Technical Comment on "The Placental Mammal Ancestor and the Post −K-Pg Radiation of Placentals"

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Technical Comment on "The Placental Mammal Ancestor and the Post–K-Pg Radiation of Placentals"

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O'Leary et al. (Research Article, 8 February 2013, p. 662) examined mammalian relationships and divergence times and concluded that a single placental ancestor crossed the Cretaceous-Paleogene (K-Pg) boundary. This conclusion relies on phylogenetic analyses that fail to discriminate between homology and homoplasy and further implies virus-like rates of nucleotide substitution in early Paleocene placentals.

O'Leary *et al.* (*1*) analyzed mammalian relationships using a large supermatrix that combined phenomic and genomic data. By contrast with molecular clock studies that support Cretaceous interordinal diversification (*2*, *3*), O'Leary *et al.* (*1*) suggest "that ~10 interordinal speciation events might have occurred in as little as 200,000 years" just after the Cretaceous-Paleogene (K-Pg) extinction. These conclusions are underpinned by phylogenetic analyses that fail to discriminate between common ancestry and convergent evolution and imply implausible rates of molecular evolution in mammalian genomes.

Morphological and molecular data often result in similar topologies (*4*), but there is strong discordance in the case of higher-level relationships among placental mammals (*5*). This is not surprising, given that the global scope of mammalian evolution includes similar habitats in far-flung regions of Earth that promote the evolution of ecological vicars and thus morphological convergence—for example, myrmecophagy has evolved independently in Xenarthra, Pholidota, and Tubulidentata. Darwin (*6*) was aware of this problem and remarked that adaptation to similar conditions in distinct lineages will result in external resemblances that will conceal, rather than reveal, genealogical relationships.

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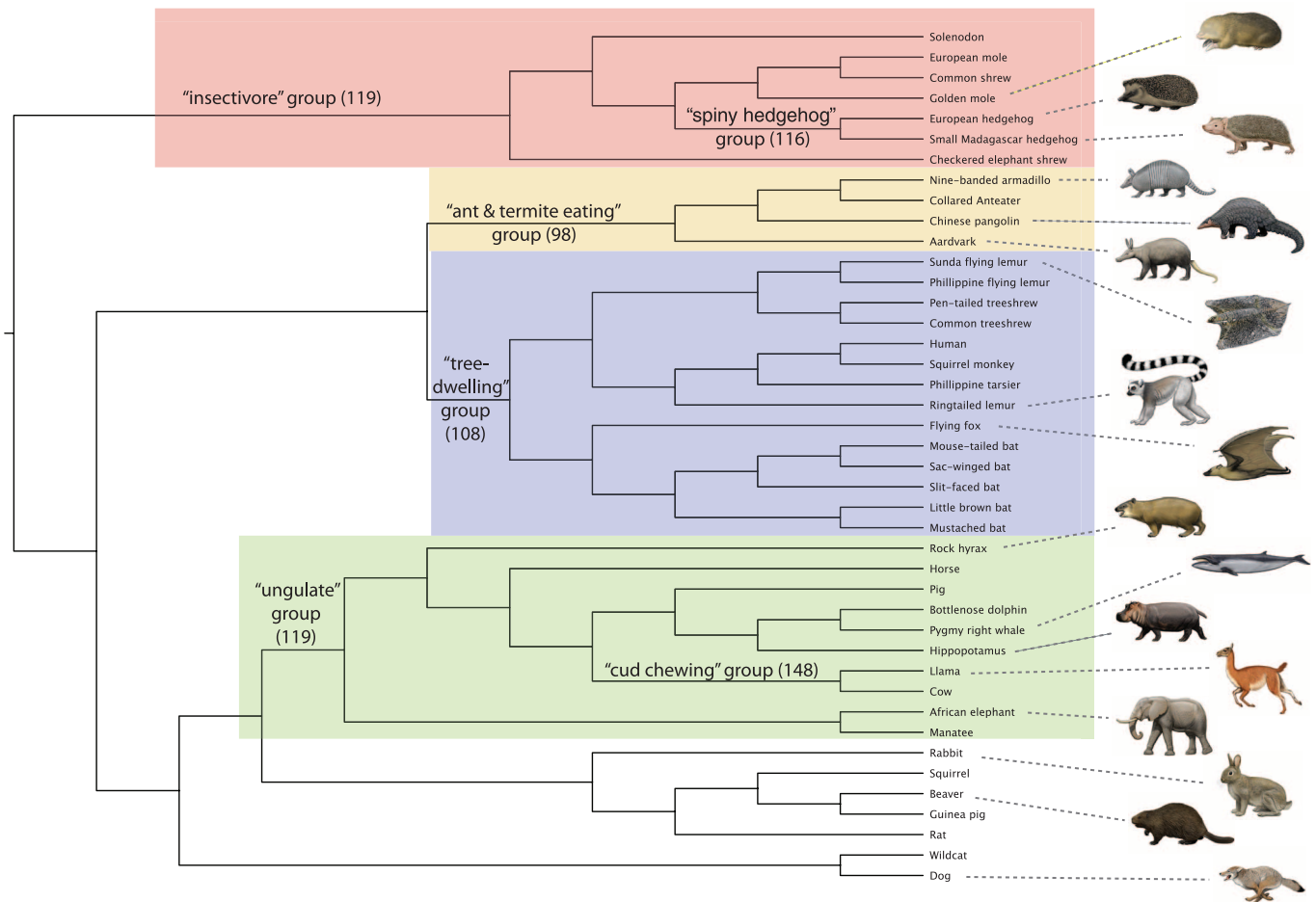*Corresponding author. E-mail: mark.springer@ucr.edu (M.S.S.); wmurphy@cvm.tamu.edu (W.J.M.)

