MBE Advance Access published July 27, 2013

Making the Impossible Possible: Rooting the Tree of Placental Mammals

Emma C. Teeling[1] and S. Blair Hedges*[,2]

[1]School of Biology and Environmental Science, University College Dublin, Dublin, Ireland

[2]Department of Biology, Pennsylvania State University, University Park

***Corresponding author:** E-mail: sbh1@psu.edu.

Associate editor: Sudhir Kumar

Abstract

Untangling the root of the evolutionary tree of placental mammals has been nearly an impossible task. The good news is that only three possibilities are seriously considered. The bad news is that all three possibilities are seriously considered. Paleontologists favor a root anchored by Xenarthra (e.g., sloths and anteater), whereas molecular evolutionists have favored the two other possible roots: Afrotheria (e.g., elephants, hyraxes, and tenrecs) and Atlantogenata (Afrotheria + Xenarthra). Now, two groups of researchers have scrutinized the largest available genomic data sets bearing on the question and have come to opposite conclusions, as reported in this issue of *Molecular Biology and Evolution*. Needless to say, more research is needed.

***Key words:* mammals, phylogeny, genome, biogeography, evolution.**

Editorial

Living mammals (~5,500 species) exist in every biome on earth and are considered to be one of the most phenotypically diverse groups of vertebrates (Wilson and Reeder 2005). Approximately 95% of mammals are placentals, and their evolutionary relationships have rapidly come into focus through dozens of molecular analyses over the past two decades. By any standard, the change has been revolutionary, from the paleontological view of an explosive, post-dinosaur radiation with hoofed mammals (e.g., horses, cattle, and elephants) joined in a group (Novacek 1999) to the molecular view of deeper origins, reflecting Earth history (Hedges et al. 1996; Meredith et al. 2011). However, despite the abundance and congruence of most molecular phylogenetic studies there are still major nodes in the molecular tree of mammals that remain unresolved and highly controversial.

Two articles in this issue (Morgan et al. 2013; Romiguier et al. 2013) address one such node, the root of the tree of living placental mammals, and come to different conclusions. The timing of the splitting event—approximately 100 Ma based on molecular clocks—is not in debate, at least among molecular evolutionists (Hedges et al. 1996; Meredith et al. 2011). Rather the question is the branching order of the three major lineages: afrotherians (e.g., elephants, manatees, hyraxes, elephant shrews, aardvarks, and tenrecs), xenarthrans (sloths, anteaters, and armadillos), and boreoeutherians (all other placentals; fig. 1). If we speak of the root as the earliest splitting branch with fewest species, paleontologists prefer a xenarthran root (O'Leary et al. 2013), whereas molecular studies have equally supported the two other possibilities: an Afrotherian root and Atlantogenata (Afrotheria + Xenarthra). Researchers have found this node to be one of the "hardest" to resolve in the mammalian phylogenetic tree, if not impossible (Nishiara et al. 2009). The hope has been that large phylogenomic studies, despite their statistical challenges (Kumar et al. 2012), will solve this puzzle (Murphy et al. 2007).

Both Morgan et al. (2013) and Romiguier et al. (2013) concatenate and analyze some of the largest phylogenomic mammalian data sets to date. Morgan et al. (2013) utilize heterogenous models to account for tree and dataset heterogeneity and find strong support for Atlantogenata. They argue that the "unresolvability" of the placental root stems from the past use of suboptimal models and smaller data sets with little power. Romiguier et al. (2013), on the other hand, divide their data set into GC- and AT-rich genes, analyzing the support for the alternate roots. They show that GC-rich genes are most likely to support egregious topologies and suffer from long-branch attraction, whereas AT-rich genic regions had a five times lower error rate. Interestingly, AT-rich genes support an Afrotherian root, whereas GC-rich genes support Atlantogenata, leading Romiguier et al. (2013) to conclude that the placental rooting conflict stems from unreliable GC-rich genes being used to build phylogenies. This finding could explain why similar coalescent analyses of different regions of the genome supported different roots: ultraconserved noncoding elements predominantly found in AT-rich isochores support an Afrotherian rooting (McCormack et al. 2012), whereas coding regions with higher GC content support Atlantogenata (Song et al. 2012). Considering the current deluge of whole genome data, it is important to continue developing methods like these to analyze heterogeneous data sets correctly and, in some cases, combining methods may be fruitful.

