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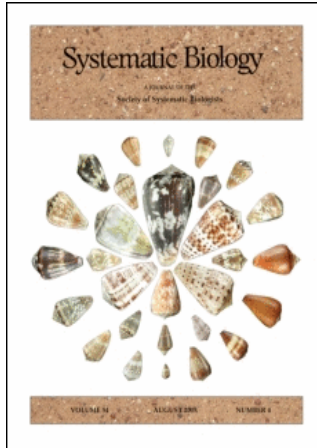
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Time to Standardize Taxonomies

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Taxonomic assignments are grossly nonstandardized in current biological classifications. For example, some genera such as *Drosophila* are an order of magnitude older than others such as *Pan* or *Gorilla*; and, furthermore, because of an “apples-versus-oranges” problem, a genus-level (or any other) designation for particular assemblages of fruit flies and primates provides almost no information on whether such disparate groups encompass comparable amounts of phenotypic, genetic, or evolutionary variation. Another aspect of nonstandardization is that some taxa (e.g., Reptilia) are paraphyletic as traditionally delimited, whereas others (e.g., Aves) are monophyletic. Although it is sometimes proclaimed that taxa afforded the same taxonomic rank should in principle be more or less equivalent by *some* criterion (Van Valen, 1973; Minelli, 2000), what that universal criterion might be and how to implement it have received scant attention (Dubois, 2005).

In principle, a “temporal-banding” strategy (Hennig, 1966; Avise and Johns, 1999) for classification could remedy this situation by moving taxonomy closer to both of its two ideal functions (Mayr, 1982): to provide a universal system for information storage and retrieval and to encapsulate an evolutionary interpretation of biological diversity. For any phylogenetic tree with internal nodes reliably dated (from molecular clocks, biogeographic data, fossils, or other evidence), extant species comprising any clade would be assigned a taxonomic rank determined by the temporal window (band) in which the basal node for that clade resides. (Although nodal dates can be notoriously difficult to estimate, rapid progress is being made for many clades thanks especially to the availability of extensive molecular sequence data; e.g., Springer et al., 2003; Moreau et al., 2006.) Because clades in any phylogeny are hierarchically arranged, each resulting classification would also be hierarchical (as under traditional Linnaean schemes) but with the added benefit of now being calibrated and standardized by a universal yardstick: evolutionary time.

Temporal banding could provide a simple way to equilibrate taxonomic ranks across any extant forms of life. The boundaries of the temporal windows to be associated with each rank are inherently arbitrary. However, once formally ratified by a consensus among systematists, they would thereafter provide an objective and universal standard for classifying any group of extant organisms for which a well-dated phylogeny is available.

A serious problem with the temporal-banding scheme (as formulated above) is that it would necessitate dramatic rank changes for many taxa. Taxonomic stability is also important in biology (Godfray and Knapp, 2004), so any wholesale taxonomic revision would be counterproductive if it complicated more so than facilitated effective communication and information retrieval. Here we suggest a simple and straightforward taxonomic tactic by which the epistemological advantages of temporal banding could be achieved without abandoning tried-and-comfortable Linnaean ranks and nomenclatures. Although we prefer the retention of ranking hierarchies in biological classifications, our current proposal could also be implemented in rank-free systems such as PhyloCode (see de Queiroz and Gauthier, 1992).

TIMECLIP PROPOSAL

We propose that a timeclip be attached to the traditional taxonomic name of any set of extant lineages (preferably a clade, but paraphyletic groups could be time-clipped as well) for which the geological age of origin is empirically established. Each timeclip could reference, for example, a standard era, period, or epoch in the geological record (Table 1). A timeclip attached to a conventional taxon would denote the window of time within which the extant species of that clade began their cladogenetic diversification from a shared ancestral node. That node (not earlier points in the stem leading to it) is thus the focal point of the timeclip designation.

