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REVIEW ARTICLE

On the temporal inconsistencies of Linnean taxonomic ranks

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The inconsistency problem in systematics refers in part to the fact that disparate taxa of identical Linnean rank are not necessarily similar or even readily comparable in any other specifiable biological feature. This shortcoming led to a 'temporal banding' proposal in which extant clades associated with particular taxonomic ranks would be standardized according to a universal metric: the absolute time of evolutionary origin. However, one underexplored possibility is that same-level taxa in disparate organismal groups already might be similar (fortuitously so) in evolutionary age. In the present study, we explicitly address this possibility by reviewing published molecular inferences about the known or suspected origination dates of taxonomic genera, families, and orders in diverse organismal groups. Our findings empirically confirm that currently recognized taxa are far from temporally standardized, thereby adding support for the contention that this kind of taxonomic inconsistency should ultimately be rectified in our biological classifications. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **102**, 707–714.

ADDITIONAL KEYWORDS: classification – nomenclature – phylogeny – systematics – taxonomy.

The hierarchical Linnean scheme of organismal classification, in which genera are nested within families, families with orders, orders within classes, and so on, has endured for more than 250 years. Originally designed by Linnaeus (1758) to catalogue the biological products of a supernatural Creator, the Linnean system of ranking has survived major transformations in biology, such as the elucidation of evolution and its principal driving force in the 1800s, the rise of genetics and population genetics in the first half of the 20th Century, and several more recent metamorphoses in systematics including the spread of a revised concept of monophyly (Hennig, 1966), as well as the ongoing revolutions in molecular phylogenetics (Hillis, Moritz & Mable, 1996; Nei & Kumar, 2000; Avise, 2004, 2006). Yet the basic Linnean system lives on, having accommodated itself to each such conceptual shift in biology. For example, beginning with Darwin (1859), the hierarchical categories that Linnaeus first erected as an organizational tribute to God's creations were reinterpreted by the scientific community to be logical outcomes of an evolutionary process that successively crafts new species by natural selection; furthermore, *sensu* Hennig (1966), many systematists simply reinterpreted Linnean ranks to be nested clades that arise naturally from successive cladogenetic events in phylogenetic trees. Nevertheless, as bemoaned by de Queiroz & Gauthier (1992), 'biologists still have not developed a phylogenetic system of taxonomy.'

TWO PERCEIVED PROBLEMS

Despite its resiliency and continued widespread deployment, the traditional Linnean nomenclatural system has come under criticism in recent years as a result of (1) instabilities and (2) inconsistencies (i.e. absences of standardization) in its nomenclatural assignments.

INSTABILITY

In translating the standard Linnean framework into a working taxonomy, one operational problem has been

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*Corresponding author. E-mail: javise@uci.edu an instability of taxon names partly as a result of historical shifts in the meanings attached to ranked taxa (de Queiroz & Gauthier, 1990, 1992, 1994). Traditionally, taxa were treated (implicitly or explicitly) as abstract classes of organisms based on shared traits rather than shared ancestry *per se*. However, even when taxa were interpreted under a strict phylogenetic framework to be monophyletic assemblages or clades (which themselves can have several different meanings; de Queiroz, 2007), cascades of name changes for Linnean ranks often have been necessitated when new taxa were discovered or previously named taxa were either split or lumped subsequent to reinterpretations of new or existing data.

Systematists have attempted to alleviate the instability problem in various ways. The mainstream approach has been to adopt and periodically update an official *International Code of Zoological Nomenclature* that formalizes how to name organisms (Polaszek & Wilson, 2005), whereas proponents of an entirely different approach known as the PhyloCode (Cantino & de Queiroz, 2007) want to convert to a system in which clade names (traditionally referring to taxonomic rank) are redefined as clade types delimited in the context of a phylogeny. Depending on how it might be implemented, the PhyloCode would either jettison Linnean ranks or retain a rank concept but do so in a different and more stabilized nomenclatural framework (de Queiroz, 2006).

