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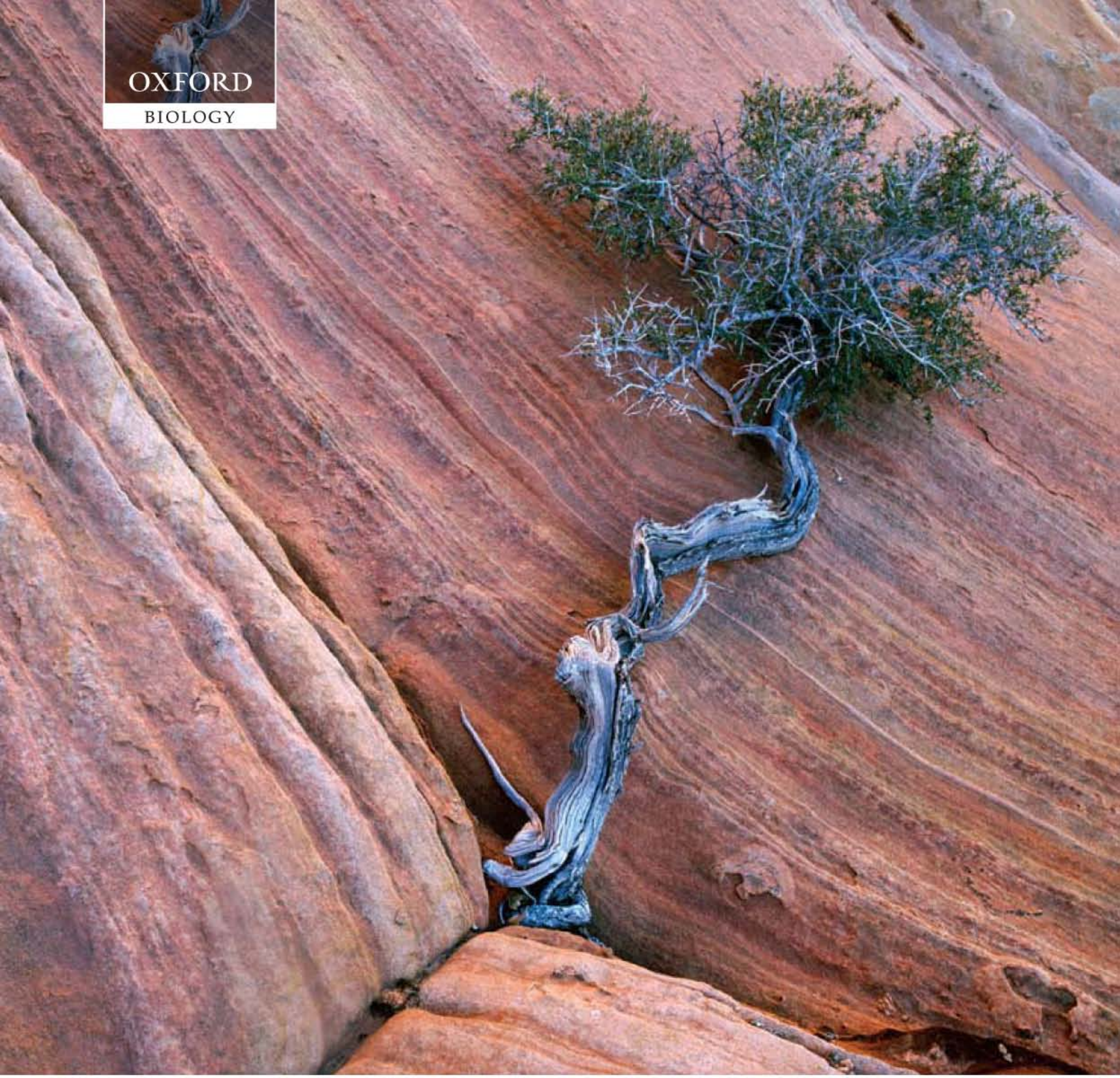

the TIMETREE of LIFE

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Hedgehogs, shrews, moles, and solenodons (Eulipotyphla)

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Abstract

Hedgehogs, shrews, moles, and solenodons (~450 sp.) are grouped into four to five families within the mammalian Order Eulipotyphla. Molecular phylogenetic analyses have resulted in major changes in their classification. Former allies have been excluded from what was previously called Lipotyphla or Insectivora. Hedgehogs are considered closest relatives of shrews, with solenodons as the most basal offshoot. The Eulipotyphla timetree shows that the major groups diversified ~80 million years ago (Ma) in the late Cretaceous. Events that led to the mass extinction at the end of the Cretaceous period (66 Ma) might have been instrumental in separating the ancestral shrews and hedgehogs.

