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TECHNICAL COMMENT

Comment on "Molecular Phylogenies Link Rates of Evolution and Speciation" (II)

Webster *et al*. (*1*) compared "the net number of speciation events to underlying genetic change using 56 published phylogenies inferred from gene-sequence data" and reported a correlation between rates of genetic evolution and speciation. They argued that their findings lend support to the hypothesis that the greater the number of speciation events in a given lineage, the longer the branch lengths associated with that clade.

Examination of their source data sets [see Supplementary Online Material in (*1*)] reveals a number of problems. First, at least three studies from which a data set was drawn do not contain "phylogenies inferred from gene-sequence data." Georgiadis *et al*. (*2*) and Weller *et al*. (*3*) [see figure 1A in (*1*)] reported allozyme trees, and Petren *et al*. (*4*) presented a microsatellite tree. It is not clear that the units of genetic change from these sources are commensurate with branch lengths based on numbers of nucleotide substitutions in DNA sequences.

A second problem is that Webster *et al*. equate each inferred node of a phylogenetic tree with a speciation event, yet many of the data sets employed examine relationships among terminal taxa that do not represent species-level variation. For example, Liu and Beckenbach (*5*) examined mitochondrial DNA (mtDNA) sequences from 13 taxa representing 10 orders of insects. Clearly, branch lengths among taxa exemplifying families and orders, which reflect cumulative evolutionary divergence accrued over hundreds or thousands of bifurcations, have little to do with the rate of genetic evolution attending individual speciation events. At the other end of the spectrum, Zamudio (*6*) examined 37 mtDNA haplotypes among three closely related species of horned lizard. MtDNA often exhibits phylogenetic structure within and among populations below the species level, but demonstration of such intraspecific polymorphism actually undermines the hypothesis of punctuated evolution—which predicts that most evolutionary change is associated with speciation events.

Another difficulty is that the phylogenetic trees presented in many of the source studies including (*7*) and (*8*) are based on parsimony analysis and do not contain any information on branch lengths. However, the Nexus files included in the supplementary material for (*1*) are presented in a uniform format, with branch lengths for each node that imply these data were extracted from the cited papers. How Webster *et al.* calculated these numbers [and where tree topology originated from in (*9*), for example, which presented no phylogenetic analysis] is not described. Since the topology of the tree is fundamental to the calculation of the branch lengths and since both topology and branch length may vary greatly under alternative methodological interpretations, we believe that it is a major shortcoming of the methodology to have neglected to present the means by which these values were derived.

Finally, it is well known that denser taxon sampling tends to reveal homoplasy in sequence data, resulting in longer branches. The much-touted phenomenon of "long branch attraction" in phylogenetic inference occurs when representatives of poorly sampled taxa group together due to apparently homologous, but independently derived character states. Thus, a correlation between branch length and number of nodes in "30 to 50% of cases" selected by Webster *et al*. is not surprising. Since most systematists do not sample taxa at random, it is very difficult to tease apart the effects of sampling from the intrinsic diversity of the clades being sampled—an issue that Webster *et al*. do not address in their effort to correct for nonrandom sampling. Because the source data sets used in (*1*) are heterogeneous, it is not obvious how many of them provide appropriate tests of the hypothesis. In my view, insufficient description of the analytical methods used further adds to the difficulty in interpreting or repeating the Webster *et al*. analyses.

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