Inconsistency (nonstandardization)

Another obvious flaw of the traditional Linnean system is that its implementation to date has not entailed any serious attempt to standardize taxonomic ranks across different kinds of organisms. This problem has both conceptual and empirical aspects. One conceptual inconsistency arises because some traditional Linnean taxa of a given rank (such as Class Aves) are monophyletic, whereas others of identical rank (such as Reptilia) are paraphyletic or even polyphyletic. The empirical inconsistencies originate because disparate groups of organisms of identical rank in the traditional Linnean hierarchy are not necessarily identical or even similar in other attributes such as morphological diversity, rate of phenotypic evolution, contribution to extant biodiversity, diversity of ecological roles, or any other biological or evolutionary features of which we are aware. For example, some genera have dozens of species, whereas others are monotypic; species in some genera are phenotypically diverse, whereas those in other genera are almost indistinguishable in morphology; some taxonomic families encompass major components of an ecosystem, whereas others include only rare species of negligible impact; some taxonomic families are quite ancient, whereas others are relatively young; and so on. These points all have been made before repeatedly (Laurin, 2008; Lee & Skinner, 2007; Minelli, 2000) but, in any event, the undisputed fact is that conventional Linnean ranks are blatantly nonstandardized and thus inconsistent. In other words, under the current Linnean system, a taxonomic genus or family of insects, for example, does not necessarily compare in any specifiable way to a genus or family of plants, fungi, birds or amphibians.

This type of inconsistency is not just a minor inventorial glitch in taxonomy but, rather, it is a fundamental impediment to cross-taxon research and interdisciplinary communication in the biological sciences. If, instead, classifications were standardized such that the taxonomic assignments themselves conveyed meaningful relational information about clades across diverse types of organisms, novel questions and research opportunities in countless areas of comparative evolutionary biology would be promoted (Avise, 2009).

In this brief commentary, we first elaborate on temporal banding and the challenge of standardization in comparative taxonomy. We will then address whether traditional Linnean taxa of specified rank already might be serendipitously standardized to some extent with respect to known or suspected dates of evolutionary origin.

TEMPORAL BANDING: A SOLUTION TO INCONSISTENCY?

Hennig (1966) may have been the first to make explicit a suggestion that the absolute time of evolutionary time of origin should be the ultimate 'gold-standard' for synchronizing Linnean taxonomic ranks such that, for example, a genus-level or family-level clade of extant insects would have arisen, by definition, within the same specified window of evolutionary time as its taxonomic counterparts in fungi, birds, and mammals, or any other type of organism. Avise & Johns (1999) elaborated on Hennig's (1966) suggestion and named it the 'temporal-banding' approach. The exact temporal bands (windows of evolutionary time) to be associated with particular Linnean ranks are in principle arbitrary and, initially, would have to be ratified by the systematics community; thereafter, they would provide a universal basis for objectively assigning particular Linnean ranks to particular clades. There is no dispute that every biological clade had some true time of evolutionary origin. Thus, at least in principal, geological time is one (and arguably the most useful) universal yardstick for comparing clade ranks within and among any organismal groups. As noted by Hennig (1966), 'If systematics is to be a science it must bow to the self-evident requirement that objects to which the same name is attached must be comparable in some way.'

Unfortunately, temporal-banding as originally formulated by Avise & Johns (1999) would necessitate wholesale nomenclatural changes because the current Linnean assignments would have to be modified to accommodate the new formulation for ranks based on dates of evolutionary origin. Thus, this proposed route to solving taxonomy's inconsistency problem would exacerbate the instability problem. This latter drawback subsequently was addressed by Avise & Mitchell (2007) who suggested a simple remedy that still remains consistent with the general notion of temporal banding: merely append suitable 'time-clips' to existing taxon names as the origination dates of clades become adequately documented from molecular data, fossils or other evidence.

APPLES VERSUS ORANGES IN THE MOLECULAR ERA

Much of the inconsistency problem described above relates to the proverbial 'apples versus oranges' issue: how can anyone meaningfully compare the phenotypes, ecologies, or any other attributes of organisms, as different as primates, fruit flies, fungi, and plants? Without a common yardstick for cross-taxon comparisons, the challenge of standardizing Linnean ranks has appeared to be insurmountable.