Hedgehogs, shrews (Fig. 1), moles, and solenodons form a single, natural group of small mammals, the Order Eulipotyphla. The 452 currently recognized species (*1*) belong to four living families: Erinaceidae (hedgehogs; two subfamilies, 10 genera, and 24 species), Soricidae (shrews; three subfamilies, 26 genera, and 376 species), Talpidae (moles; three subfamilies, 17 genera, and 39 species), Solenodontidae (solenodons; one genus and four species), and the recently extinct Nesophontidae (West Indian shrews; one genus and nine species). Shared morphological characters include a simple hindgut without a caecum, typically long narrow snouts, and reduced to absent eyes. However, the lack of unique derived characters has convinced many zoologists that they resemble the basic stock that gave rise to most eutherian lineages. Here, we review the relationships and divergence times of these four living families. We begin by first placing them in the context of what has long been considered as a taxonomic wastebasket, the Insectivora.

Under its broadest meaning the former Order Insectivora *sensu* Wagner encompassed 10 distinct families: Eulipotyphla plus Tenrecidae (tenrecs), Chrysochloridae (golden moles), Macroscelidae (elephant shrews), Tupaiidae (tree shrews), and Cynocephalidae (flying lemurs). However, since Wagner (*2*), the taxonomic content of the order has gradually decreased. In one of the first attempts to accommodate heterogeneity within Insectivora, Haeckel (*3*) proposed to split insectivores into two suborders, Menotyphla for insectivores with a caecum (elephant shrews, tree shrews, and flying lemurs) and Lipotyphla for insectivores without a caecum (Eulipotyphla, tenrecs and golden moles). However, evidence arguing against the Menotyphla concept accumulated and these three families were consecutively placed in their own orders. First Leche (*4*) removed flying lemurs in 1885 but they were not assigned to their own order until 1945 (*5*). Then Butler (*6, 7*) assigned ordinal status to both elephant shrews and tree shrews, in 1956 and 1972, respectively. Contrary to this gradual sundering of Menotyphla, morphological studies never challenged the reality of the Suborder Lipotyphla. Regarding

Fig. 1 A Water Shrew (*Neomys fodiens*), Family Soricidae. Credit: P. Vogel.

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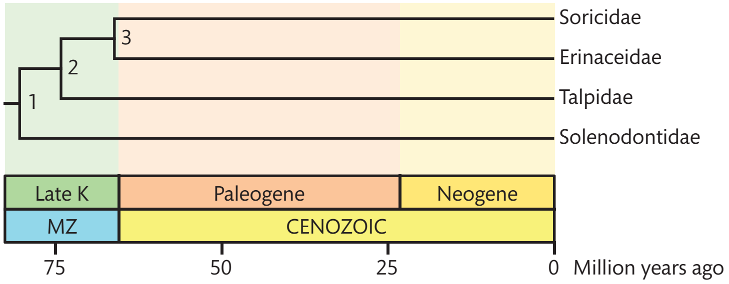

Fig. 2 A timetree of hedgehogs, shrews, moles, and solenodons (Eulipotyphla). Divergence times are from Table 1. *Abbreviations*: MZ (Mesozoic) and K (Cretaceous).

this last group, only the interfamilial and interordinal relationships were questioned (e.g., *8, 9*). Unfortunately, and as suggested earlier, the morphological "primitiveness" of this group (i.e., they resemble the "undifferentiated eutherian," *10*), which makes them key taxa in understanding mammalian body plan evolution, has also made difficult attempts at deriving their evolutionary history using morphological data.

