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Mesozoic origin for West Indian insectivores

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The highly endangered solenodons, endemic to Cuba (*Solenodon cubanus*) and Hispaniola (*S. paradoxus*), comprise the only two surviving species of West Indian insectivores^{1,2}. Combined gene sequences (13.9 kilobases) from *S. paradoxus* established that solenodons diverged from other eulipotyphlan insectivores 76 million years ago in the Cretaceous period, which is consistent with vicariance, though also compatible with dispersal. A sequence of 1.6 kilobases of mitochondrial DNA from *S. cubanus* indicated a deep divergence of 25 million years versus the congeneric *S. paradoxus*, which is consistent with vicariant origins as tectonic forces separated Cuba and Hispaniola^{3,4}. Efforts to prevent extinction of the two surviving solenodon species would conserve an entire lineage as old or older than many mammalian orders.

Solenodons are small (1 kg) fossorial (burrowing) insectivores, and are among the few native non-flying mammals that survived human settlement of the islands of the West Indies^{1,2}. They inhabit the forests of Cuba and Hispaniola to elevations of 2,000 m, and shelter in caves, crevices, logs and extensive tunnel networks at a depth of >20 cm (refs 5 and 6). The dearth of Late Cretaceous or early Tertiary fossils from the West Indies has constrained resolution among alternative hypotheses regarding the origin of solenodons and their affinity to other mammals^{1,7}.

Some have suggested a close relationship to soricids (shrews) but not to talpids (moles)^{8,9}, or to soricids but not erinaceids (hedgehogs and gymnures)^{9–11}, and/or to fossil North American 'apternodontids' such as *Apternodus*, or geolabidids such as *Centetodon*^{10,12–15}. A few authorities have suggested an affinity of solenodons to Afro-Malagasy tenrecs (both have zalambdodont molars)^{12,15,16} and a trans-Atlantic dispersal event was suggested to explain this apparent relationship^{12,16}. Recent molecular studies have placed the tenrecs firmly within Afrotheria, a superordinal mammalian group with

African origins^{17,18}, while placing shrews, moles and erinaceids in a distinct clade (Eulipotyphla) within Laurasiatheria, a superordinal mammalian group most probably of Northern Hemisphere origins¹⁸. For solenodons, only a few mtDNA sequences of *S. paradoxus* have been available for analyses; these have rejected a close affinity between solenodons and tenrecs¹⁷. One study has placed *Solenodon* as a sister group to soricids + talpids but not to erinaceids, although the bootstrap support for this placement (51%) was quite weak¹⁷; a second molecular analysis has positioned *Solenodon* as sister to a clade of rodents¹⁹.

To examine the origin of *Solenodon* and its relationship to other mammals, we sequenced portions of 16 nuclear and three mitochondrial genes as previously described¹⁸ using DNA extracted from a blood sample of a wild-born male *S. paradoxus* from the northern Dominican Republic (Cordillera Septentrional, Provincia de Espaillat), kept at the National Zoological Park (ZOODOM) in Santo Domingo. *S. paradoxus* DNA sequences were aligned (13,885 base pairs (bp) after removal of regions of ambiguous homology) to those of taxa from all extant eutherian orders of mammals¹⁸. Figure 1 depicts the phylogenetic position of solenodons relative to other eulipotyphlan insectivores (including the results of a separate analysis to place *S. cubanus*, see below). *Solenodon* grouped with eulipotyphlan insectivores with 100% maximum-likelihood bootstrap support and bayesian posterior probability (BPP) of 1.00. Putative affinities of *Solenodon* to tenrecs^{12,15,16} or to rodents¹⁹ received no support (Supplementary Information). There was high support for *Solenodon* being the most basal eulipotyphlan (95% maximum-likelihood bootstrap support; BPP of 1.00). *Solenodon* had a more basal position than had been suggested by previous molecular or morphological reports, relative to talpids^{8,9} and/or to erinaceids^{9–11,17}.

We used well-established fossil dates²⁰ as minimum and maximum calibration points to estimate, using the method of Thorne–Kishino^{21,22}, the divergence date for *Solenodon* versus other placental mammals to be 76 million years (Myr) ago (95% credibility interval (CI) of 72–81 Myr ago) (Fig. 1 and Supplementary Information). The estimate for solenodon divergence (76 Myr ago) is comparable to or older than the estimated dates of some interordinal splits in mammals (for example, pangolins versus carnivores, or manatees versus elephants)²⁰, and considerably older than the basal divergence of most mammalian orders. The point estimate is 11 million years before the Cretaceous/Tertiary boundary at 65 Myr ago^{3,7}, with the 95% CI for solenodon divergence falling completely within the Mesozoic. The Mesozoic divergence date contrasts with previously reported support for Cenozoic divergence versus extant mainland forms for eight of nine distinct West Indian amphibian lineages, 67 of 68 reptile lineages, all 300–500 independent colonizations by birds, all 42 bat lineages, and the eight non-flying non-insectivore mammalian lineages⁴.