Molecular yardsticks and clocks

In the latter part of the 20th Century, molecular genetic approaches appeared to offer some hope of escape from the apples versus oranges problem. All extant organisms employ nucleic acids as genetic material and proteins as metabolic workforces. By comparing homologous DNAs or protein molecules even in disparate kinds of organisms of specified taxonomic rank, the desired common yardstick might finally have been found. Alas, it soon became apparent that same-level taxa in different organismal groups are far from consistent with respect to magnitudes of genetic divergence at homologous proteins, loci, or even entire genomes (such as mitochondrial DNA). Among vertebrate animals, for example, congeneric species and confamilial genera of endotherms (birds and mammals) often show much smaller genetic distances than counterpart taxa of reptiles and amphibians (Avise & Aquadro, 1982; Johns & Avise, 1998).

Another sobering realization came with the elucidation of rate heterogeneities in molecular evolution at several levels: across nucleotide sites within a gene; across nonhomologous loci within a lineage; across comparable genomes; and at homologous loci across taxonomic lineages (Gu & Li, 1992; Rand, 1994; Ayala, 1997; Li, 1997; Kumar & Hedges, 1998). Thus, early hopes for a universal and metronomic 'molecular clock' (Zuckerkandl & Pauling, 1965) were dashed, as were prospects that genetic distances might be an ideal universal metric for standardizing Linnean ranks. This is not to say that molecular timepieces were discarded; by contrast, stochastic or 'relaxed' molecular clocks remain extremely helpful for reconstructing and provisionally dating nodes in phylogenetic trees. Nevertheless, dating exercises are challenging and their results often remain problematic in some instances. Much discussion has surrounded how best to combine molecular and fossil data with those from biogeography, morphology or other phenotypic evidence (Benton & Ayala, 2003; Donoghue & Benton, 2007; Marjanović & Laurin, 2007; Padial *et al*., 2010), as well as how best to calibrate and constrain molecular clocks in phylogeny reconstruction (Kumar, 2005; Benton, Donoghue & Asher, 2009; Hedges & Kumar, 2009b). We will not discuss such implementational issues here, although they have major implications for the reliability and precision of reported dates for phylogenetic nodes (Graur & Martin, 2004; Ho *et al*., 2005; Pulquério & Nichols, 2006; Ho & Phillips, 2009).

DNA barcoding

In recent years, an exploding literature on this topic attests to the widespread appeal of standardization in taxonomy. The basic idea of 'DNA barcoding' is to use the magnitude of sequence divergence in a 'master molecule' (typically a mitochondrial cytochrome oxidase gene) as a consistent metric to identify species in any organismal group (Hebert *et al*., 2003; Stoeckle, 2003). The approach not only has great promise, but also potential pitfalls (Moritz & Cicero, 2004), including the arbitrariness of any sequence divergence threshold for species recognition.

To date, DNA barcoding has been the major generator of enthusiasm for standardization in taxonomy. We find this situation quite ironic because 'species' is the one-and-only level in the Linnean hierarchy not recommended for inclusion in the temporal-banding proposal by Avise & Johns (1999) (i.e. under the biological species concept, reproductive isolation already serves as a universal standard for demarcating sexual species, at least in principle). Of course, DNA barcoding could be extended to higher Linnean ranks by assigning arbitrary sequence-divergence cutoffs for genera, families, orders, and so on; however, we still would argue that the ages of clades would ultimately be a better standard for any universal earmarking of supra-specific taxa.

ABSOLUTE TIME: THE ULTIMATE ARBITER?

Under the general temporal-banding framework, taxonomic ranks of extant clades would be standardized (or at least time-clipped) according to dates of origin. However, one key issue not well addressed is whether same-level taxa in different organismal assemblages already might be somewhat similar in evolutionary age. Although systematists apparently have made no conscious efforts to time-standardize taxonomies across (or even within) organismal groups, it remains possible that some degree of standardization has arisen *de facto* because: (1) most systematists have strived to assign Linnean ranks to clades (as opposed to grades or artificial groups); (2) such clades typically are nested, meaning that lower-ranked clades almost inevitably are younger than higher-ranked clades in any organismal group; and (3) many biogeographical events associated with the geological timescale may have concordantly shaped the cladograms of multiple taxa in ways that should be reflected to some degree in current taxonomies.

