



Editorial

Tree thinking and species delimitation: Guidelines for taxonomy and phylogenetic terminology

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ABSTRACT

By tradition, phylogenetic trees are presented in such a way that species-poor taxa are placed on the left side and their more diverse sister taxa on the right (usually with humans on the far right). This often leads to reading the tree as a "ladder of progress" from left (allegedly primitive, basal or even ancestral) to right (allegedly advanced, derived, descendant). Although biologically and logically wrong and often bemoaned, the evolutionary literature teems with language perpetuating this phylogenetic misconception. Likewise, the splitting of one into two or more species based on different versions of the Phylogenetic Species Concept has recently found a growing number of adherents, resulting, in the eyes of many, in a trivialization of the species category ("taxonomic inflation"). This editorial briefly summarizes these phylogenetic and taxonomic issues and provides guidelines to authors submitting their studies to *Mammalian Biology* in order to avoid errors in phylogenetic discussions and to do justice to the fundamental nature of species in biology.

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Introduction

This editorial is aimed at authors submitting their papers to *Mammalian Biology*. We receive quite a number of manuscripts dealing with phylogenetic relationships among mammal taxa and/or the splitting and description of (new) mammalian species. Most of these papers are good studies, reporting methodologically sound analyses and results and drawing appropriate conclusions from them. There are, however, even in otherwise good studies, often very specific shortcomings, errors or inconsistencies. With respect to phylogenetics, they usually result from an erroneous interpretation of trees as "ladders of progress" resulting in, subsequently, phylogenetically inappropriate terminology ("higher", "lower", "basal" and "ancestral" groups). In taxonomy and species splitting/description, matters are more complicated and less straightforward, but using monophyly/paraphyly of gene trees or mere diagnosability as species criteria will inevitably lead to taxonomic inflation (Isaac et al. 2004). This kind of taxonomic proliferation is strongly discouraged here, and at the very least, authors should explicitly name their criteria for species status (i.e. the species concept adopted). Both topics are too complex to be covered in detail in an editorial like this, and below only a few general

points and guidelines will be given. None of the points mentioned here are novel insights (for tree interpretation, see Baum et al. 2005; Omland et al. 2008; there is even a very similar editorial to this one, published for the same reasons: Krell and Cranston 2004; for the species debate, the list of publications is all but infinite, cf. Heller et al., 2013, 2014; Zachos et al. 2013a; Zachos 2015, in press; for an opposing view, see Groves 2013; Cotterill et al. 2014). However, the same issues and misconceptions arise again and again and are perpetuated in quite a number of papers, so that emphasis and reinforcement of the guidelines below are still needed. *Authors submitting phylogenetic and taxonomic papers to Mammalian Biology should follow them whenever possible.*

Phylogenetic trees and how not to read them

Phylogenetic trees depict evolutionary relationships among taxa. In cladograms, the only information conveyed is the topology itself, i.e. the succession of branching events resulting in a nested pattern of relationships. Other kinds of phylogenetic trees also contain information on evolutionary rates (depicted by branch lengths, phylograms) or absolute time (chronograms). In any case, it never makes a difference which taxa are drawn on the right side of the tree and which on the left (the same holds for the upper and lower sides in horizontal trees). Relationships (i.e. the recency of common ancestors) are only represented by the succession of

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splitting events, and therefore, in a vertical tree, only the *y*-axis (time) contains information. The *x*-axis does not contain directional information, i.e. whether a group is more basal than or ancestral to another! (In horizontal trees, it is the other way around, but I will only discuss vertical trees as shown in Fig. 1). Phylogenetic trees consist of branching lineages, each node (unless it is a polytomy) gives rise to two sister taxa. Sister taxa are, by definition, of the same age, and none of them can be more basal than or even ancestral to the other. Which of the two is depicted on the right and which on the left side is irrelevant and just a matter of convention or, perhaps more precisely, tradition. The latter has it that species-poor lineages (or those falsely deemed more “primitive”) are usually shown on the left side, the species-rich sister taxa on the right (“ladderize right” trees). This invites a common misconception, namely to read or interpret trees from “left to right” and to conclude that there is an element of progress from left to right when there is not (the so-called “primitive lineage fallacy”, Omland et al. 2008). All branches can be freely rotated around the nodes without changing the topology or any other information content of the tree. Consequently, all three trees in Fig. 1 are actually exactly the same tree, although we are clearly more used to seeing version A than B or C. Interpreting trees as ladders of progress also introduces another linguistic mistake: taxa do not branch off the tree. This would imply a main trunk, i.e. a main direction of the tree (as in the famous Tree of Life by Ernst Haeckel). Such a main trunk, however, does not exist; all possible trajectories from the root of the tree to any of its tips are equivalent! There is only branching (into sister groups), no branching off. In the words of Omland et al. (2008, p. 863): “Stating which is the lineage to ‘branch off’ requires a fixed reference that defines where evolution is heading” – clearly a long-outdated view of evolution as a predetermined (“orthogenetic”) process.

