diversity of mammals versus afrotherian sengis), and spines (true hedgehogs versus afrotherian tenrecid hedgehogs in Madagascar).

Likewise, hyracoids share enough detailed morphological similarities with perissodactyls that a close relationship between the two orders has been championed by morphologists until very recently (Prothero *et al.* 1988, Fischer 1989). Another convergence has only been revealed recently; this shows that the diverse radiation of extant hyraxes contained cursorial bovid-like forms (Rasmussen & Simons 2000). Early proboscideans such as *Mastitherium* were likely to have had life styles directly comparable with those of somewhat aquatic tapirs (Kingdon 1979). The most parsimonious explanation for the evolution of detailed morphological convergences is that these adaptations evolved in response to similar selection pressures on disjoint landmasses. Otherwise, direct competition between taxa with such similar evolutionary trajectories would have led to character displacement or early extinction in their evolutionary histories. It is for these and other reasons, we are unconvinced by the recent arguments of Asher *et al.* (2003) and Zuck *et al.* (2005) that

post afrotheria orders originating on northern continents, alongside demonstrably convergent clades.

A major argument against Holarctic origins for Afrotheria is the implication that most afrotherian lineages dispersed to Afro-Arabia independently, via crossings of the Tethys Sea, at times when such dispersals would have been highly unlikely. Although it is clear that primates had arrived in Afro-Arabia by the late Palaeocene, ~56 mya (Sigé *et al.* 1990) and rodents had invaded Africa by the early or middle Eocene, perhaps as early as 50 mya (Vianey-Liaud *et al.* 1994, Marivaux *et al.* in press), these colonizations do not offer compelling evidence for a 'swapsake' route that could also explain multiple afrotherian arrivals. Primates and rodents are, for whatever reason, remarkably adept at colonizing distant landmasses; for instance, members of both groups managed to subsequently colonize the distant South American landmass from Africa whereas no other mammals have. Primate and rodent groups have also crossed the Mozambique Channel to colonize Madagascar.

In evaluating the hypothesis of extra-African origins for Afrotheria, the likelihood that all the different members of a diverse, closely related group of mammals such as Afrotheria would have coincidentally (and unsuccessfully) crossed the Tethys Sea independently, is almost infinitesimal. In spite of morphological resemblances, hypotheses that taxa such as hypospionids, phoracanthids and lepidictids should be aligned with afrotherians now have to be rejected in spite of the fact that such extant taxa have left behind no DNA. Affinities suggested on the basis of a few widely distributed morphological features are no different from the taxonomic arrangements that have been erroneously erected over the course of the last two centuries. Had perissodactyls, lagomorphs, pholidotans or solenodonts gone extinct and left no DNA perhaps their few resemblances could have bolstered claims that these taxa too were afrotherians, aligned with hyracoids, sengis, aardvarks and tenrecs, respectively. It may also be the case that previous phylogenetic studies simply did not adequately sample the morphological information that has been provided by the radiation of living and extinct mammals. This possibility would appear to be supported by the recent outgroup and character-rich analysis of Wible *et al.* (2007), which, unlike the studies of Asher *et al.* (2003) and Zuck *et al.* (2005), placed North American taxa such as *Hyopsodus*, *Meniscotherium* and *Phenacodus* far outside of the afrotherian radiation rather than placing them as stem paenungulates.

The oldest, undisputed members of afrotherian orders appear in the Palaeocene of north-west Africa, where the earliest proboscidean *Eutherium* is now known (Gheerbrant 2009). However, Palaeocene African mammals are still scarce, deriving largely from a few micro mammalian sites in Morocco. These have produced numerous insectivores (Gheerbrant 1992, 1994, 1995, Gheerbrant *et al.* 1998), and a few isolated specimens of erodonts (Gheerbrant 1995, Solé *et al.* 2009) and primates (Sigé *et al.* 1990), as well as some indeterminate fragments of woodrat teeth. It is possible that some of the late Palaeocene insectivores are actually aligned with the tenrecid-chrysochlorid clade (Seiffert 2010, Goswami *et al.* 2011) but it is not yet possible to identify possible late Palaeocene stem members of the Tubulidentata on the basis of isolated teeth, because the only unambiguous fossil aardvark appears in the early Miocene with essentially modern, specialized, enamel-less, poly-lith teeth (MacInnes 1956). One possibility is that the order traces back to the peculiar platanoids, which are now known from the late Eocene,

early Oligocene, and early Miocene of Africa (Cote *et al.* 2007, Seiffert 2007).