Here, we review recently published molecular information on suspected evolutionary ages of taxonomic genera, families, and orders in diverse organismal groups. The results strongly imply that currently recognized Linnean taxa are indeed highly nonstandardized, temporally.

Our analysis was prompted by the recent publication of *The Timetree of Life* (Hedges & Kumar, 2009a), a synthetic phylogenetic treatise from which most of our temporal estimates of clade origins and taxonomic assignments were extracted. This edited volume consists of more than 80 chapters devoted to family-level-and-above taxa in particular extant groups of animals, plants, and microbes, with each chapter typically including a 'best-estimate' of a timetree (a cladogram with evolutionary dates) as reconstructed by systematic experts on each organismal group. Most of the estimates of divergence time in *The Timetree of Life* came from molecular clocks (often based primarily on mitochondrial DNA) as calibrated using fossil or biogeographic evidence. In the present commentary, 'evolutionary age' or 'date of origin' will refer to the nodal timepoint at which each taxonomic clade was reported to have arisen.

Because *The Timetree of Life* treated only taxa at and above the taxonomic level of families, we supplemented our analysis with previously estimated divergence dates for selected genera in various organismal groups, based on our own literature survey (see Supporting information, Appendix S1). Here, we focus mostly on vertebrate taxa because these animals have attracted special interest in discussions of comparative molecular evolutionary patterns. We also have summarized timetree data for decapod crustaceans (Decapoda) because published estimates are available for many genus- and family-level taxa in this arthropod group. Table 1 summarizes these published estimates of evolutionary ages (inferred dates of origin) for traditionally recognized genera, families, and orders in the various vertebrate groups and decapods; the data are graphically portrayed in Figures 1, 2, 3.

One major point to emerge is that each Linnean rank within a group appears to be associated with a wide range of evolutionary ages. Within mammals, for example, some extant genera provisionally date back only 100 000 years, whereas others are as old as 40 Myr; and, within reptiles, coalescent points for extant members of various genera range from approximately 7–160 Mya. Similar statements apply to the taxonomic ranks of families and orders. For example, the provisional evolutionary ages of amphibian families range from 43–226 Myr, and dates for mammalian families range from 7–80 Myr.

The second major point from these data is that mean evolutionary age generally increases with taxonomic rank within each vertebrate group. Within birds, for example, a traditional genus arose on

Table 1. Summary of published evolutionary ages (Myr) estimated for genera, families, and orders within each of four major vertebrate groups, and also for decapod crustaceans among the invertebrates (see text)

	Orders			Families			Genera		
Taxon	*N*.	Age (mean ± SE)	Ranges	*N*	Age (mean ± SE)	Ranges	*N*	Age (mean ± SE)	Ranges
Amphibia	3	274.0 ± 10.0	264.0–294.0	76	101.3 ± 5.5	43.2–226.4	84	37.3 ± 1.7	14.3–110.7
Reptilia	3	240.5 ± 15.9	219.2–271.5	72	86.4 ± 4.8	32.9–209.4	137	31.5 ± 2.2	6.9–159.0
Aves	31	85.5 ± 3.0	53.0–106.9	149	42.9 ± 1.7	11.3–97.9	201	27.7 ± 1.1	0.4–80.0
Mammalia	26	81.2 ± 5.3	60.7–202.2	141	37.1 ± 1.3	7.3–80.5	597	9.6 ± 0.3	0.1–40.0
Decapoda	1	437	NA	25	200.9 ± 16.1	94.0–430.0	57	60.2 ± 4.2	16.8–135.1

NA, not available.

