

# Afrotheria: Plate tectonics meets genomics

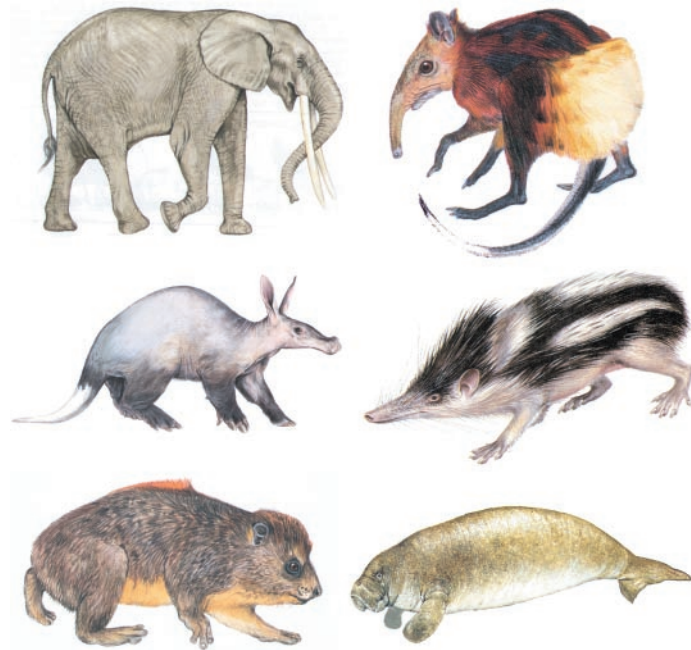
S. Blair Hedges\*

Department of Biology, Institute of Molecular Evolutionary Genetics, and Astrobiology Research Center, 208 Mueller Laboratory, Pennsylvania State University, University Park, PA 16802

**A**frotheria is one of the most remarkable hypotheses in mammal evolution. It suggests that one-third of the orders of placental mammals form an ancient group that evolved on Africa when that continent was isolated from others through plate tectonics (1). Although this hypothesis has been predicted by molecular clock studies (2), evidence for it has emerged only in the last 3 years from phylogenetic analyses of DNA and protein sequence data (1, 3–6). Many mammalogists remain baffled and see no support from traditional sources of data such as anatomy (7). The recognition of Afrotheria splits apart other established groups of mammals, including ungulates and insectivores, yet it is the most strongly supported grouping of mammalian orders in molecular phylogenies (4). In this issue of PNAS, van Dijk *et al.* (8) take a slightly different approach in analysis of molecular data and find additional support for Afrotheria.

The 4,700 species of living mammals are placed in about 20 orders, including such groups as the rodents (Order Rodentia), primates (Primates), and bats (Chiroptera) (9, 10). In systematics, taxonomic names often are treated as evolutionary hypotheses, implying that members of the group are more closely related to each other than to other species or groups. Afrotheria is a superorder (4) that contains six orders: the elephants (Order Proboscidea), sea cows (Sirenia), hyraxes (Hyracoidea), armadillo (Tubulidentata), elephant shrews (Macroscelideia), and golden moles and tenrecs (Afrosoricida) (Fig. 1). Some of the smallest (Lesser long-tailed tenrec, 5 g) and largest (African elephant, 5,000 kg) species of mammals belong to this group, and its members fill a diversity of ecological niches (11).

