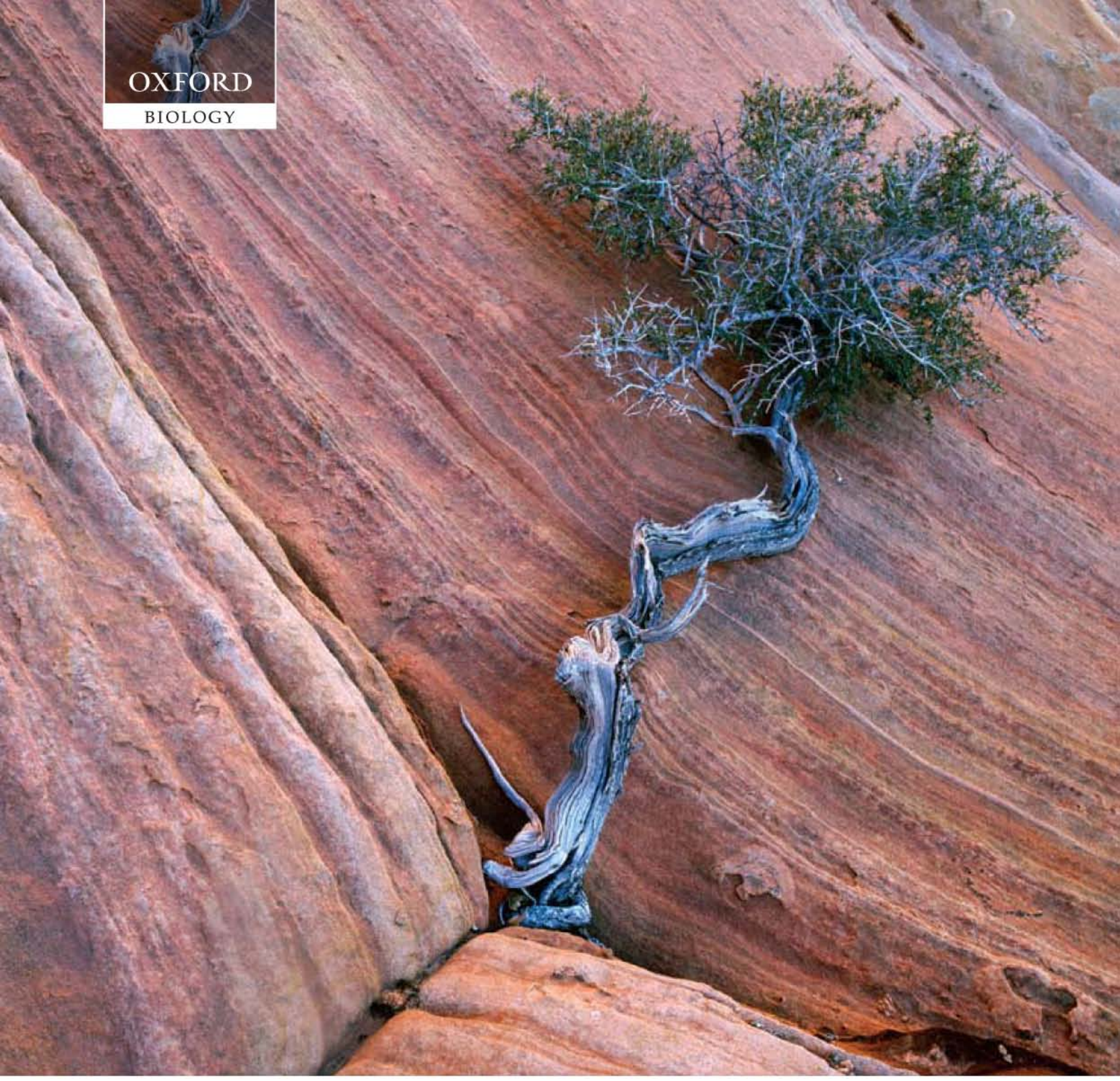

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Tenrecs and golden moles (Afrosoricida)

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Abstract

Afrosoricida is an order represented by two families (54 species) of largely insectivorous mammals, Tenrecidae (tenrecs) and Chrysochloridae (golden moles), distributed in sub-Saharan Africa and Madagascar. Most morphological studies have not supported the joining of these two families in a natural group, yet it has been supported in all molecular phylogenies. Molecular studies also have shown that Afrosoricida is a member of the Superorder Afrotheria and not related to other insectivorous mammals in the Order Eulipotyphla. Several studies have addressed the timeline of afrosoricid evolution, suggesting that tenrecids diverged from chrysochlorids 67–63 million years ago (Ma).

The mammalian Order Afrosoricida is composed of two families, the tenrecs (Tenrecidae; Fig. 1) and golden moles (Chrysochloridae) (*1*). The name Afrosoricida, coined by Stanhope *et al.* (*1*), has been debated (*2*), but is now broadly accepted and used in the literature. The order includes 10 genera and 33 species of tenrecs and nine genera and 21 species of chrysochlorids. Among the tenrecs, the most species-rich genus is *Microgale*, which accounts for two-thirds of the overall tenrec diversity and for which new species are still being discovered (*3*).

The distribution of afrosoricids is restricted to sub-Saharan Africa and Madagascar. All golden moles are blind subterranean species, of which the greatest diversity has been recorded in Southern Africa (*2*). In contrast, only one of the tenrec subfamilies is present on the African mainland. All other tenrec subfamilies are endemic to Madagascar. Tenrecs display a high level of adaptation to their environment and are remarkable examples of convergent morphological evolution with other insectivores, notably shrews, hedgehogs, and moles (*4*). This makes it difficult to understand their origin and phylogenetic interrelationships on the basis of morphological characters alone. Here, the molecular and morphological data that form the basis of our current understanding of the relationships and the divergence times of Afrosoricida will be reviewed, with emphasis on the time of divergence of the two families.