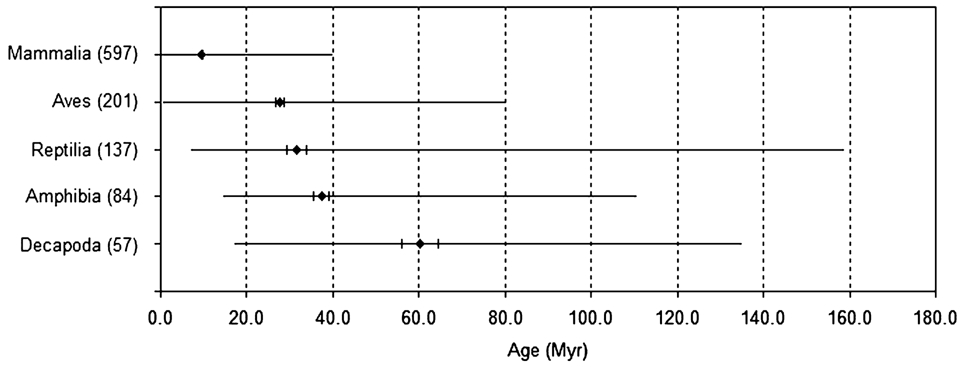

Figure 1. Published evolutionary ages of surveyed genera within each of four major vertebrate groups, and also for decapod crustaceans among the invertebrates. Mean dates, SEs, and ranges are shown.

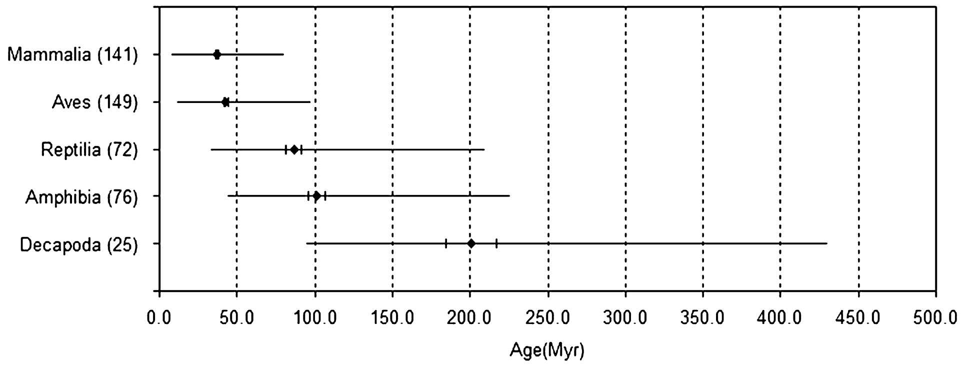

Figure 2. Published evolutionary ages of surveyed taxonomic families within each of four major vertebrate groups, and also for decapod crustaceans among the invertebrates. Mean dates, SEs, and ranges are shown.

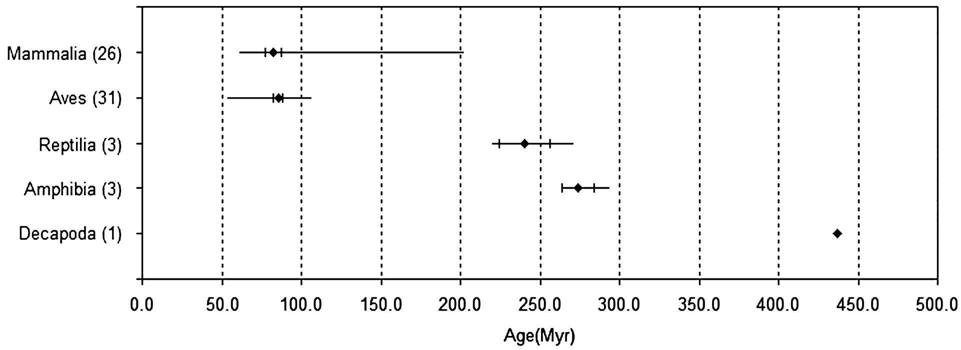

Figure 3. Published evolutionary ages of surveyed orders within each of four major vertebrate groups, and also for decapod crustaceans among the invertebrates. Mean dates, SEs, and ranges are shown.

average approximately 28 Mya, a taxonomic family arose 43 Mya, and an order originated approximately 86 Mya. A general association of higher Linnean rank with older evolutionary age is of course not unexpected. Nevertheless, for each vertebrate group, we conclude that clades of a given taxonomic rank can be associated with a wide range of evolutionary ages, meaning that there is little consistency with respect to time of origin.

