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Editor's Choice Article

Waking the undead: Implications of a soft explosive model for the timing of placental mammal diversification

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ABSTRACT

The explosive, long fuse, and short fuse models represent competing hypotheses for the timing of placental mammal diversification. Support for the explosive model, which posits both interordinal and intraordinal diversification after the KPg mass extinction, derives from morphological cladistic studies that place Cretaceous eutherians outside of crown Placentalia. By contrast, most molecular studies favor the long fuse model wherein interordinal cladogenesis occurred in the Cretaceous followed by intraordinal cladogenesis after the KPg boundary. Phillips (2016) proposed a soft explosive model that allows for the emergence of a few lineages (Xenarthra, Afrotheria, Euarchontoglires, Laurasiatheria) in the Cretaceous, but otherwise agrees with the explosive model in positing the majority of interordinal diversification after the KPg mass extinction. Phillips (2016) argues that rate transference errors associated with large body size and long lifespan have inflated previous estimates of interordinal divergence times, and further suggests that most interordinal divergences are positioned after the KPg boundary when rate transference errors are avoided through the elimination of calibrations in large-bodied and/or long lifespan clades. Here, we show that rate transference errors can also occur in the opposite direction and drag forward estimated divergence dates when calibrations in large-bodied/long lifespan clades are omitted. This dragging forward effect results in the occurrence of more than half a billion years of 'zombie lineages' on Phillips' preferred timetree. By contrast with ghost lineages, which are a logical byproduct of an incomplete fossil record, zombie lineages occur when estimated divergence dates are younger than the minimum age of the oldest crown fossils. We also present the results of new timetree analyses that address the rate transference problem highlighted by Phillips (2016) by deleting taxa that exceed thresholds for body size and lifespan. These analyses recover all interordinal divergence times in the Cretaceous and are consistent with the long fuse model of placental diversification. Finally, we outline potential problems with morphological cladistic analyses of higher-level relationships among placental mammals that may account for the perceived discrepancies between molecular and paleontological estimates of placental divergence times.

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1. Introduction

The radiation of placental mammals in relationship to the KPg boundary (~66 Ma) is one of the most contentious problems in paleontology and systematics. Archibald and Deutschman (2001) suggested three competing models for placental diversification.

Abbreviations: KPg, Cretaceous–Paleogene; PAML, phylogenetic analysis by maximum likelihood; PAUP, phylogenetic analysis using parsimony.

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The explosive model, which is favored by many paleontologists (e.g., O'Leary et al., 2013), posits interordinal and intraordinal diversification after the KPg boundary. This model is underpinned by morphological cladistic analyses that place Cretaceous eutherians outside of crown Placentalia (Wible et al., 2009; O'Leary et al., 2013; Zhou et al., 2013; Chester et al., 2015). The long fuse model agrees with the explosive model in positing most intraordinal diversification after the KPg boundary, but positions nearly all interordinal diversification before the KPg boundary. Support for the long fuse model derives from a wide array of molecular timetree

analyses (Hasegawa et al., 2003; Springer et al., 2003, 2005; Delsuc et al., 2004; Meredith et al., 2011; dos Reis et al., 2012; Lartillot and Delsuc, 2012; Slater, 2013; Emerling et al., 2015; Foley et al., 2016; Tarver et al., 2016). Archibald and Deutschman's (2001) third model, the short fuse model, posits interordinal and some intraordinal diversification well before the KPg boundary. This model is supported by Bininda-Emonds et al.'s (2007) analysis of a supertree phylogeny with local molecular clocks.

Advocates of the explosive model have argued that both long fuse and short fuse models are in direct conflict with the fossil record because of their implied ghost lineages (O'Leary et al., 2013). However, ghost lineages are a logical extension of an incomplete fossil record and cannot be dismissed out of hand (Springer and Lilje, 1988; Strauss and Sadler, 1989; Marshall, 1990; Springer, 1990; Teeling et al., 2005; Johnson et al., 2006; Meredith et al., 2008). Also, the explosive model is predicated on the accuracy of morphological cladistic analyses that place Cretaceous eutherians outside of Placentalia. Morphological cladistics has a poor track record of recovering superordinal clades of even extant placental mammals and is prone to cluster taxa together based on ecomorphological convergence. Furthermore, most morphological studies utilize matrices in which many of the taxa (fossils) are missing the majority of the characters because of incomplete fossil preservation (Springer et al., 2007a, 2008, 2013; Sansom and Wills, 2013). Finally, the explosive model requires viral-like rates of evolution in mammalian lineages during the interval immediately following the KPg boundary (Springer et al., 2013).