The remarkable diversity that is now evident among Palaeocene and early Eocene proboscideans (Gheerbrant *et al.* 2002, 2005, Gheerbrant 2009) is consistent with molecular estimates of divergence dates within Paenungulata, which would place proboscidean origins well back into the Palaeocene (Springer *et al.* 2003). For the next 35 million years or so, paenungulates would dominate Africa's large mammal fauna with morphologically diverse hyracoids, proboscideans and the extinct embriothopos occupying a variety of browsing and grazing niches. Afrotherian dominance was first challenged (apparently, not too seriously) by a trans-Tethyan dispersal of the semi-aquatic anthracotheriid artiodactyls, which first appear in Africa as fossils during the earliest part of the late Eocene, about 36 mya. Note the less, paenungulates continued to be the dominant large-bodied herbivores in Africa until at least the latest Oligocene, about 25 mya, shortly after which the first major exchange of fauna took place between Africa and Eurasia. There is still no evidence for any other artiodactyls or perissodactyls having dispersed from northern continents before this time (Kappelman *et al.* 2003, Rasmussen & Gutiérrez 2009). There is still no evidence for lagomorphs or eulipotyphlans in Africa until the Miocene. No other group of placental mammals is known to have existed in Africa before the Afrotheria. Still important elements of the continent's fauna, they represent a continuous presence for at least 50 million years and perhaps as much as 80 million years.

The molecular and palaeontological data provide a broad view of the phylogenies and biogeographical relationships of the different clades making up the Afrotheria, but these data fail to tell us much about the ecological relationships of current afrotherians. Two features of the extant afrotheria fauna are striking: first, compared with other placental radiations, species diversity is low (with the exception of the tenrecs on Madagascar and, to a lesser degree, the golden-moles in southern Africa). Secondly, the extant species are



Comparisons between an Afrotherian and an unrelated species with convergent features: Mammalian Banded Anteater *Myrmecobius fasciatus* (above) and Giant Sengi *Rhinoceros* sp. (below).

very highly specialized in terms of their morphology or ecology or both, and this specialization is probably related to low species diversity and to the advantages, for such lineages, of a long head-start in adapting to difficult niches.

Currently, there are about 78 species of extant afrotherians, including three elephants (though there is some controversy regarding current recognition of two African species), four sirenians (dugongs and manatees), five hyraxes, one aardvark, 15 sengis, 30 tenrecs and 21 golden-moles. As was pointed out earlier, many, if not most of these, have ecologically convergent forms on other continents, but some do not and there are generally quite plausible reasons for both the presence and the lack of convergence. For example, the afrotherian golden-moles are remarkably similar to the marsupial moles (genus *Notoryctes*) and various Holarctic talpid moles, adaptive niches in which an early occupation of the continent has to be particularly advantageous, given how much body modification is necessary. The afrotherian Aardvark is broadly comparable to the Giant Anteater *Mylodon darwini* of South America in size and habitat, while afrotherian hyraxes, particularly the higher altitude forms, have many ecological similarities with the pikas (family Ochotoniidae) in Eurasia and North America. The three afrotherian species of Potamogalini are convergent with various aquatic sorial shrews and dormice in the Holarctic region and with the marsupial Duck-billed Platypus *Ornithorhynchus anatinus* - in Australia. Interestingly, the only tenrecs on the African continent are the three highly specialized aquatic potamogalines while the 27 others are confined to the island of Madagascar, where they occupy ecological positions similar to a diversity of Australasian marsupials, Caribbean solenodons and a variety of shrews and hedgehogs from other areas and continents. Although the larger sengis (*Mylodon*) superficially resemble hedgehogs and the solenodons of Cuba and Hispaniola, the smaller species (e.g. *Elephantulus*) do not have many resemblances with other small mammals. In addition, sengi life history sets them apart from any other group of mammal, with features that are uniquely African and might best be thought of as a cross between a miniature antelope and small ungulate! Despite such specializations, sengi occupies the extremes of terrestrial habitats - from gravel plains of the Namib Desert and boulder fields in north-west Africa to tropical forests of central and eastern Africa.