As a consequence, no terminal taxon in a phylogenetic tree (cladogram, phylogram, chronogram) can be basal (basal to what anyway? It is just as “far away” from its ancestor as its sister group). Basal taxa exist, but not at the tips of trees, they are internal ancestral or stem species (see circles 1 and 2 in Fig. 1). The first split in Fig. 1 is indeed more basal (older) than split 2, but apart from this specific context there is no use for the term basal when describing a tree. Nor can taxa as a whole be primitive, plesiomorphic, advanced, progressive or apomorphic; these terms apply to characters and their various states – species and other taxa are always an amalgam of plesiomorphies and apomorphies. The platypus, sometimes viewed as the archetypically primitive mammal (after all, it lays eggs) is in point of fact highly derived with respect to a number of characters (the bill with its electroreception and the venom spur, to name just the two most obvious ones) (see Omland et al. 2008 for a web search of the platypus as being primitive). With the possible exception of surviving stem species (a highly contentious issue in phylogenetics), no extant taxon can be ancestral to another. As Omland et al. (2008) rightly state, phylogenies of extant (perhaps better: terminal) species “show ‘evolutionary cousin’ relationships and should not imply one species is more primitive, whereas another is more advanced” (p. 856; they illustrate this with a pedigree of the Kennedy family).

Still, the evolutionary and phylogenetic literature teems with these biologically incorrect expressions. Omland et al. (2008) give examples of which mammal species they found to be called primitive (expectedly, the opossum, monotremes, shrews and tenrecs ranked first). And consider this quote from the English Wikipedia site on mammals (<https://en.wikipedia.org/wiki/Mammal>, accessed on 4 October 2015, italics added): “The relationships between these three lineages is contentious, and three different hypotheses have been proposed with respect to which group is *basal* with respect to other placentals. These

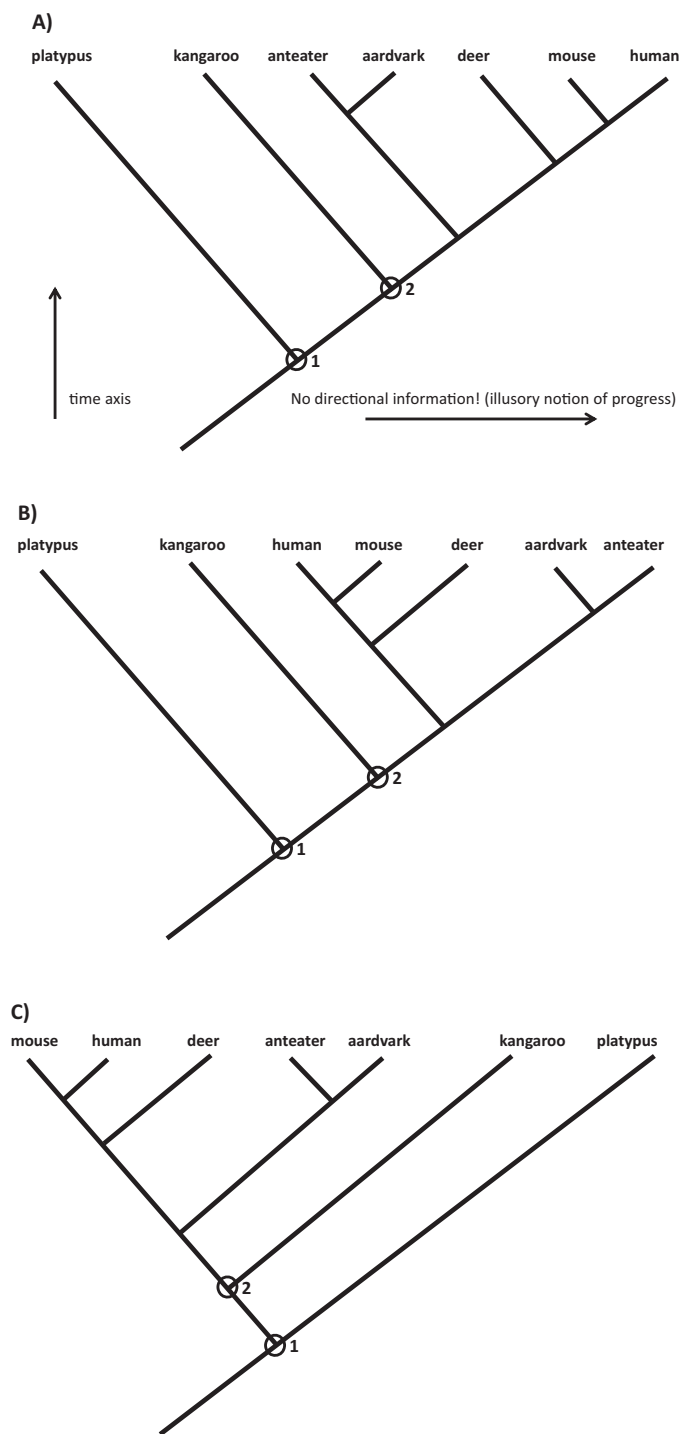


Fig. 1. Three equivalent depictions of the same phylogenetic tree of representatives of major mammalian taxa: Monotremata (platypus), Marsupialia (kangaroo), and different groups within the Placentalia (Xenarthra: anteater, Afrotheria: aardvark, Laurasiatheria: deer, Euarchontoglires: mouse and human). Whether xenarthrans and afrotherians are really sister taxa is still being debated, but this is irrelevant for the present purpose. Version A shows the traditional way of representation with monotremes on the far left, followed by marsupials and placental mammals. Humans are usually shown on the far right, implying a “ladder of progress” from “primitive” monotremes and “slightly less primitive” marsupials to more “derived” placental mammals with humans at the top. This, however, is not implied in any of the three trees, nor is it (bio-)logically correct. Only the *y*-axis, but *not* the *x*-axis, carries directional information (time). The circles with numbers 1 and 2 denote the first (and indeed most basal) split in the tree, i.e. the stem species giving rise to monotremes and therians, and the second (less basal) split of the therian stem species giving rise to marsupials and placental mammals.

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