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Editor's Choice Article

Appropriate fossil calibrations and tree constraints uphold the Mesozoic divergence of solenodons from other extant mammals

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ABSTRACT

The mammalian order Eulipotyphla includes four extant families of insectivorans: Solenodontidae (solenodons); Talpidae (moles); Soricidae (shrews); and Erinaceidae (hedgehogs). Of these, Solenodontidae includes only two extant species, which are endemic to the largest islands of the Greater Antilles: Cuba and Hispaniola. Most molecular studies suggest that eulipotyphlan families diverged from each other across several million years, with the basal split between Solenodontidae and other families occurring in the Late Cretaceous. By contrast, Sato et al. (2016) suggest that eulipotyphlan families diverged from each other in a polytomy ~58.6 million years ago (Mya). This more recent divergence estimate for Solenodontidae versus other extant eulipotyphlans suggests that solenodons must have arrived in the Greater Antilles via overwater dispersal rather than vicariance. Here, we show that the young timetree estimates for eulipotyphlan families and the polytomy are due to an inverted ingroup-outgroup arrangement of the tree, the result of using Tracer rather than TreeAnnotator to compile interfamilial divergence times, and of not enforcing the monophyly of well-established clades such as Laurasiatheria and Eulipotyphla. Finally, Sato et al.'s (2016) timetree includes several zombie lineages where estimated divergence times are much younger than minimum ages that are implied by the fossil record. We reanalyzed Sato et al.'s (2016) original data with enforced monophyly for well-established clades and updated fossil calibrations that eliminate the inference of zombie lineages. Our resulting timetrees, which were compiled with TreeAnnotator rather than Tracer, produce dates that are in good agreement with other recent studies and place the basal split between Solenodontidae and other eulipotyphlans in the Late Cretaceous.

1. Introduction

The mammalian family Solenodontidae includes two extant species (*Solenodon cubanus*, *S. paradoxus*) that are endemic to Cuba and Hispaniola, respectively. Phylogenetic analyses based on nuclear and mitochondrial genes suggest that Solenodontidae is the sister taxon to a clade containing all other extant eulipotyphlan families, i.e., Talpidae (moles), Soricidae (shrews), and Erinaceidae (hedgehogs) (Roca et al., 2004; Meredith et al., 2011; Emerling et al., 2015; Foley et al., 2016; Brandt et al., 2017). Recently, Brace et al. (2016) obtained sequences for species of the extinct nesophontid *Nesophontes* (West Indies shrews), which used to live in the Greater Antilles, and showed that a clade comprised of *Solenodon* and *Nesophontes* is the sister group to other eulipotyphlans. Brace et al. (2016) suggested the name Solenodonota for the clade that includes Solenodontidae and Nesophontidae. Most timetree estimates place the age of the basal split in Eulipotyphla in the Late Cretaceous (Roca et al., 2004; Meredith et al., 2011; Emerling

et al., 2015; Brace et al., 2016; Foley et al., 2016; Springer et al., 2017). These divergence times are compatible with the vicariant separation of *Solenodon* + *Nesophontes* in the proto-Antilles from other eulipotyphlans in mainland North America during the Late Cretaceous (Hedges et al., 1992; Iturralde-Vinent and MacPhee, 1999; Roca et al., 2004; Iturralde-Vinent, 2006). The aforementioned molecular dating studies also suggest that interfamilial divergences within extant Eulipotyphla occurred over a temporal window of ~4.7–12 million years (Table 1).

By contrast with these studies, Sato et al. (2016) have suggested that the basal split in Eulipotyphla occurred 58.6 Mya in the Paleocene. This divergence date is believed to be incompatible with the vicariance hypothesis and suggests that the ancestor of *Solenodon* dispersed from North America to the Greater Antilles (Cuba + Hispaniola) in the early Cenozoic after the mass extinction at the Cretaceous-Paleogene boundary (KPg). Sato et al.'s (2016) timetree dates further suggest that the base of Eulipotyphla is a polytomy and that all of the interordinal

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Table 1

Divergence time estimates in millions of years for interfamilial splits within Eulipotyphla (95% CIs are in parentheses when numerical values were reported).