Without surprise, it appears that molecular approaches have significantly transformed our perception of the group. One of the first successes of molecular tools applied to insectivore-like taxa was the corroboration of the close affinity of flying lemurs (Dermoptera), tree shrews (Scandentia), and Primates (e.g., *11–13*). Unexpectedly, de Jong *et al.* (*14*) placed elephant shrews within the African supraordinal clade, which is known as Afrotheria (*15*). This position for elephant shrews has now been corroborated by numerous other molecular studies (e.g., *16–20*) and by some paleontological evidence (*21*). Moreover, Douzery and Catzeflis (*22*) suggested an association between chrysochlorids and afrotherians, which were represented in their study by a golden mole (*Amblysomus*) and a hyrax (*Procavia*), respectively.

More recently, several significant improvements in understanding lipotyphlan relationships were obtained with expanded sampling of species. Springer *et al.* (*17*), Stanhope *et al.* (*15*), and Douady *et al.* (*23*) demonstrated that two former members of Lipotyphla belong in Afrotheria. Interestingly, these two taxa, golden moles and tenrecs (Afrosoricida), had previously been associated in morphological phylogenies (*24, 25,* but see *8*), but within an intact (earlier) concept of Lipotyphla. Based on these new results, remaining lipotyphlans (hedgehogs, moles, shrews, and solenodons) were placed in a new order coined Eulipotyphla (*26*).

Phylogenetic inferences based on complete mitochondrial genomes even suggested that these remaining taxa may not constitute a natural grouping. Indeed, while the European hedgehog (*Erinaceus europaeus*) was generally identified as the first offshoot of the placental tree (*27, 28*), other eulipotyphlans such as the European mole (*Talpa europaea*) seemed more closely related to Laurasiatheria (*29*) (bats, cetartiodactyls, perissodactyls, carnivores, and pangolins). However, this hypothetical diphyly of Eulipotyphla was soon rejected. First, nuclear studies based on up to 19 nuclear and three mitochondrial gene fragments (*30, 31*) and data from species representing all subfamilies (*32*) did not corroborate a basal hedgehog position (*13, 30–33*). Second, improved mitogenomic analyses favored eulipotyphlan monophyly (*34–37*). Denser taxonomic sampling and better suited models of sequence evolution indeed suggested that the basal position first reported for hedgehog was mostly due to an artifact potentially resulting from their peculiar base composition (*35–39*).

Molecular evidences have also challenged intraordinal associations. Morphology had suggested a fundamental split of Lipotyphla into Erinaceidae and all other families (Erinaceomorpha vs. Soricomorpha *sensu 25*). Stanhope *et al.* (*15*) refuted the Soricomorpha concept by exclusion of tenrecs and golden moles from this group. Then, a definite rejection of shrews–moles affinities came from Murphy *et al.* (*30, 31*) and Douady *et al.* (*23, 32*). Considering hedgehogs, shrews and moles as representative, they both supported erinaceomorph hedgehogs as the closest relative of soricomorph shrews. Roca *et al.* (*41*) even further discredited the soricomorph assemblage in supporting solenodontids as the most basal lineage in Eulipotyphla. This evidence based on 19 nuclear and three mitochondrial gene fragments conclusively resolved the position of the sole living family that was absent from the already well-established eulipotyphlan phylogeny (Fig. 2). Now, ancient DNA studies are awaited to elucidate the phylogenetic affinities of the last family,

Table 1. Divergence times (Ma) and their confidence/credibility (CI) intervals among hedgehogs, shrews, moles, and solenodons (Eulipotyphla).

Timetree		Estimates									
Node	Time	Ref. (*41*)(a)		Ref. (*41*)(b)		Ref. (*43*)(a)		Ref. (*43*)(b)		Ref. (*43*)(c)	
		Time	CI	Time	CI	Time	CI	Time	CI	Time	CI
1	80.5	85	95–75	76	81–72	–	–	–	–	–	–
2	74.3	73	86–61	73	78–68	69.8	81–59	72.9	82–64	82.8	93–72
3	66.2	65	80–51	65	71–60	62.8	74–52	65.2	75–56	72.8	83–62

Note: Node times in the timetree represent the mean of time estimates from different studies and methods. Results from ref. (*41*) are based on the analysis of (a) three mitochondrial rRNA and (b) 16 nuclear and three mitochondrial rRNA genes. Results from ref. (*43*) are from analysis of (a) 1st + 2nd codon positions of three nuclear genes, (b) amino acid sequences of three nuclear genes, and amino acid sequences of eight nuclear genes.