Table 1 and Figures 1, 2, 3 also permit comparisons of mean evolutionary ages of taxa across these groups. Taxonomic inconsistency is evident from this perspective also. For example, whereas a mammalian genus reportedly averages an age of only 10 Myr, an amphibian genus typically arose approximately 35 Mya. Furthermore, whereas a typical mammalian family arose approximately 40 Mya, a typical amphibian family arose more than 100 Mya. At the ordinal

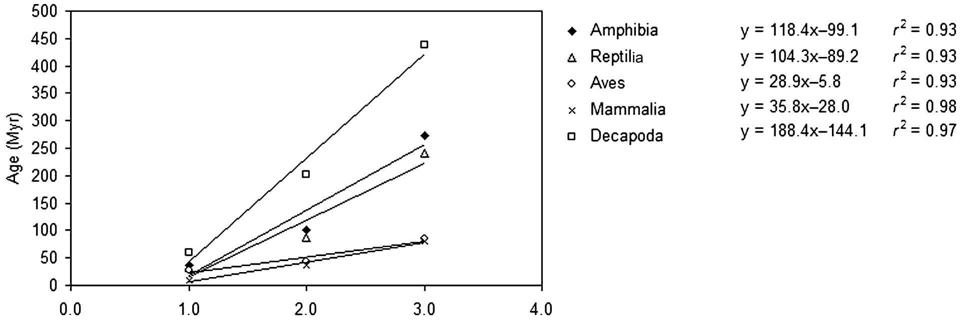

Figure 4. Regressions showing the relationships between evolutionary ages of taxa and their Linnaean ranks in current classifications. For this analysis, genera, families, and orders were arbitrarily assigned numerical values of 1, 2, and 3.

level, estimated mean ages of taxa range from a low of approximately 80 Myr in mammals and birds to highs of approximately 240 and 270 Myr in reptiles and amphibians, respectively.

The heterogeneity of origination dates for a specified-level taxon becomes even more pronounced when an invertebrate group (Decapoda) is also considered; in our survey, the 25 taxonomic families and 57 genera within this taxonomic order originated on average approximately 200 Mya, and 60 Mya, respectively; or approximately five-fold longer ago in each case than the same-level taxa of mammals.

The heterogeneity of taxonomic assignments with respect to absolute evolutionary time of origin across major vertebrate groups has been illustrated previously (Hedges & Kumar, 2009b: 15), and it is further demonstrated by significantly different slopes for these groups in the regressions between evolutionary age and taxonomic rank (Fig. 4). In this representation, it appears to be the case, for example, that reptilian and amphibian taxa not only are consistently older at each taxonomic level than their counterpart taxa among the birds and mammals, but also that their evolutionary ages increase faster with increasing levels of Linnean taxonomic rank.

One goal of this commentary has been to consider the degree to which clades currently assigned a given taxonomic rank might already be somewhat consistent, with respect to age of origin, across extant members of disparate organisms. At issue is not so much whether higher ranks within a specified group tend to be more ancient than lower ranks (this is to be expected under nearly all taxonomic and evolutionary scenarios), rather, the more salient questions are: (1) are identical taxonomic ranks in the same and different organismal groups consistent with respect to evolutionary age and (2) are the slopes in the regressions between taxonomic rank and evolutionary age consistent across different kinds of creatures? For animals included in our survey, the answers to both questions are 'no'; the evolutionary ages of taxa are not consistent across (or even within) specified organismal groups. Furthermore, the inconsistencies are even more pronounced when highly disparate kinds of organism are considered.

Thus, evolutionary dates of origin can now be added to the pantheon of biological variables for which nested ranks in current Linnean taxonomies are highly inconsistent. Other such variables include such diverse features as numbers of species per taxon, magnitudes of phenotypic divergence (e.g. in morphology, behaviour, physiology, etc.), ecological roles, speciation rates, geographic ranges, genetic distances in proteins or nucleic acids, calibrations for molecular clocks, and just about any other biological variable that you might think of. In other words, even two-and-a-half centuries after Linnaeus, systematists have yet to standardize (or even develop criteria for standardizing) the nested Linnean categories (ranks) that serve as the organizational and nomenclatural foundation for essentially all areas of biology.