West Indian insectivores are therefore the only tetrapod lineage for which strong evidence supports Mesozoic divergence versus extant mainland forms, with the possible exceptions of the frog genus *Eleutherodactylus* and the Cuban xantusiid lizard *Cricosaura typica*^{4,7}. For the frog *Eleutherodactylus*, an intra-Antillean split within the genus has been previously dated to 70 ± 6.8 Myr ago⁴. For *Cricosaura typica* and related mainland lizards, we applied the Thorne–Kishino dating method^{21,22} to previously published sequences²³. While uncertain fossil constraints for xantusiids did not allow the definitive establishment of a Mesozoic origin for *Cricosaura* (95% CI of 57–101 Myr ago), the point estimate for the divergence of Cuban versus mainland xantusiids was 76 Myr ago (Supplementary Information).

Various biogeographic hypotheses have been proposed to account for the presence of solenodons only in the Antilles¹². These invoke vicariance (biogeographic separation caused by the tectonic motion of land masses or rising sea levels) or dispersal (for example, rafting across the sea on vegetation) or some combination

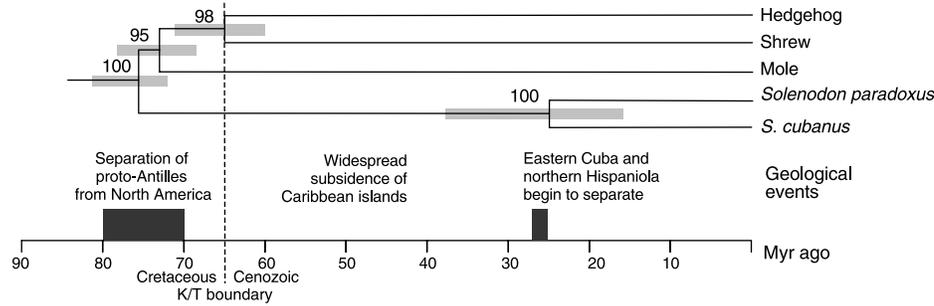


Figure 1 Phylogeny and molecular timescale for solenodons and other eulipotyphlan insectivores. The phylogeny depicted is based on analysis of a DNA sequence alignment (13.9 kb after removal of ambiguous regions) of nuclear and mitochondrial genes from *Solenodon paradoxus* and 42 other eutherian taxa²⁰, and a separate analysis of 1.6 kb of mtDNA that included *S. cubanus* (Supplementary Information). Only eulipotyphlan taxa are depicted, with nodes positioned on the basis of divergence times estimated by the Thorne–Kishino method^{21,22} using twelve fossil constraints²⁰ (Supplementary Information). Shading along each node indicates the 95% credibility interval for the

estimated divergence dates. Nodes are labelled with maximum-likelihood bootstrap support; relationships depicted were also supported by maximum-parsimony, minimum-evolution and bayesian analyses (Supplementary Information). Geological events indicated include severing of the proto-Antillean land connection to the North American mainland 70–80 Myr ago^{3,7}, the Cretaceous/Tertiary (K/T) boundary, widespread subsidence of Caribbean islands in the Tertiary^{3,4,7,26}, and the separation of eastern Cuba and northern Hispaniola, which began subsequent to 25–27 Myr ago^{3,4,7}.

of the two^{1,12,14–16}. The proto-Antillean arc, which moved north-eastward relative to the North American mainland to form part of the West Indies, was in close proximity to the mainland in the Late Cretaceous period^{3,24}. The most recent overland connection between the proto-Antilles and the North American mainland was severed 70–80 Myr ago^{3,7}. The timing of this separation is consistent with vicariance, as contemporaneous divergence dates were estimated for *Solenodon*, *Eleutherodactylus* and *Cricosaura*, even though the vicariance hypothesis must be evaluated in the context of subsequent events, notably the extraterrestrial bolide 10 km in diameter that struck the nearby Caribbean at Chicxulub 65 Myr ago^{3,4,7,25}, and the widespread subsidence of Caribbean islands in the Tertiary period^{3,4,7,26} (Fig. 1).

Dispersal during the Tertiary of a now-extinct North American mammal, such as *Apternodus* or *Centetodon*^{10,12–15}, has also been suggested to account for the presence of solenodons in the Antilles. However, a recent phylogenetic analysis has concluded that several fossil North American zalambdodonts, including *Apternodus*, were more closely related to soricids than to solenodons²⁷, which suggests that these zalambdodont taxa could not have been dispersing ancestors of solenodons. We performed a parsimony analysis of living and fossil insectivores using the same morphological data set²⁷, while employing the tree derived from our molecular analysis as a constraint. Although bootstrap values were low, solenodons were only distantly related to the soricid-fossil zalambdodont clade, or to *Centetodon* (Supplementary Information). Thus the morphological analysis does not diminish the possibility of vicariance, although it remains possible that solenodons could derive from dispersal during the Tertiary of a now-extinct North American mammal.