For the timeclips, we suggest a three-letter format. The first letter in the code, printed in uppercase font, designates the clade’s nodal origin: A in the Recent epoch; B, Pleistocene; C, Pliocene; and so on consecutively back to the Archaean (R). (Other temporal bands and/or codes could be substituted if systematists so decide collectively.) This first letter is followed by a colon and then by two lowercase letters mnemonically abbreviating the geological episode. We further suggest that the timeclip be printed in **bold**, bracketed as [...], and connected directly to the clade’s taxon name as either a prefix or a suffix (e.g., [**D:mi**] Hominoidea; or *Drosophila* [**F:eo**]). For publication or other formal purposes, the authority for the temporal estimate could be appended to the timeclip (e.g., *Drosophila* [**F:eo Johndoe, 2000**]) with the source cited in references.

As reliable origination dates for various clades become established from empirical evidence, timeclips could be

TABLE 1. Suggested timeclips and a few taxonomic examples involving various taxa of primates, bats, fruit flies, ants, and horsetail plants mentioned in the text.

Timeclip	Geological episode	Temporal window (Mya)	"Equivalency list" (of taxa mentioned in Fig. 1 or in the text)
[A:re]	Recent	0–0.01	
[B:pl]	Pleistocene	0.01–2	
[C:pc]	Pliocene	2–5	<i>Pan</i> , <i>Gorilla</i>
[D:mi]	Miocene	5–24	Hominoidea, Pteropodidae
[E:ol]	Oligocene	24–33	
[F:eo]	Eocene	33–56	Yangochiroptera, Rhinolophoidea, Emballonuroidea, Noctilionoidea, Vespertilionoidea, <i>Equisetum</i> , <i>Drosophila</i>
[G:pa]	Paleocene	56–65	Chiroptera, Yinpterochiroptera Myrmicinae
[H:cr]	Cretaceous	65–145	
[I:ju]	Jurassic	145–205	
[J:tr]	Triassic	205–250	
[K:pe]	Permian	250–290	
[L:cb]	Carboniferous	290–350	
[M:dv]	Devonian	350–410	
[N:si]	Silurian	410–440	
[O:od]	Ordovician	440–500	
[P:ca]	Cambrian	500–550	
[Q:pr]	Proterozoic	550–2500	
[R:ar]	Archaean	2500–3600	

attached to traditional taxonomic lists as well as used in other suitable settings such as publications or seminars. Timeclips would not specify precise dates of origin (such details are best reserved for primary scientific treatises), but they would give consumers an informative sense of the approximate evolutionary depths of the taxa in question.

TIMECLIP EXAMPLES

Based on molecular genetic data and fossil discoveries, extant members of the horsetail plant clade (genus *Equisetum*) began their diversification early in the Cenozoic, as did extant members of the bat clade (order Chiroptera) (Fig. 1). To equilibrate these assemblages under the original temporal-banding scheme, *Equisetum* could, for example, be renamed and elevated to subordinal level, or Chiroptera could be renamed and demoted to generic status. Under the new proposal, the taxonomic designations *Equisetum* and Chiroptera would be retained but simply appended with timeclips [F:eo] and [G:pa] denoting origination dates in the Eocene and Paleocene, respectively. Other well-dated clades within these two groups could likewise receive appropriate timeclips, thereby enabling any observer to arrange and compare these taxa in terms of their approximate evolutionary ages (Table 1). Furthermore, with timeclips linking the origins of taxa to well-known geological episodes, possible historical associations of biological events (such as adaptive radiations) with physical events (such as the asteroid holocaust at the K-T boundary) might often suggest themselves as interesting hypotheses for further scientific inquiry.

Moreau et al. (2006) recently provided another illustration of how evolutionary dates can be of interest. From extensive DNA sequence data and fossil evidence, they concluded that an early radiation of myrmicine ants occurred during the Cretaceous (much earlier than formerly supposed). Thus, readers seeing a timeclip [H:cr] attached to Myrmicinae might be stimulated to think about causal hypotheses for this evolutionary proliferation, such as that it might be ecologically associated with Angiosperm plant radiations that were also taking place at about that same time. Such hypotheses might then be worthy of further scientific investigation.

TIMECLIP BENEFITS

A timeclip system would standardize and convey far more information than do current taxonomies and would thus facilitate research and communication in nearly all areas of comparative phylogenetics. Furthermore, time is the denominator in any rate equation, so timeclips would stimulate comparisons of evolutionary tempos in anatomies, behaviors, or other phenotypes within and across clades. For example, simply knowing that *Equisetum*, *Drosophila*, and Chiroptera are of roughly similar evolutionary age, or that all of these taxonomic groups are far more ancient than Hominoidea, raises intriguing questions about how and why morphological evolution seems to have proceeded at grossly different paces across these clades.