Fig. 1. Polyphyletic ecomorphology groups. Polyphyletic ecomorphology groups from figure S2 (phenomic tree) of O'Leary *et al.* (*1*). Fossils and nonplacentals were pruned to highlight relationships among living placentals. Numbers next to groups indicate the number of "apomorphies" with Deltran optimization (*13*). [Paintings by Carl Buell]
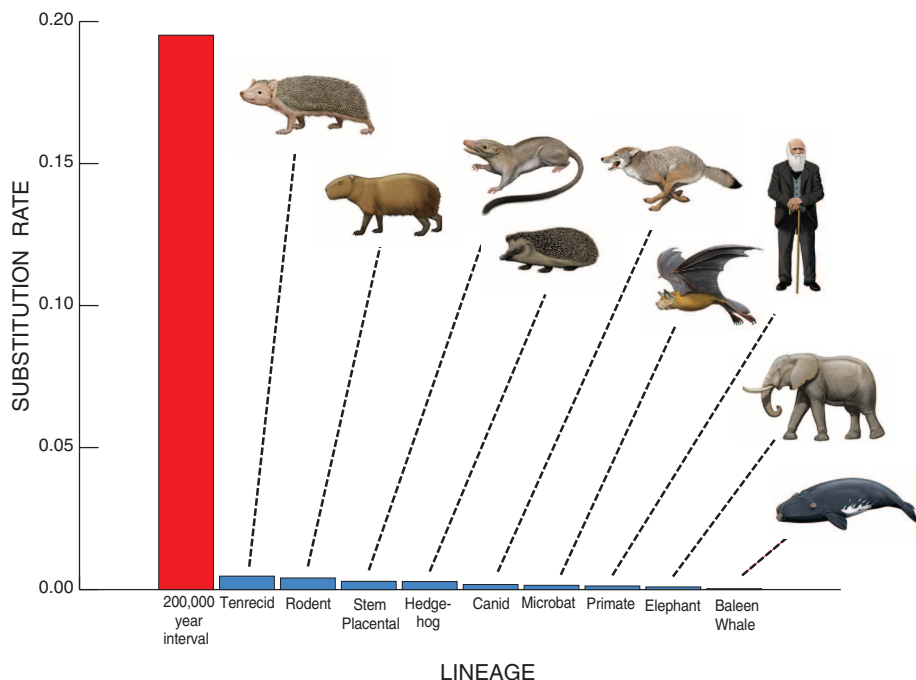
Fig. 2. Substitution rates. Substitution rates (substitutions per nucleotide per million years) for 26 nuclear genes based on O'Leary *et al.*'s (*1*) hypothesis that ~10 interordinal speciation events occurred within 200,000 years. The rate for the 200,000-year interval (red bar) was calculated for the internal branches that lead from the placental common ancestor to the common ancestor of Macroscelidea and Afrosoricida, assuming ages of 64.95 and 64.75 million years, respectively, for these nodes (*1*). Other rates (blue bars) were calculated based on ages in table 1 and table S2 of O'Leary *et al.* (*1*). Molecular branch lengths are from Meredith *et al.*'s (*2*) DNA tree (TreeBase S11872). "Stem placental" is the branch leading from the most recent common ancestor of Theria to that of Placentalia. [Paintings by Carl Buell]