What is the significance of knowing the correct root? First, it may help us understand how traits evolved that are shared among major groups of placental mammals. Second, it will have biogeographic implications. The fact that xenarthrans and afrotherians are so closely tied to South America and

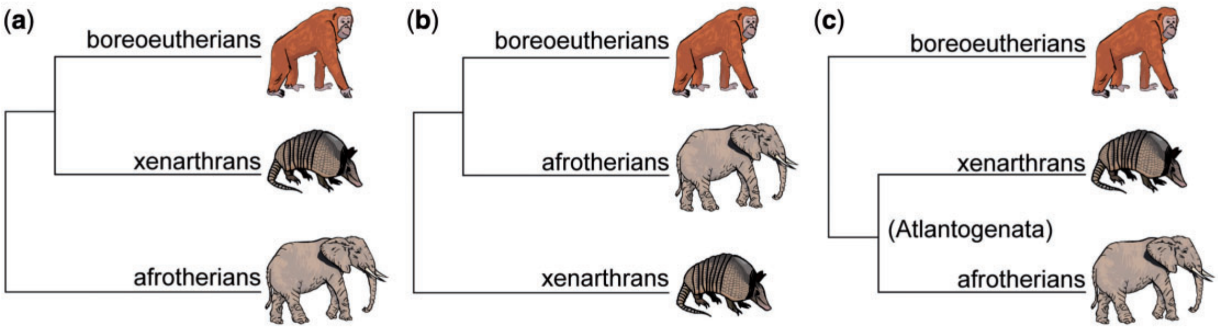

Fig. 1. The root of the evolutionary tree of living placental mammals. (*a*) Afrotherian root, (*b*) Xenarthran root, and (*c*) Atlantogenatan root.

Africa, respectively, continents that separated at about the same time (~100 Ma) as those groups, is hard to ignore, suggesting that some vicariance was involved regardless of the root. If, on the other hand, Afrotheria arose in the New World (O'Leary et al. 2013), then the biogeographic story is not as simple. Clearly, we have more to learn about the early evolution of placental mammals.

References

Hedges SB, Parker PH, Sibley CG, Kumar S. 1996. Continental breakup and the ordinal diversification of birds and mammals. *Nature* 381: 226–229.

Kumar S, Filipski AJ, Battistuzzi FU, Pond SLK, Tamura K. 2012. Statistics and truth in phylogenomics. *Mol Biol Evol.* 29:457–472.

McCormack JE, Faircloth BC, Crawford NG, Gowaty PA, Brumfield RT, Glenn TC. 2012. Ultraconserved elements are novel phylogenomic markers that resolve placental mammal phylogeny when combined with species tree analysis. *Genome Res.* 22:746–754.

Meredith RW, Janecka JE, Gatesy J, et al. (22 co-authors). 2011. Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* 334:521–524.

Morgan C, Foster PG, Webb A, Pisani D, McInerney JO, O'Connell M. 2013. Heterogeneous models place the root of the placental mammal phylogeny. *Mol Biol Evol.* Advance Access published June 29, 2013, doi:10.1093/molbev/mst117.

Murphy WJ, Pringle TH, Crider TA, Springer MS, Miller W. 2007. Using genomic data to unravel the root of the placental mammal phylogeny. *Genome Res.* 17:413–421.

Nishihara H, Maruyama S, Okada N. 2009. Retroposon analysis and recent geological data suggest near simultaneous divergence of the three superorders of mammals. *Proc Natl Acad Sci U S A.* 106: 5235–5240.

Novacek MJ. 1999. 100 million years of land vertebrate evolution: the cretaceous-early tertiary transition. *Ann Missouri Bot Garden.* 86: 230–258.

O'Leary MA, Bloch JI, Flynn JJ, et al. (23 co-authors). 2013. The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* 339:662–667.

Romiguier J, Ranwez V, Delsuc F, Galtier N, Douzery EJ. 2013. Less is more in mammalian phylogenomics: AT-rich genes minimize tree conflicts and unravel the root of placental mammals. *Mol Biol Evol.* Advance Access published June 29, 2013, doi:10.1093/molbev/mst116.

Song S, Liu L, Edwards SV, Wu S. 2012. Resolving conflict in eutherian mammal phylogeny using phylogenomics and the multispecies coalescent model. *Proc Natl Acad Sci U S A.* 109:14942–14947.

Wilson DE, Reeder DM, editors 2005. Mammal species of the world. Baltimore (MD): Johns Hopkins University Press.