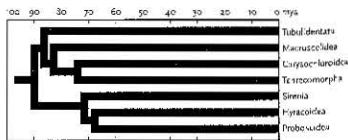
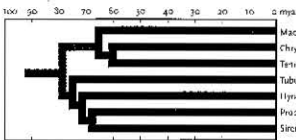
All the smaller afrotheres continue to be restricted to the Afro-Arabian region, plus Madagascar, but the two clades with representatives with the largest body mass dispersed to other continents. The elephants were well represented in North America and Asia and the sirenians radiated into the world's tropical oceans at a very early date, in addition to the North Pacific, and the Amazon

River system. Although elephants and sirenians are wide ranging, they are both morphological specialists. In addition, sirenians are obligate aquatic herbivores and as such have no ecological equivalents outside the afrotherian radiation.

The palaeontological record suggests that the highly specialized nature of extant afrotheres may not have been so marked in the past. For example, the diversity of sengis in the Miocene included six subfamilies, which included several herbivores, based on the morphology of their dentition. Only two subfamilies are extant, and all taxa in these two subfamilies have retained somewhat hypsodont dentition as well as a caecum, which strongly implies herbivorous ancestors. The herbivorous macroscelidians became extinct in the Mio Pliocene; perhaps they could not effectively compete with newly arriving rodents, hares and ungulates coming in from the north. The extant sengis seem to have escaped competition with these invaders by secondarily becoming invertebrate specialists, especially ant-eaters, where a head-start in adapting to soil chemistry must be an advantage. Likewise, the palaeontological history of hyraxes suggests that only those species that were raptorial or arboreal were able to escape competitive extinction with hares, rodents and ungulates.

A similar argument does not explain the high species diversity in the very recent past, of elephants and dugongs and manatees compared with their current sorry status, and most available evidence suggests that predation by humans might have played a decisive role in some of their extinctions. The diversity of tenrecs on Madagascar apparently suffered less from the impact of incoming rodents, undoubtedly because there was no competition for food between the herbivorous rodents and insectivorous tenrecs. Golden-moles similarly escaped competition from other insectivores by being fossorial. It thus appears that an important factor in the relatively small number of extant afrotheres is their ecological specialization, which allowed them to avoid extinction in the face of invading faunas from outside Africa. Although this specialization has served the extant afrotheres well in the past, their low species diversity, often accompanied by highly restricted distributions and ecological specializations, makes many forms especially vulnerable to another wave of extinctions - at the hands of humans. This is especially the case with the potamogalines, several golden-moles and the forest-dwelling sengis. These taxa all occupy highly restricted habitats that are being increasingly degraded by human activities. Because of the low species diversity of the extant afrotheres, extirpations will have an especially severe impact on an already depauperate group.

Jonathan Kingdon, Erik R. Seiffert, Blair Hedges & Galen Rathbone



Tentative phylogenetic relationships of afrotherian mammals (left) based on a combined analysis of DNA from living species and morphology of living and extinct species (after Seiffert 2007), and (right) based on analysis of genomic data alone (after Meredith et al. 2011).

Cohort PAENUNGULATA

Cohort Paenungulata Simpson 1947, Bulletin of the American Museum of Natural History 55: 131.

