

The soft explosive model of placental mammal evolution

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Addressing claims of “zombie lineages” on Phillips’ (2016) timetree

Phillips [1] found extreme divergence underestimation among large, long-lived taxa that were not calibrated, and argued that calibrating these taxa instead shifted the impact of the underlying rate model misspecification to inflating dates deeper in the tree. To avoid this “error-shift inflation”, Phillips [1] first inferred divergences with dos Reis *et al.*’s [2] calibrations, most of which are set among taxa with plesiomorphic life-history (tree 1). Next, the final timetree (tree 2) was inferred with further calibrations added among large, long-lived taxa, but with maximum bounds on several superordinal clades based on broad agreement between tree 1 and fossil records for major diversification following the KPg.

Here we consider Springer *et al.*’s [3] claims that divergences among small, short-lived taxa in Phillips [1] are underestimated relative to first fossil appearances. Each of these claims is invalid. For 20 of the 22 clades, either (1) the fossil placement is incorrect or poorly supported (see text below) or (2) the molecular and fossil dates are consistent, with the fossil date falling within the 95% CI from Phillips’ [1] tree 1 (Table S1). For the remaining two clades, the 95% CIs from Phillips’ [1] final molecular dates (tree 2) are entirely older than the proposed fossil minima. The tree 2 analysis was primarily designed to test rate variation hypotheses, and still retains some dubious fossil calibrations from Meredith *et al.* [2]. But it is notable that our primary (dR40) dating estimates in the present study are also consistent with these proposed fossil minima (Supplemental file 3). Thus, Springer *et al.*’s [3] claim of “zombie” lineages among smaller, shorter lived taxa is unfounded.

Incorrect or poorly supported fossil placements

1. Hyracoidea (*Dendrohyrax*, 6.08 Ma): Pickford and Hlusko [4] assigned fragmentary material to *Dendrohyrax*, primarily on the presence of ridges on the base of the mandibular symphysis that are “usually only found in *Dendrohyrax*”, although even in *Dendrohyrax* they are often absent. This similarity criterion is not a phylogenetic statement, because no outgroups or other rationale for determining polarity were employed to distinguish the character as synapomorphic for *Dendrohyrax* or primitive for Procaviidae. The authors also note another similarly aged hyrax assigned to *Dendrohyrax*, but again, whether the assignment is based on apomorphic or

plesiomorphic similarity is not tested. Moreover, our tree, and that of Springer *et al.* [3] does not include *Dendrohyrax*. Springer *et al.* [3] assume that *Dendrohyrax* is sister to *Procavia*, but this is not the traditional morphological relationship. Even the molecular analysis of Kuntner *et al.* [5] does not robustly resolve affinities among hyraxes, although weakly favours *Dendrohyrax/Procavia*. If however, the total evidence analysis of Puttick and Thomas [6] is correct, then *Dendrohyrax* falls outside of the hyraxes that are included in the present study (*Heterohyrax* and *Procavia*), delegitimizing the calibration.

2. *Prionodon* – *Felis* and **3. *Felidae* – *Eupleridae*** (*Proailurus*, *Stenogale*, 28. 1 Ma): See Supplemental file 2: “New calibrations” (3. Feliformia) for discussion on the inappropriateness of *Proailurus* and *Stenogale* as reference taxa for calibrating these clades.

4. *Ferae* (=Ostentoria, cat – pangolin divergence) (*Ravenictis*, 64 Ma): *Ravenictis* was regarded as a stem carnivoran based on a single upper molar [7]. A further two, rather damaged lower molars from the same Rav W-1 horizon within a quarry in the Ravenscrag Formation were also attributed to an unnamed carnivoran by Fox *et al.* [8]. Neither of these papers provided any formal phylogenetic analysis (matrix based or otherwise) and instead relied on similarity. Perhaps more importantly, neither paper considered pangolins (the modern sister group of Carnivora). Inferring whether *Ravenictis* and the unnamed lower molar taxon diverged from the carnivoran stem before or after pangolins is not directly possible, because pangolins lack teeth. Even the extinct, probable pangolin relatives, the palaeonodonts have reduced or derived molars, thus clouding their deeper affinities based on teeth. Without being able to confidently place the origin of pangolins within this carnivorimorph framework the Rav W-1 teeth cannot be used to calibrate *Ferae*. Some authors have also instead placed *Ravenictis* with cimolestids (e.g. [9]).