In most classifications, elephants, hyraxes, and the armadillo are considered close relatives of other hoofed mammals (ungulates) such as horses, rhinos, and allies (Order Perissodactyla) and cattle, deer, and allies (Artiodactyla). With the exception of the ant-eating armadillo, ungulates typically are herbivores. Golden moles and tenrecs previously have been classified with other insectivores such as shrews and moles (Insectivora or Lipotyphla). The living elephant shrews, mouse-like in appearance, are



**Fig. 1.** Representatives of the six orders of mammals comprising the Superorder Afrotheria: (Upper Left) African forest elephant (*Loxodonta africana*); (Upper Right) Golden-rumped elephant shrew (*Rhynchocyon chrysopygus*); (Middle Left) Armadillo (*Orycteropus afer*); (Middle Right) Streaked tenrec (*Hemicentetes nigriceps*); (Lower Left) Eastern tree hyrax (*Dendrohyrax validus*); and (Lower Right) Dugong (*Dugong dugon*). [Images of tenrec and dugong reproduced with permission from Andromeda Oxford Limited (18); other images reproduced with permission from Jonathan Kingdon.]

insectivorous, but their ancestors were herbivores; morphological classifications usually place them with rabbits (Lagomorpha) and rodents (12). The elephant shrews were so named because of their elephant-like snout (Fig. 1) and not because of any presumed close ties to elephants. Although sirenians appear the most ecologically and morphologically divergent members of Afrotheria, their anatomy and fossil record have indicated a close relationship with proboscideans and hyraxes (9). In general, the fossil record (12) and distribution of afrotherians suggest an origin in Africa.

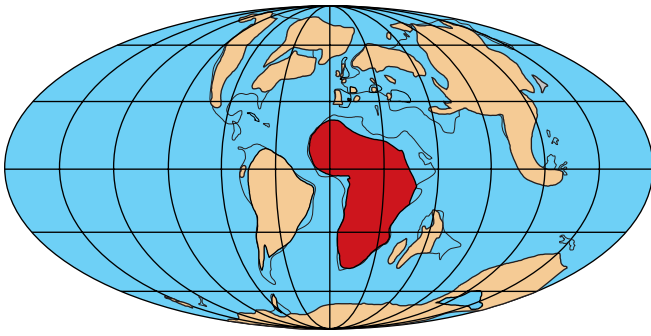
The discovery of Afrotheria places more importance on plate tectonics in the early evolution of placental mammals (2, 13). However, this is another issue that is hotly debated (14). Molecular clocks derived from large numbers of genes have indicated that placental mammals not only were present deep in the Cretaceous [≈100 mil-

lion years ago (mya)] but were already diverging from one another into clades that eventually led to the present-day orders (2, 15). Today, Africa is connected to Europe and Asia, facilitating dispersal of mammals among these three continents. But in the early Cretaceous (≈120 mya), Africa was connected to South America, with the two continents separating about 105 mya (16). Africa was relatively isolated between 105 and 40 mya (Fig. 2), and during this time afrotherians likely were evolving and adapting to different ecological niches. Around 30 mya, Africa began to collide with Europe and Asia, and since then these areas have been closely associated.

van Dijk *et al.* (8) subject existing molecular data sets to additional scrutiny by searching for specific amino acid replace-

See companion article on page 188.

\*E-mail: sbh1@psu.edu.



**Fig. 2.** Plate tectonic reconstruction for the late Cretaceous (85 mya) at a time when Africa was separated from other continents, and afrotherians presumably were evolving in isolation. Land areas are orange, Africa is red, and current coastlines are included for reference (adapted from ref. 16).

ments that might support Afrotheria. As expected, they identify a large number of sites in which an amino acid residue is uniquely shared (more or less) by afrotherians in three selected proteins. Next, they collected sequence data from other afrotherian species to see whether they possessed these diagnostic amino acid residues. In all six sites that were selected, the additional species were found to possess the diagnostic residues. Finally, the data were subjected to some statistical analyses that are unique but are not necessarily an improvement over current analytical methods. For example, the presence or absence of diagnostic sites typically contributes to statistical support in the widely used bootstrap method (17) and with fewer assumptions. Nonetheless, van Dijk *et al.* present new sequence data for the African otter shrew and other species that are important evidence in support of Afrotheria.