A close relationship between hyraxes, manatees and dugongs, elephants and the extinct Palaeocene order Embriothopoda was first explicitly recognized by Gregory (1910), thanks in large part to fossil discoveries made in the late nineteenth and early twentieth centuries in the Fayoum Depression of northern Egypt (Andrews 1906). Simpson eventually coined the name Paenungulata for this clade, but also included a variety of other extinct taxa whose affinities are now believed to lie elsewhere. The taxon Paenungulata has since been used by different authors to include very different assemblages of living and extinct placental (Lucas 1993), but is now generally recognized as the afrotherian radiation that produced the orders Hyracoidea, Sirenia, Proboscidea, and the extinct Embriothopoda and Desmostylia (e.g. Gheerbrant et al. 2005a). In the past, many morphological features that paenungulates share with paenungulates are evolutionary convergences (Springer et al. 2004).

The tiny Palaeocene proboscidean *Leptacromis* from Morocco, is the oldest unambiguously paenungulate (Gheerbrant 2009). More derived proboscideans (*Desmosterium* and *Platybelodon*) and the oldest known hyraxoid (*Sigacanthus*) have been found in earliest Eocene sediments of the same basin (Ouled-Abdoum) (Gheerbrant et al. 2003; Gheerbrant et al. 2003b). By the early Eocene, hyracoidea are morphologically distinct and there is already considerable morphological diversity within Proboscidea, suggesting that the evolutionary histories of both clades will eventually be traced much further back into the early Palaeocene. As yet basal sirenians are missing from the early African record, and the oldest forms are from

the early middle Eocene of Jamaica (Savage et al. 1994). However, by that time, sirenians already exhibit clear morphological adaptations for an aquatic existence.

With the recognition of Afrotheria, a number of the morphological features that have been proposed as evidence for paenungulate monophyly now must be re-evaluated. For instance, one of the key features that was thought to align paenungulates to the exclusion of other 'ungulates' is a serial arrangement of the orbital and zygomatic bones (i.e. no contact between the astragalus and the cuboid in the foot, and no contact between the lunar and unciform in the wrist) (Basuelsen et al. 1990). However, there is also no astragalus-cuboid contact in most other afrotherians (e.g. duikers, tenrecs, golden-moles), and there is no lunar-unciform contact in tenrecs, golden-moles and primitive sengis or elephant-shrews. As such, the serial corpus and tarsus could either be primitive within Placentalia or could represent afrotherian synapomorphies, but these characters can no longer be confidently interpreted as paenungulate synapomorphies. Other features, such as a tectiform articular process in tenrecs, golden-moles and primitive sengis or elephant-shrews, the cup-like astragalus cotylar fossa (which articulates with an enlarged medial malleolus of the tibia), enlargement of the central upper incisors and caudal extension of the jugal to the glenoid fossa, are also seen in various other non-paenungulate afrotherians, suggesting a more ancient origin for these characters. Placement of the orbit over the premaxillars, which is seen in living and extinct tethytherians and extant procanid hyracoidea, is absent in primitive fossil hyracoidea and so likely evolved convergently within Paenungulata.

Paenungulates can be distinguished from other afrotherians by a number of derived dental features and muscular arrangements (Storch 1993), in addition to postcranial characters such as loss of the clavicle and metacromion, an increase in the number of rib-bearing thoracic vertebrae, loss of the humeral entepicondylar foramen (though present, perhaps secondarily, in the early proboscidean *Numidotherium*), and, possibly, wide and flaring iliac ilae. Amantely remains as a probable cranial synapomorphy of Paenungulata, while other possible synapomorphies include loss of lacrimal-palatine contact, presence of an alisphenoid canal, presence of a ptiliform foramen rostral to the petrosal, a weakly excavated subnasale fossa and a vertical to anterior orientation of the mandibular ascending ramus. However, these, and many other, candidate cranial synapomorphies of Paenungulata must be tested with fossil evidence from early stem and crown paenungulates.

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Alternative tree of phylogenetic relationships of afrotherian mammals based on a combined analysis of DNA from living species and morphology of living and extinct species, showing recovery of Tethytheria within Paenungulata (after Asher et al. 2003).