Another slight variation on this calibration is that Fox *et al.* [8] acknowledge that “correlation of the Rav W-1 horizon has been contentious”, and that it is possibly middle or upper Puercan, such that the appropriate bound would be 63.3 Ma. Hence, even if the Rav W-1 fossils could be assigned to Carnivora with confidence, the 63.3 Ma fossil date is consistent with our dR40 timetrees, falling within the 95% CIs for *Ferae* (Auto: 62.1-65.4 Ma, Ind: 60.7-64.8 Ma).

5. *Emballonuroidea* and **6. *Emballonuroidea* – *Noctilionoidea*** (*Tachypteron*, 47.8 Ma): As discussed in the main text, *Tachypteron* was assigned by Storch *et al.* [10] only on the basis of similarities, and within a framework that considered emballonurids as sister to rhinolophoids.

These two groups are now known to fall on opposite sides of the chiropteran root [11], and some other Eocene European bats previously assigned to Emballonuridae and Rhinolophoidea have since been placed in a new family of uncertain affinities [12]. *Tachypteron* was not considered in that study. Ravel *et al.*'s [13] cladistic analysis of *Tachypteron* and *Vespertiliavus* included only emballonuroids among crown bats. Hence, the placement of *Tachypteron* requires confirmation. Noctilionoids were also not considered in these studies.

7. Erinaceidae – Soricidae, 8. Erinaceidae/Soricidae – Talpidae, and 9. Eulipotyphla

(*Adunator*, 61.6 Ma): Springer *et al.* [3] cite five articles in support of *Adunator* being an 'erinaceimorph', but all are secondary references (including their own previous molecular dating studies) and rely on the calibration compendia of Benton *et al.* [14, 15]. Looking within these compendia, two primary research sources are cited, but neither provides a compelling argument for placing *Adunator* within Lipotyphla, let alone as a stem erinaceid. One of these studies, Novacek *et al.* [16], states that *Adunator* is in "limbo between primitive insectivorans and primitive condylarths", and "we do not exclude the possibility that *Adunator* is a very primitive hyopsodontid". The other study, Smith *et al.* [17], only sampled *Adunator* alongside the nyctithere, *Leptacodon* (which was assumed to be 'basal') and five species of the putative lipotyphlan fossil genus *Macrocranion* in unrooted maximum parsimony analyses. Hence, Smith *et al.* [17] could only be used to infer whether the affinities of *Adunator* lie within or outside the sampled genus *Macrocranion*. Another more recent study [18], which admittedly also sampled few lipotyphlans, instead places *Adunator* with elephant shrews and several enigmatic Paleogene taxa. The affinities of *Adunator* remain unclear.

Even if *Adunator* could be confidently assigned as a lipotyphlan, the 61.6 Ma fossil date is consistent with our dR40 timetrees, falling within the 95% CIs for Lipotyphla (Auto: 59.4-62.9 Ma, Ind: 59.0-62.6 Ma) and for Erinaceidae/Soricidae – Talpidae (Auto: 58.7-62.3 Ma, Ind: 58.4-61.9 Ma), but not for Erinaceidae-Soricidae (Auto: 55.0-59.3 Ma, Ind: 54.8-58.8 Ma).

10. Lorisiformes (*Saharagalago*, 38 Ma): As discussed in the main text, *Saharagalago* is known from just two molars. Phillips ([1], fig. 2) showed this calibration to be an extreme outlier for apparent dating error (or rate distortion). The most likely explanation is that *Saharagalago* (and *Karanisia* from the same locality) falls outside Lorisiformes, as two recent phylogenetic analyses found [19, 20].

11. Lagomorpha (Vastan ankle bones, 53.7 Ma): In the main text we argue that the Vastan ankle bones do not provide a robust reference for the minimum age of crown lagomorphs. Firstly, Rose *et al.* [21] did not consider sampling error and noted that the morphological signal may be confounded by functional similarities. Secondly, Zhang *et al.*'s [22] μ CT scans show that a key character, the calcaneal canal, is also present in stem lagomorphs. Our reanalysis of Rose *et al.* [21] excluding the calcaneal canal character places the Vastan ankle bones outside crown lagomorphs, although their affinities remain statistically unresolved (fig. S1).