Reference	Clade				
	Eulipotyphla	Talpidae + Soricidae + Erinaceidae	Talpidae + Soricidae	Erinaceidae + Soricidae	Solenodonota
Roca et al. (2004) ^A	77 (72, 82)/76 (72, 81)	74 (68, 79)/73 (68, 78)	NR	66 (59, 72)/65 (60, 71)	NR
Meredith et al. (2011) DNA ^B	77.4 (71.7, 85.8)	76.4 (70.4, 84.8)	NR	71.9 (65.6, 80.4)	NR
Meredith et al. (2011) amino acids ^B	77.2 (70.7, 84.0)	73.6 (66.7, 80.9)	68.0 (62.4, 75.3)	NR	NR
dos Reis et al. (2012)	NR	61.5 (60.9, 62.0) ^K	NR	61.4 (60.6, 62.1) ^L	NR
Emerling et al. (2015)	78.0	77.1	NR	73.3	NR
Brace et al. (2016) ^C	72.3 (67.5, 78.9)	69.4 (65.2, 75.6)	NR	65.0 (61.9, 70.8)	57.3 (43.6, 68.6)
Foley et al. (2016)	74.2 (72.9, 75.5)	71.8 (70.5, 73.2)	NR	62.2 (61.6, 63.7)	NR
Phillips (2016) ^D	59.1 ^M	58.5 ^M	NR	55.3 ^M	NR
Sato et al. (2016) ^E	58.6 (57.3, 60.8) ^M	58.6 (57.3, 60.8) ^M	NR	58.5 (57.3, 60.4) ^M	NR
Tarver et al. (2016)	NR	NR	NR	64.4 (61.5, 67.6)	NR
Ronquist et al. (2016) ^F	57 ^M	49 ^M	NR	42 ^M	NR
Ronquist et al. (2016) ^G	54 ^M	47 ^M	NR	40 ^M	NR
Brandt et al. (2017) ^H	78.2 (62.1, 98.6)	NR	68.0 (47.8, 95.80)	NR	NR
Springer et al. (2017) ^I	69.0 (66.5, 73.0)	67.6 (65.3, 71.8)	NR	62.7 (60.5, 67.0)	NR
This study ^J	71.9 (65.4–78.5)	68.6 (63.9–74.0)	NR	63.6 (61.5–65.7)	NR

Abbreviations: NR, not reported.

^A Nuclear + mitochondrial supermatrix with both species of *Solenodon* and with *S. paradoxus* only.^B Mean of four divergence dates based on 26 nuclear loci (DNA analyses) or 22 protein-coding loci (AA analyses) and different combinations of autocorrelated versus independent rates and hard-bounded versus soft-bounded calibrations.^C Nuclear + mitochondrial supermatrix.^D 26 nuclear genes from Meredith et al. (2011).^E Five nuclear genes.^F Approximate dates estimated from Fig. 7 in Ronquist et al. (2016) that does not include fossils.^G Approximate dates estimated from Fig. 8 in Ronquist et al. (2016) that does include fossils.^H Mitochondrial genomes.^I Mean of four divergence dates based on 26 nuclear genes from Meredith et al. (2011) and four different combinations of autocorrelated versus independent rates and hard-bounded versus soft-bounded calibrations. 95% CIs are based on the most extreme values (youngest, oldest) from four different analyses.^J Estimated dates based on Sato et al.'s (2016) nuclear supermatrix with enforced monophyly and updated calibrations as in Fig. 3.^K Analysis based on nuclear + mitochondrial genes.^L Mean of analyses with three different trees based on nuclear genes.^M Zombie lineages for point estimate assuming that *Litolestes* is a stem erinaceid (O'Leary et al., 2013).

splits within Eulipotyphla are effectively coincident with each other at ~58.6 Mya (their Fig. 1 and Table S2). This convergence of eulipotyphlan interfamilial divergence times at ~58.6 Mya is surprising in view of other timetree studies that deploy these cladogenic events over a much longer time window (Table 1).