O'Leary *et al.*'s (*1*) unprecedented phenomic data set is ~10 times as large as its predecessors and provides an exceptional opportunity to examine whether phenome-genome antagonism in mammalian phylogeny reconstruction is a consequence of small sample size in previous phenomic data sets. However, O'Leary *et al.*'s massive (*1*) phenomic data set only supports 20 of 44 nodes within Mammalia that are upheld by molecular data [figure S2 in (*1*)], and the morphology tree provides robust support for numerous polyphyletic taxa (Fig. 1). O'Leary *et al.*'s (*1*) phenomic data set therefore provides additional support for the inadequacy of morphology in higher-level mammalian phylogenetics (*7*). This problem is rectified for living taxa by combining phenomic and genomic data, but genomic data are unavailable for most fossils.

O'Leary *et al.*'s (*1*) data set also includes highly diachronous terminals, including extant species and ~200-million-year old Mesozoic fossils. The inclusion of these taxa in a single analysis raises the possibility of clustering of the Recent, which is a form of long-branch attraction, and may be exacerbated if parallel evolutionary constraints have acted on the phenomes of living taxa (*8*, *9*).

O'Leary *et al.* (*1*) suggest that ~10 interordinal cladogenic events may have occurred in the 200,000 years just after the K-Pg extinction. This hypothesis implies that substitution rates were accelerated by a factor of more than 60 relative to the ancestral placental rate and were similar to long-term substitution rates in double-stranded DNA viruses (*10*, *11*) (Fig. 2). These results require unrealistic mammalian generation times on

the order of a few days (or hours), low-fidelity DNA polymerases, or genome-wide positive selection on the affected branches. Currently, there is no evidence to support these hypotheses. Instead, the extension of a few ghost lineages into the Cretaceous is a much simpler hypothesis. O'Leary *et al.*'s (*1*) nodal ages should logically be viewed as minima rather than actual divergence times.

The discordance between phenomic and genomic topologies (*1*) suggests that caution should accompany the interpretation of phylogenies based on combined data. The nonspecialist is left to assume that the combined tree is a robust phylogeny of living and extinct mammals. However, given the pervasive convergence in morphology, the placement of fossil taxa for which molecular data are unavailable is uncertain (*7*, *12*). Similarly, estimates of divergence times that discount molecular branch lengths are unsatisfactory.

Careful examination of O'Leary *et al.*'s (*1*) data and implied interordinal divergence times suggests that molecular phylogenies and time trees (*2*, *3*) are more credible than phenome-based phylogenies of distantly related mammalian taxa whose evolution has been strongly influenced by ecomorphological convergence.

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