Individuals of *S. cubanus* are only very rarely caught, and the species has been considered extinct at various times during the past century. We used three museum samples of *S. cubanus* to examine molecular divergence in a 2.5-kilobase (kb) DNA fragment spanning portions of both mitochondrial ribosomal RNA genes. Aligning the sequence to the same mtDNA region of *S. paradoxus* and other eutherian mammals (1,624-bp alignment after removing regions of ambiguous homology), we estimated that the two *Solenodon* species diverged 25 Myr ago (95% CI of 16–38 Myr ago; Fig. 1 and Supplementary Information). For part of the Cenozoic, eastern Cuba and northern Hispaniola were attached, but after 27–25 Myr ago they began separating^{3,4,7} (Fig. 1). Our date estimate is consistent with intra-Antillean vicariance separating solenodons into two distinct island taxa. The large molecular genetic separation between the species is comparable to the divergence between

distinct mammalian families, for example, deer versus bovids (23 Myr ago)²⁸, dolphins versus whales (30 Myr ago)²⁰, or humans versus Old World monkeys (23 Myr ago)²⁸. While almost all authorities have classified Hispaniolan and Cuban solenodons as distinct species within a single genus, *Solenodon*¹, our results lend support to an alternative proposal that Cuban solenodons be classified in a distinct genus, *Atopogale*²⁹. The large genetic distance between *Solenodon* taxa may also raise the possibility that insectivore-grade early eutherian fossil taxa may be more disparate than suggested by morphological differences.

Solenodons today are threatened by deforestation, increasing human activity, the negative impacts of predation by introduced cats, dogs and mongooses, and possibly by competition from introduced rodents^{1,6}. They have survived human settlement of the islands of the West Indies, which probably eliminated two other solenodon species and eleven species of the extinct genus *Nesophontes*^{1,2}, possibly related to solenodons^{4,8–10,14}. Both solenodons are listed as endangered and declining in population by the IUCN Red List of threatened species, alongside 867 other threatened Caribbean taxa³⁰. Our results indicate that extinction of solenodons would represent the loss of an entire evolutionary lineage whose antiquity predates the extinction of the dinosaurs. They emphasize the urgent need for conservation measures on behalf of native West Indian wildlife. □

Methods

Solenodon paradoxus DNA was extracted from a fresh blood sample using a column-based kit (Qiagen), and amplified, sequenced and aligned as previously described¹⁸, resulting in a 13,885-bp data set. DNA was also successfully extracted from three museum samples of *S. cubanus* (of five individuals attempted) in a physically isolated ancient DNA laboratory, with some extractions repeated in different locations. Segments of the 12S, transfer RNA valine and 16S mitochondrial genes were amplified in overlapping fragments by nineteen pairs of primers.

Maximum-likelihood analyses were performed with PAUP* 4.0b10 and employed heuristic searches using a neighbour-joining starting tree and tree-bisection–reconnection branch swapping. Nonparametric maximum-likelihood bootstrap analysis was performed using 100 heuristic replicates with nearest-neighbour-interchange branch swapping. Settings for the GTR + Γ + I model of DNA sequence evolution were estimated initially using Modeltest and then optimized in PAUP* by additional heuristic searches. Bayesian phylogenetic analyses were performed using MrBayes v3.0b4. Maximum-parsimony and minimum-evolution analyses of *Solenodon* DNA sequences were also performed using PAUP*. To examine the relationship of *Solenodon* to fossil insectivores, a parsimony tree was generated using the morphological data set of ref. 27, employing a tree scaffold based on our molecular phylogeny.

To estimate divergence times, we used the Thorne–Kishino method^{21,22}, which permits multiple simultaneous constraints from the fossil record while allowing rates of molecular evolution to vary on different branches of a phylogenetic tree. Branch lengths were estimated with the *estbranches* program of ref. 21; divergence times were estimated using the program *divtime5b*^{21,22}. Divergence dates were established using different DNA

sequence data sets for *S. paradoxus* versus other mammals, for *S. paradoxus* versus *S. cubanus*, and for *Cricosaura typica* versus other xantusiid lizards.

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Convergence across biomes to a common rain-use efficiency

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Water availability limits plant growth and production in almost all terrestrial ecosystems^{1–5}. However, biomes differ substantially in sensitivity of aboveground net primary production (ANPP) to between-year variation in precipitation^{6–8}. Average rain-use efficiency (RUE; ANPP/precipitation) also varies between biomes, supposedly because of differences in vegetation structure and/or biogeochemical constraints⁸. Here we show that RUE decreases across biomes as mean annual precipitation increases. However, during the driest years at each site, there is convergence to a common maximum RUE (RUE_{max}) that is typical of arid ecosystems. RUE_{max} was also identified by experimentally altering the degree of limitation by water and other resources. Thus, in years when water is most limiting, deserts, grasslands and forests all exhibit the same rate of biomass production per unit rainfall, despite differences in physiognomy and site-level RUE. Global climate models^{9,10} predict increased between-year variability in precipitation, more frequent extreme drought events, and changes in temperature. Forecasts of future ecosystem behaviour should take into account this convergent feature of terrestrial biomes.

There is a compelling need to understand how terrestrial ecosystems respond to precipitation and other external drivers to permit the forecasting of potential biosphere feedback to natural and anthropogenic changes in the climate system¹¹. This is especially