Another advantage is that timeclips could be incorporated piecemeal, as secure phylogenies for various taxonomic groups emerge from empirical studies. Any timeclip attached to a given taxon should be considered provisional and subject to change with new information, but such flexibility is scientifically desirable. Furthermore, taxonomic stability under the timeclip system is retained by the continued use of traditional taxon names to which timeclips are appended. Finally, the mere adoption of a timeclip protocol would encourage desirable scientific efforts to estimate nodal dates, in addition to branch topologies that often have been the sole focus of traditional phylogenetic analyses. Of course, origination dates are currently unknown for many clades, but for these no timeclips need be attached. These taxa would simply be interpreted as *incertae sedis* with respect to evolutionary age (this information itself is important because it pinpoints gaps in knowledge that might warrant further investigation).

SYNOPSIS

Systematists for years have engaged in debates about whether to retain, overhaul, or abandon conventional Linnaean frameworks for biological classification. A popular compromise stance was stated by Dubois (2005): "the current system of zoological taxonomy and nomenclature... has a number of merits, has been in existence for more than 250 years, and... should be saved rather than thrown away; this does not mean that this information should remain unchanged..." Our timeclip

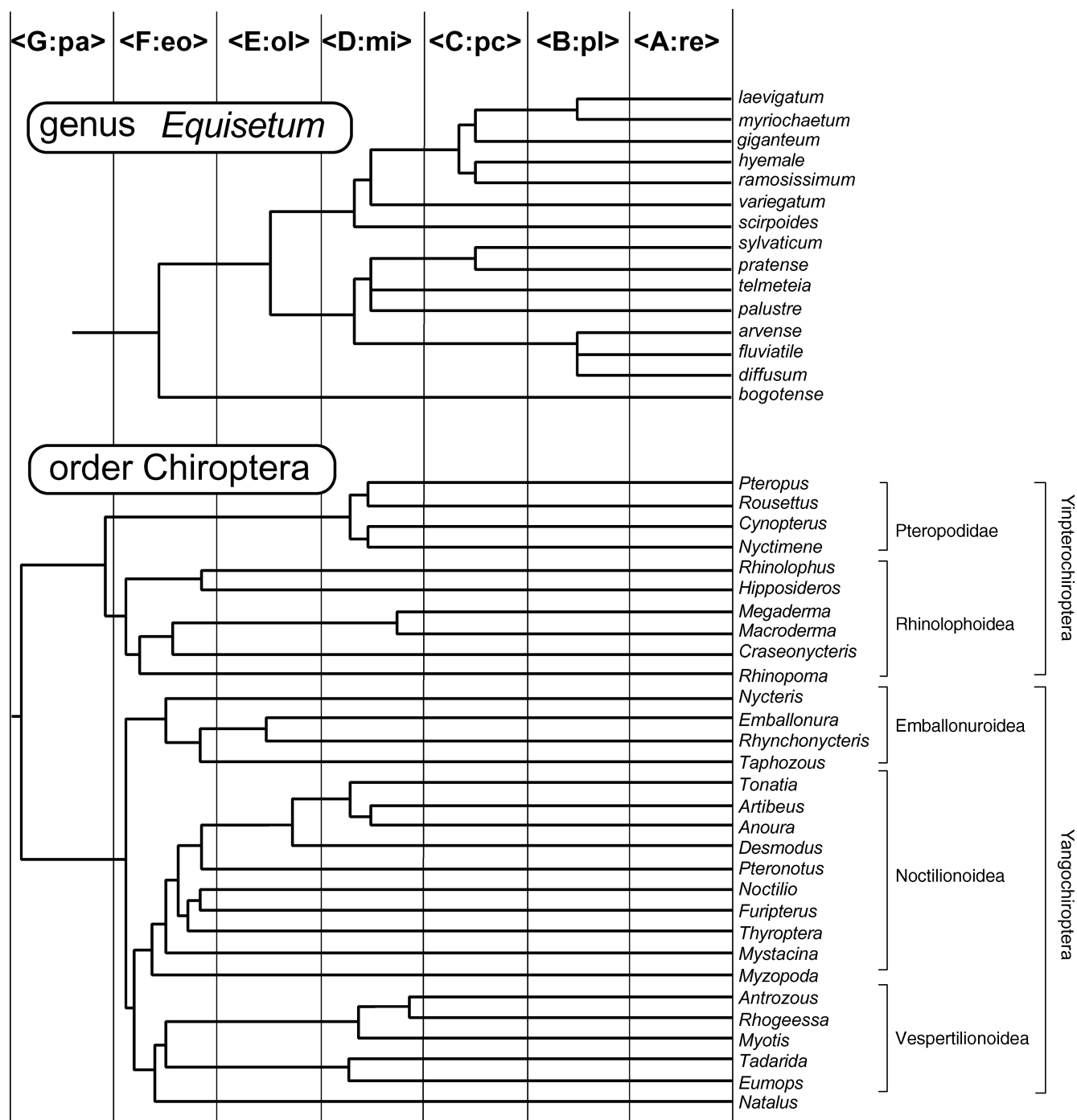


FIGURE 1. Phylograms drawn on the same temporal axis for horsetail plant species in the genus *Equisetum* (Des Marais et al., 2003) and various bat lineages in the order Chiroptera (Teeling et al., 2005). For simplicity, the seven temporal bands associated with successive epochs of the Cenozoic Era are drawn here as equal in width, but their actual durations vary.

proposal provides a practical way to retain the familiar Linnaean system *and* simultaneously promote the incorporation of new phylogenetic discoveries from molecular biology, paleontology, or other relevant evolutionary disciplines. By enabling biologists to signify and sort traditional Linnaean taxa according to their approximate dates of origin, timeclips would add materially to the

information content of biological classifications, help to equilibrate nonstandardized taxonomic ranks across disparate forms of life, promote novel avenues of thought about comparative evolutionary rates of organismal phenotypes and genotypes, and in general facilitate nearly all types of scientific research in comparative phylogenetics (Avice, 2006).