Most recently, Phillips (2016) proposed a fourth model, the soft explosive model, which allows for cladogenic separation of the four major clades of placental mammals (Afrotheria, Xenarthra, Laurasiatheria, Euarchontoglires) in the Cretaceous, but otherwise agrees with the explosive model in positioning the bulk of interordinal diversification in Placentalia after the KPg boundary. Phillips (2016) argued that support for the long fuse model in previous timetree analyses results from rate transference errors that inflate estimates of interordinal divergence times, and that most interordinal divergences are positioned after the KPg boundary when rate transference errors are avoided by eliminating calibrations in large-bodied/long lifespan clades that are the source of these errors. Here, we discuss fundamental problems with Phillips' (2016) timetree analyses and show that they result in 'zombie' lineages, which are the antithesis of ghost lineages and occur when estimated divergence dates are younger than minimum ages implied by the fossil record. We show that when divergence dates in large-bodied/long lifespan clades are not calibrated and are underestimated (i.e., too young), as in Phillips (2016), they can drag forward deeper nodes and result in estimates of interordinal divergence times that are in direct conflict with the fossil record. We also present the results of new timetree analyses that circumvent the rate transference problem highlighted by Phillips (2016) by deleting taxa that exceed thresholds for body size and lifespan. The results of these analyses again position all interordinal divergence times in the Cretaceous and support the long fuse model of placental diversification. Finally, we review potential problems with the results of morphological cladistic analyses of higher-level relationships among placental mammals that challenge the stem status of all Cretaceous placentals.

2. Methods

2.1. Molecular dating analyses

Molecular data analyses with Meredith et al.'s (2011) DNA data set were performed with the mcmctree package in PAML 4.8 (Yang, 2007). Analyses were performed with both autocorrelated and

independent rates, as well as with hard-bounded and soft-bounded calibrations. Each mcmctree analysis was run twice to check for convergence. As in Meredith et al. (2011), each gene was allowed to have its own model of sequence evolution following Meredith et al. (2011). We set 1 time unit = 100 million years. Analyses were run with cleandata = 0. Shape (α) and scale (β) parameters for rgene_gamma, which describes the gamma prior for the overall rate parameter μ , were as in Meredith et al. (2011). Similarly, shape and scale parameters for sigma_gamma, which describes the gamma prior for the rate-drift parameter (σ^2), were taken from Meredith et al. (2011). Analyses were run for 100,000 generations following a burn-in of 10,000 generations. Each chain was sampled every 20 generations.

Timetree analyses with too few calibrations in large-bodied/long lifespan clades (Phillips, 2016) may drag divergence times of deeper nodes toward the present owing to underestimation of divergences in the large-bodied clades. Instead of dropping all or most calibrations in large-bodied clades, which would have the effect of forcing rates from small-bodied taxa onto their branches, we employed an alternate strategy (Springer et al., 2003) and excluded taxa with average adult body mass >10 kg and/or maximum longevity >40 years (thresholds suggested by M. Phillips, pers. comm.). Body size data are from Pantheria (Jones et al., 2009) and longevity data are from Magalhães and Costa (2009). The resulting topology included 122 of 169 taxa from Meredith et al. (2011) and excluded all members of Proboscidea, Sirenia, and Perissodactyla; all Cetartiodactyla except for *Tragulus* (mouse-deer); all Anthroproidea with the exception of *Callithrix* (marmoset); nine of 16 carnivorans including all three pinnipeds and *Ailuropoda* (giant panda); and assorted taxa in other clades such as *Pteropus* (flying fox), *Myrmecophaga* (giant anteater), and *Hydrochoerus* (capybara). After excluding these taxa, this 122-taxon data set retained at least one representative of all placental orders except for Proboscidea, Sirenia, Tubulidentata, and Perissodactyla. Analyses were performed with an updated set of 62 calibrations that reflect newly described fossils and recommendations from a variety of other timetree studies (Table 1). Analyses were performed with all four combinations of hard-bounded versus soft-bounded constraints and autocorrelated versus independent rates. All four timetrees are available at TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S19854>).

2.2. Parsimony analysis

Maximum parsimony analyses of Wible et al.'s (2009) data set were performed with PAUP* 4.0a147 (Swofford, 2002). Analyses were performed after excluding *Alymlestes* because of a high percentage (94.9) of missing data for this taxon. Searches for optimal trees, with or without phylogenetic constraints, employed 100 random addition sequences with tree-bisection and reconnection branch swapping. Trees with minimum branch lengths of zero were collapsed using the "-amb" option in PAUP. Templeton and winning-sites tests were also performed with PAUP to compare parsimony scores for different trees to each other.

2.3. Molecular timetree diversification patterns and the fossil record

We used the R package paleobioDB (Varela et al., 2014) to acquire eutherian fossil data from each geological stage ranging from the Berriasian (Lower Cretaceous) to the Priabonian (Eocene). For each stage, we downloaded all records of eutherian families, genera, and species, recorded the standing diversity for each taxon, and quantified the number of new taxa in each category. We estimated new lineage accumulation rates for each stage by dividing the number of new lineages by the stage's time duration, and then calculated the percentage increase or decrease across each stage

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