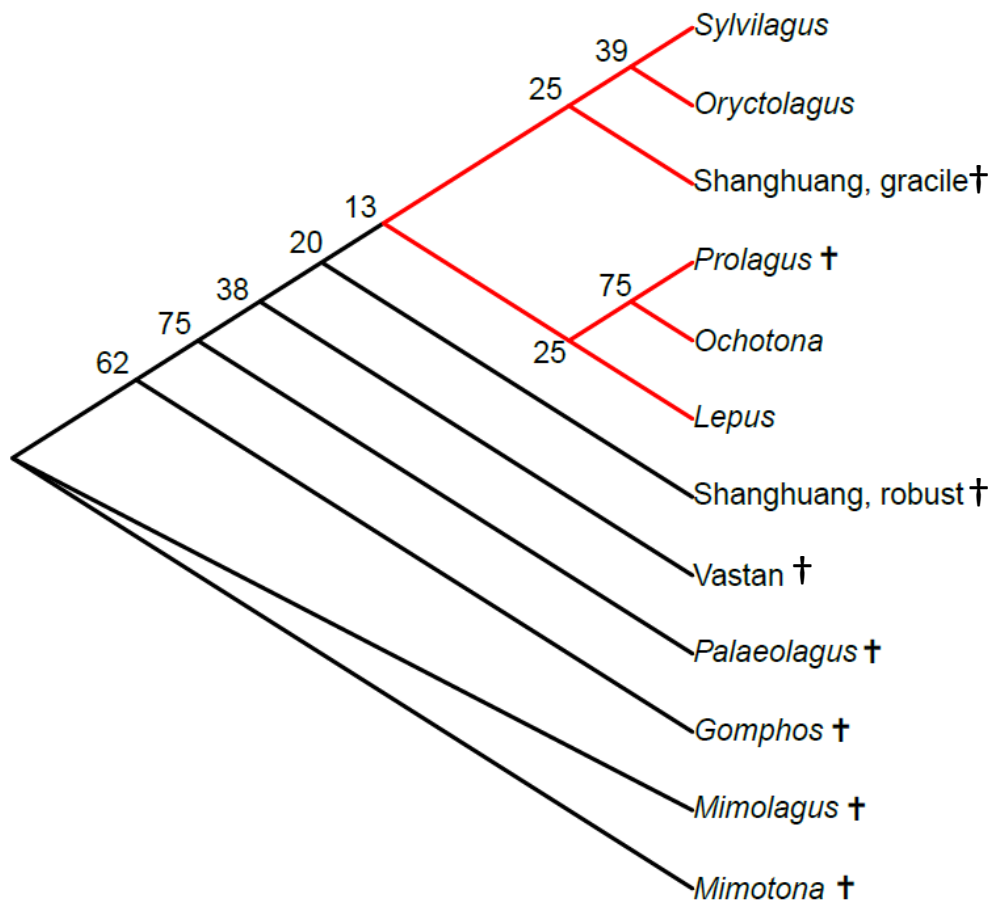


Figure S1: Lagomorph phylogeny from 500 maximum parsimony bootstrap pseudoreplicates, with the crown branches indicated red. The very large number of equally parsimonious trees among Rose *et al.*'s [21] full (71 taxa) dataset may explain why they did not bootstrap their data. However, bootstrapping becomes tractable when including only the lagomorphs.

12. Aplodontidae – Sciuridae (*Spurimus*, 45.7 Ma): *Spurimus* has been excluded from most phylogenetic analyses. When *Spurimus* was included by Heissig [23] it was placed with primitive ischyromyids that fall far deeper in the rodent phylogeny when datasets have been extended beyond dental characters [24, 25]. Korth's [26] placement of *Spurimus* as an aplodontoid was a "secondary" derivation, based on its potential as an ancestor to *Pelycomys*, and not based on any

unambiguous synapomorphies. Hence, *Spurimus* is not acceptable as a reference taxon for strong priors. Even the placement of *Pelecomys* is somewhat ambiguous. Hopkins [27] showed affinities of several putative aplodontoids, including *Pelycomys* lying outside Aplodontoidea, and regardless of the root position, being separated from these by ischyromyids (which may not even be crown rodents). Vianey-Liaud *et al.* [28] did group *Pelycomys* with aplodontoids, but did not include Springer *et al.*'s [3] poorly known reference taxon, *Spurimus* or the apparently non-monophyletic ischyromyid taxa that were included by Hopkins [27].