Sato et al. (2016) performed their molecular dating analyses with BEAST and summarized their ingroup divergence times with Tracer rather than TreeAnnotator. In addition to representative eulipotyphlans, which belong to the mammalian superorder Laurasiatheria, Sato et al. (2016) included three outgroups from the laurasiatherian order Carnivora (*Herpestes javanicus*, *Mustela erminea*, *M. itatsi*) and two outgroups from the mammalian superorder Euarchontoglires (*Tupaia belangeri*, *Mus musculus*). Divergence times between ingroup and outgroup taxa were not reported by Sato et al. (2016). Furthermore, Sato et al.'s (2016) BEAST analyses were performed without any constraints on the monophyly of ingroup or outgroup taxa (J. Sato, pers. comm. to M.S.S., W.J.M., and A.L.R.), which leaves open the possibility that well-established clades in the BEAST analyses may not have been reconstructed as monophyletic given that BEAST returns a rooted phylogeny. Given these anomalies and potential concerns with Sato et al.'s (2016) molecular dating analyses, we sought to determine whether unusual features of their timetree are the result of employing Tracer rather than TreeAnnotator to reconstruct their timetree, or of failing to constrain the monophyly of ingroup and outgroup taxa. We therefore performed analyses using the original and modified versions of Sato et al.'s (2016) data set.

2. Methods

2.1. BEAST analyses

We used BEAST 1.7.2 (Drummond et al., 2006, 2012) to analyze

Sato et al.'s (2016) original “Strategy 1” xml file (Supplementary XML File 1) that included constraints for four nodes: Erinaceidae to Soricidae (59–57 Mya), Erinaceidae (49–37 Mya), Soricidae (33–25 Mya), and Talpinae to Scalopinae (37–34 Mya). Sato et al.'s (2016) mcmc chains were run for 10 million generations and were based on a data set that included five nuclear genes (*APOB*, *ATP7A*, *BDNF*, *BRCA1*, *RAG1*) and 13 partitions. We also analyzed a modified version of Sato et al.'s (2016) Strategy 1 xml file that enforced the monophyly of Euarchontoglires, Laurasiatheria, and Eulipotyphla (Supplementary XML File 2). Finally, we analyzed a modified version of Sato et al.'s (2016) Strategy 1 xml file that enforced monophyly as above, modified Sato et al.'s (2016) calibration for Erinaceidae to Soricidae, and added an additional calibration for Euarchontoglires (Supplementary XML File 3). These changes were employed because analyses with Sato et al.'s (2016) original calibrations resulted in zombie lineages (Springer et al., 2017), i.e., lineages for which estimated divergence dates are younger than minimum ages that are implied by crown fossils. We modified the calibration for Erinaceidae to Soricidae because the maximum age attributed to this node by Sato et al. (2016), which was not justified by these authors, is younger than the oldest stem erinaceid fossils (Benton et al., 2009, 2015; O'Leary et al., 2013). The minimum age of *Adunator ladae* is 61.6 Mya (Benton et al., 2015). Hooker and Russell (2012) suggested that *Adunator* is a stem macroscelidean, but their analysis did not include any other erinaceids (or other eulipotyphlans) and it is therefore difficult to argue in favor of macroscelidean affinities based on Hooker and Russell's (2012) results. Even if *Adunator* is not a stem erinaceid, *Litolestes ignotus* from the Danian has a minimum age of 61.7 Mya and is regarded as a stem erinaceid (O'Leary et al., 2013; Paleobiology Database). We therefore used a minimum age of 61.7 Mya and a maximum age of 66.0 Mya (base of Danian) for the age of the erinaceid-soricid split. For Euarchontoglires (*Mus* to *Tupaia*), we used a minimum age of 65.5 Mya based on the crown euarchontan fossil

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