An extensive literature, special symposia, and even a formal organization (International Society for Phylogenetic Nomenclature) have been devoted to various other taxonomic proposals some of which seem far more radical and/or less utilitarian than the timeclip proposal advanced here. Thus, we now invite open discussion on the temporal-banding strategy and on timeclip-like tactics that could greatly enrich existing taxonomies while still maintaining established Linnaean traditions and nomenclatures.

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Opinions on Multiple Sequence Alignment, and an Empirical Comparison of Repeatability and Accuracy between POY and Structural Alignment

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The concept of homology is pivotal to Darwin's paradigm of descent with modification. However, in molecular phylogenetics, the process of alignment is often overlooked as a critical step. The data in molecular phylogenetic studies are not individual sequences, but rather, columns of putatively homologous nucleotides, or arguably, reconstructed presumed homology pathways in direct optimization (see Wheeler, 1996). Simplified, alignment is the assignment of homology.

Although it would be unthinkable for morphologists to ignore issues of homology, many investigators do not carefully consider alignment of molecular data. Some simply use default parameters with their data in Clustal (Thompson et al., 1994) or some other automated alignment program, perhaps manually deleting "unalignable" regions. This is a mistake, because there

are many examples where alignments, and the assumptions that go into them, will produce different trees (e.g., Mindell, 1991; Wheeler, 1995; Morrison and Ellis, 1997; Kjer, 1995; Hickson et al., 2000; Wheeler et al., 2001; Xia et al., 2003; Ogden and Whiting, 2003; Kjer, 2004).

Approaches to alignment for phylogenetic studies can be divided into two broad categories; manual alignment and computer-based alignment. A diagram of the types of alignment and their relationship to one another is provided in Figure 1. In a survey of phylogenetic papers in *Systematic Biology*, *Molecular Biology and Evolution*, and *Cladistics* from the last 3 years, we find that 76% of the papers that utilized rRNA were manually aligned (Table 1). Automated methods can be performed in a variety of programs (e.g., Clustal [Thompson et al., 1994], Divide and Conquer [Stoye, 1998], and T-Coffee [Notredame