13. Geomyoidea (*Proheteromys*, 31.4 Ma): The heteromyid affinities of *Proheteromys* within Geomyoidea have been questioned by Wahlert [29], who was unable to rule out stem-geomyoid placement. This may in part be explained by Korth and Samuels [30] removing some species described as members of *Proheteromys* and placing them as tentative florentiamyids, which may be stem or crown geomyoids. Korth and Samuels [30] then consider that the earliest *Proheteromys* appearances are Arikarean (Ar1), and at least as old as the Blue Basin Tuff dated 28.8 Ma [31]. However, Korth [32] also places *Proharramys* as a heteromyid, and based on his interpretation of the Cedar Pass Fauna as Whitneyan, this would place a minimum bound on Geomyoidea of 30.6 Ma. However, as for *Proheteromys*, placement of *Proharramys* as a basal heteromyid is based on similarity criteria, and as far as we are aware has not been confirmed with phylogenetic analyses (matrix-based or otherwise). It is premature to calibrate or validate molecular dating with these taxa.

Even if *Proheteromys* or *Proharramys* could be assigned to Heteromyidae with confidence, the 30.6 Ma (or 31.4 Ma) fossil date is consistent with our dR40 independent rates timetree (95% CI 24.6-32.2 Ma), but not the autocorrelated rates timetree (95% CI 21.5-27.6 Ma).

14. Rhinolophidae-Hipposideridae (*Hipposideros*, 38 Ma): Springer *et al.* [3] cite papers that include bat fossil record compendia as secondary references for the first appearance of *Hipposideros*. But see our discussion on Rhinolophidae-Hipposideridae in Supplemental file 2: “New calibrations” (7. Rhinolophidae - Hipposideridae), for problems associated with calibrating this clade. Even if these fossils could be assigned with confidence, the 38 Ma fossil date is consistent with our dR40 autocorrelated rates timetree (95% CI 34.7-38.7 Ma), but not the independent rates timetree (95% CI 30.7-34.9 Ma).

Table S1. Molecular dates from Phillips’ [1] initial (tree 1) and final (tree 2) timetrees, compared with Springer *et al.*’s [3] fossil minima for the eight proposed “zombie” lineages among smaller sized, shorter longevity mammal clades that were not included in the above section, *Incorrect or poorly supported fossil placements*. Molecular date 95% CIs are shown in green when they overlap or pre-date proposed fossil minima and in red when they post-date the proposed fossil minima (inducing “zombie” lineages).

Clade	Springer <i>et al.</i> ’s [3] fossil minimum (Ma)	Reference fossil	Phillips (2016) Tree 1, 95% CI	Phillips (2016) Tree 2, 95% CI
Tardigrada	15.97	<i>Imagocnus</i>	11.7-17.1	15.1-20.6
Xenarthra	47.8	<i>Riostegotherium</i>	42.5-51.4	58.0-60.8
Carnivora	38	<i>Hesperocyon</i>	34.5-39.1	43.4-47.6
Fereuungulata	64 ^a	<i>Ravenictis</i>	59.0-64.1	64.2-65.4
Scrotifera	64 ^a	<i>Ravenictis</i>	59.1-64.2	64.3-65.5
Octodontoidea	24.5 ^b	<i>Sallamys</i> , <i>Xylechimys</i> , <i>Deseadomys</i>	21.9-24.9	24.4-27.5
Feliformia	28.1 ^c	<i>Proailurus</i> , <i>Stenogale</i>	22.3-26.1	30.3-35.3
Mustelidae/Ailuridae / Procyonidae	24.8 ^d	<i>Promartes</i>	17.4-20.5	28.5-30.7

^aThe appropriate date is 63.3 Ma for *Ravenictis*, and the phylogenetic placement of this fossil taxon is highly speculative; see “Incorrect or poorly supported fossil placements” (4. Ferae).

^bAmong two recent papers, Verzi *et al.* [33] place all three of these reference taxa within crown Octodontoidea, while Arnal and Vucetich [34] place each of these reference taxa outside or in a basal polytomy with crown Octodontoidea. In our bootstrap analyses of these datasets, neither resolves any of the reference taxa as either within or outside the octodontoid crown (not shown).

^cThere is uncertainty over the placements of *Proailurus* and *Stengale*, see Supplemental file 2: “New Calibrations” (3. Feliformia).

^dThere is uncertainty over the placement of *Promartes*, see Supplemental file 2: “New Calibrations” (4. Musteloidea).

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