Nesophontidae. Indeed, West Indian shrews presumably became extinct during post-Colombian time. However, while waiting for molecular data, it has been proposed by Roca *et al.* (*41*) that this taxon could be closely related to shrews. This result was suggested by a reanalysis of Asher *et al.*'s (*42*) morphological data set constrained by a molecular scaffold corresponding to the most likely relationships among extant taxa.

Most comprehensive molecular dating estimates for the eulipotyphlan family tree come from Douady and Douzery (*43*) and from Roca *et al.* (*41*). Both studies are strongly linked, as they rely on Bayesian relaxed molecular clocks as implemented in the Thorne–Kishino method (*44, 45*) and have partly overlapping genetic data. Douady and Douzery (*43*) used a denser taxonomic sampling, with lesser genetic coverage, but could not include the key taxa *Solenodon,* whose sequences were unavailable at the time. In regard to calibration times, both studies again show some degree of overlap. However, Roca *et al.* (*41*) followed Springer *et al.* (*46*) in choosing the most probable ages of fossils as calibrations, whereas Douady and Douzery (*43*) employed upper and lower bounds of the stratigraphic range of the geological epochs to which the fossils pertaining to the divergence under focus were assigned. The second approach is a more conservative one as it accounts for uncertainty in timing the fossil remains. Thus Douady and Douzery (*43*) assumed divergence between 24 and 5 Ma for the split between *Mus*/*Rattus* and 72 and 49 Ma for Feliformia/Caniformia, Hippomorpha/Ceratomorpha, Hippopotamidae/Cetacea and Paenungulata. In contrast, Roca *et al.* (*41*) used >12 Ma, 63–50 Ma, 58–54 Ma, >52 Ma, and 65–54 Ma for these nodes, respectively. In addition, Roca *et al.* (*41*) constrained a basal divergence among extant xenarthrans before 60 Ma, a maximum of 65 Ma for cetartiodactyl diversification, and a 60–43 Ma range for the divergence between pteropodid bats and the false vampire bat.

While some differences in estimates exist, mainly for Roca *et al.*'s (*41*) three-gene mtRNA data and Douady and Douzery's (*43*) eight-gene (nuclear) data set, overall results are similar (Table 1). Both analyses suggest that the interfamily diversification of extant eulipotyphlans took place in the late Cretaceous. The basal (early branching) position of *Solenodon* and its divergence estimate argue for a vicariant origin of this West Indian taxon. Indeed, it is well established that proto-Antilles separated from the North American mainland between 80 and 70 Ma (*47*) and the mean estimate of 80 Ma fits in this window of time. However, the complex history of the area cannot exclude other alternatives (*41*). One such alternative would disconnect speciation in the late Cretaceous and colonization of the West Indies later in the Paleogene (*48*). The split between hedgehogs and shrews is quite likely contemporaneous to the Cretaceous/Paleogene boundary. Thus, it seems plausible that events that triggered the mass extinction acted as a diversification agent for Eulipotyphla. This may have included subsequent adaptive radiation into newly available niches during the very early Paleogene. However, historical events leading to the origin of the mole lineage are much more elusive. One could argue that they were linked to some climatic or tectonic event that occurred at the boundary between the mid- and late Campanian (84–71 Ma). The time of divergence of the *Nesophontes* lineage is unclear. However, the phylogenetic position suggested by Roca *et al.*'s (*41*) reanalysis of Asher *et al.*'s (*42*) data would suggest that divergence occurred sometime after the hedgehog–shrew divergence but before separation of the Subfamilies Crocidurinae and Soricinae. Douady and Douzery (*43*) estimated the time of divergence of these subfamilies 38 Ma (95% credibility interval: 47–29). Thus, if phylogenetic assumptions are correct, the *Nesophontes*–shrew split could have occurred between 65 and 38 Ma. Additional molecular studies are still required for a better understanding of the evolution of Eulipotyphla, one of the most recently delineated orders of placental mammals.

Acknowledgments

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