On the basis of the current composition of the group and limited knowledge of relationships, the Cretaceous afrotherian ancestor likely was a small forest-dwelling insectivore or possibly herbivore. What morphological characters, if any, are uniquely shared by these mammals and represent inheritance from that common ancestor? At first glance, the most obvious shared trait is the long snout possessed by several members of the group (Fig. 1). The sirenian snout is not long but is nonetheless enlarged and is used for grasping vegetation (underwater) in a way vaguely similar to the elephant's trunk. Except for hyraxes, the snouts of all are tactile and (except in tenrecs) mobile. Structurally, however, there is no evidence that these similarities are anything but superficial and are related to the ecology of the animals. Nonetheless, afrotherians in gen-

eral have been poorly studied, and additional anatomical, developmental, and genetic studies are needed. The molecular evidence predicts that there are shared derived morphological characters that link together this odd collection of mammals. Finding those characters would help us to understand better the evolutionary history of this ancient clade of mammals.

For permission to reproduce illustrations, I gratefully thank Jonathan Kingdon for the elephant, elephant shrew, aardvark, and hyrax; Priscilla Barrett and Andromeda Oxford Limited for the dugong; and Dennis Ovendon and Andromeda Oxford Limited for the tenrec. I thank Alan Walker and Sudhir Kumar for discussion and Anthony Geneva for assistance with graphics. This work was supported by the National Aeronautic and Space Administration.

1. Springer, M. S., Cleven, G. C., Madsen, O., de Jong, W. W., Waddell, V. G., Amrine, H. M. & Stanhope, M. J. (1997) *Nature (London)* **388**, 61–63.
2. Hedges, S. B., Parker, P. H., Sibley, C. G. & Kumar, S. (1996) *Nature (London)* **381**, 226–229.
3. Madsen, O., Deen, P. M. T., Pesole, G., Saccone, C. & de Jong, W. W. (1997) *Mol. Biol. Evol.* **14**, 363–371.
4. Stanhope, M. J., Waddell, V. G., Madsen, O., de Jong, W. W., Hedges, S. B., Cleven, G., Kao, D. & Springer, M. S. (1998) *Proc. Natl. Acad. Sci. USA* **95**, 9967–9972.
5. Stanhope, M. J., Madsen, O., Waddell, V. G., Cleven, G. C., de Jong, W. W. & Springer, M. S. (1998) *Mol. Phyl. Evol.* **9**, 501–508.
6. Springer, M. S., Amrine, H. M., Burk, A. & Stanhope, M. J. (1999) *Syst. Biol.* **48**, 65–75.
7. Asher, R. J. (1999) *Cladistics* **15**, 231–252.
8. van Dijk, M. A. M., Madsen, O., Catzeflis, F., Stanhope, M. J., de Jong, W. W. & Pagel, M. (2001) *Proc. Natl. Acad. Sci. USA* **98**, 188–193. (First Published December 12, 2000; 10.1073/pnas.250216797)
9. Simpson, G. G. (1945) *Bull. Am. Mus. Nat. Hist.* **85**, 1–350.
10. Wilson, D. E. & Reeder, D. M. (1993) (Smithsonian Institution Press, Washington, DC).
11. Kingdon, J. (1997) *The Kingdon Field Guide to African Mammals* (Academic, San Diego).
12. Benton, M. J. (1997) *Vertebrate Paleontology* (Chapman & Hall, New York).
13. Easteal, S. (1999) *BioEssays* **21**, 1052–1058.
14. Benton, M. J. (1999) *BioEssays* **21**, 1043–1051.
15. Kumar, S. & Hedges, S. B. (1998) *Nature (London)* **392**, 917–920.
16. Smith, A. G., Smith, D. G. & Funnell, B. M. (1994) *Atlas of Mesozoic and Cenozoic Coastlines* (Cambridge Univ. Press, Cambridge, U.K.).
17. Felsenstein, J. (1985) *Evolution (Lawrence, KS)* **39**, 783–791.
18. *The Encyclopedia of Mammals* (1984) ed. Macdonald, D. (Facts on File Publications, New York).