Tenrecs and golden moles were originally placed within the Order Lipotyphla (= Insectivora *sensu stricto*), which was a taxonomic group based on ancestral morphological characters (*5*). They were associated with moles (Talpidae), shrews (Soricidae), and *Solenodon* in the Suborder Soricomorpha by Butler (*6*), who even proposed a common origin of chrysochlorids and tenrecids based on very few derived characters such as the basisphenoid bulla (also present in erinaceids), zalambdodont molars (also in *Solenodon*), and the orthomesometrial implantation of the blastocyst. Furthermore, Butler suggested that the high number of morphological differences between chrysochlorids and tenrecids was an indication of their early divergence. On the other hand, MacPhee and Novacek (*7*) proposed that Chrysochloridae should be elevated to the same subordinal rank as Soricomorpha because, in their opinion, they did not share any derived traits.

The Order Lipotyphla has been completely reorganized with the advent of molecular phylogenies. It is divided into two widely divergent clades, the Eulipotyphla as a

Fig. 1 A Streaked Tenrec (*Hemicentetes semispinosus*), Family Tenrecidae, from Ranomafana, Madagascar. Credit: M. Vences.

C. Poux. Tenrecs and golden moles (Afrosoricida). Pp. 479–481 in *The Timetree of Life*, S. B. Hedges and S. Kumar, Eds. (Oxford University Press, 2009).

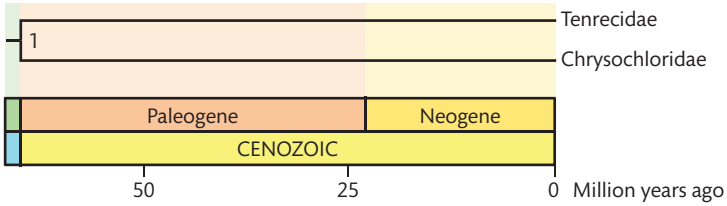

Fig. 2 A timetree of tenrecs and golden moles (Afrosoricida). Divergence times are from Table 1.

basal clade of the Superorder Laurasiatheria, and the Afrosoricida nested within Afrotheria, which regroups all mammals of African origin (*1*). This finding has been confirmed by many molecular studies (e.g., *8–11*), including those based on complete mitochondrial genome data (*12–14*). The latter studies, however, found afrosoricids to be paraphyletic (*12*) or did not include any chrysochlorid (*13, 14*). The position of Afrosoricida within the Afrotheria cannot yet be stated with certainty although the current molecular consensus favors the grouping of Afrosoricida as the closest relative of Macroscelidea (*8–11*, *15*, *16*). However, chromosome painting (*17*) and retroposon studies (*18*) support alternative hypotheses.

Several studies have provided a reliable timeline for the evolution of afrosoricids. They are of two kinds: either studies attempting to date the age of the various mammalian orders (usually based on a large number of nuclear and mitochondrial sequences but displaying one individual per family of Afrosoricida) (*19, 20*) or studies focusing on the Family Tenrecidae (based on more tenrecid samples and a smaller number of gene sequences) (*21–23*) (Table 1). Only a single study has tried to assess times of divergence within Chrysochloridae (*24*). All age estimates have been obtained using a Bayesian relaxed molecular clock approach, except for an older study (*21*) in which a linearized tree approach was used. The divergence time of the two families of Afrosoricida falls at the Mesozoic–Cenozoic boundary (66 Ma; Fig. 2). It is an average of divergence times from four studies (*19*, *20*, *22*, *23*) (Table 1). These studies are not independent, because they used some of the same genes and sequences.

Like other mammalian orders, Afrosoricida appeared during the Cretaceous (146–66 Ma) (*19*). However, there are no chrysochlorid or tenrec fossils known before the early Miocene, 23–16 Ma (*25*, *26*). This important fossil gap is possibly explained by the fact that the fossil record from the early Cenozoic of sub-Saharan Africa is rather poor (*27*). In addition, the chrysochlorid fossils from the Miocene already display a skull morphology that closely resembles that of extant species. This observation has been used to suggest that the origin of this family may be much older than the known fossil record (*25*), a hypothesis that appears to agree with recent molecular age estimates (*24*). The main debate about the evolutionary history of Afrosoricida concerns the timing of the colonization(s) of Madagascar by tenrecs (*21*, *23*, *28*), which happened after Madagascar became completely isolated from the mainland. To date, the only known tenrec fossils have been discovered on the African continent but are considered to represent lineages nested within the Malagasy tenrec subfamilies (*28*). If true, this might affect the inferred number of migrations of the Tenrecidae between the African continent and Madagascar, but not the age of the main Malagasy/African tenrec divergence that appears to be much older than the age of the fossils (*22*, *23*).

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Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among tenrecs and golden moles (Afrosoricida).

Timetree		Estimates							
Node	Time	Ref. (*19*)		Ref. (*20*)		Ref. (*22*)		Ref. (*23*)	
		Time	CI	Time	CI	Time	CI	Time	CI
1	65.4	66.4	72–60	65.4	74–57	63.0	72–53	66.9	76–58

Note: Node times in the timetree represent the mean of time estimates from different studies. All studies have overlapping data sets. The genes analyzed were: 19 nuclear and three mitochondrial genes among which *VWF, ADRA2B, BRCA1*, and *12s–16s* rRNA (*19*); 16 nuclear and three mitochondrial genes including *VWF, ADRA2B, BRCA1*, and *12s–16s* rRNA (*20*); *VWF, ADRA2B*, and *BRCA1* (*22*); and *VWF, ADRA2B*, and *AR* (*23*).

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