SYNOPSIS

In the introduction to *The Timetree of Life*, Hedges & Kumar (2009a: 16) emphasize 'the immense value of having a robust Timetree of Life for all fields of science. It will provide a means for estimating rates of change for almost anything biological; for example, morphological structures, behaviors, genes, proteins, non-coding regions of genomes – in any group of organisms. In that sense it will catalyze a Renaissance in comparative biology'. If reliable timetrees can indeed be generated for many taxa in the coming years, we agree with the sentiment by Hedges and Kumar, and would merely add that a nomenclatural scheme (such as time-clips) clearly encapsulating that temporal information might then help to catalyze a transition to comparative evolutionary thinking, which in turn could benefit many areas of biology, ranging from the phylogenetic analysis of adaptations (Harvey *et al.*, 1996; Avise, 2006) to biodiversity analyses including conservation efforts (Wilson, 1988; Purvis, Gittleman & Brooks, 2005).

In the present commentary, we have confirmed that temporal inconsistencies pervade current Linnean taxonomies. The twin problems of taxonomic instability and nonstandardization have plagued biology for more than two centuries. However, with the increased availability of timetrees for numerous taxa, perhaps a time will come when systematists rectify the inconsistency problem by somehow incorporating temporal benchmarks into their biological nomenclatures. The nonstandardization problem in taxonomy has pre-Darwinian roots and is insidious but, in principle, it can be corrected. For the first time since Linnaeus, conceptual frameworks as well as empirical approaches now exist to stabilize and universally standardize taxonomic assignments across all forms of life. The open question is: will systematists finally choose to adopt some such system?

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REFERENCES

Avise JC. 2004. *Molecular markers, natural history, and evolution*, 2nd edn. Sunderland, MA: Sinauer.

Avise JC. 2006. *Evolutionary pathways in nature: a phylogenetic approach*. Cambridge: Cambridge University Press.

Avise JC. 2009. Beyond cladograms, phenograms, and phylograms. In: Hedges B, Kumar X, eds. *Timetrees of life*. Oxford: Oxford University Press, 19–25.

Avise JC, Aquadro CF. 1982. A comparative summary of genetic distances in the vertebrates: patterns and correlations. *Evolutionary Biology* **15:** 151–185.

Avise JC, Johns GC. 1999. Proposal for a standardized scheme of biological classification for extant species. *Proceedings of the National Academy of Sciences of the United States of America* **96:** 7358–7363.

Avise JC, Mitchell D. 2007. Time to standardize taxonomies. *Systematic Biology* **56:** 130–133.

Ayala FJ. 1997. Vagaries of the molecular clock. *Proceedings of the National Academy of Sciences of the United States of America* **94:** 7776–7783.

Benton MJ, Ayala FJ. 2003. Dating the tree of life. *Science* **300:** 1698–1700.

Benton MJ, Donoghue PCJ, Asher RJ. 2009. Calibrating and constraining molecular clocks. In: Hedges B, Kumar X, eds. *Timetrees of life*. Oxford: Oxford University Press, 35–86.

Cantino PD, de Queiroz K. 2007. *International code of phylogenetic nomenclature*, Version 4b. Available at: http://www.ohiou.edu/phylocode/

Darwin CW. 1859. *On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life*. London: John Murray.

Donoghue PCJ, Benton MJ. 2007. Rocks and clocks: calibrating the tree of life using fossils and molecules. *Trends in Ecology and Evolution* **22:** 424–431.

Graur D, Martin W. 2004. Reading the entrails of chickens: molecular timescales of evolution and the illusion of precision. *Trends in Genetics* **20:** 80–86.

Gu X, Li W-H. 1992. Higher rates of amino acid substitution in rodents than in humans. *Molecular Phylogenetics and Evolution* **1:** 211–214.

Harvey PH, Leigh Brown AJ, Maynard Smith J, Nee S, eds. 1996. *New uses for new phylogenies*. Oxford: Oxford University Press.

Hebert PDN, Cywinska A, Ball SL, de Waard JR. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B Series B, Biological Sciences* **270:** 313–321.

Hedges SB, Kumar S, eds. 2009a. *The timetree of life*. Oxford: Oxford University Press.

Hedges SB, Kumar S. 2009b. Discovering the timetree of life. In: Hedges B, Kumar X, eds. *Timetrees of life*. Oxford: Oxford University Press, 3–18.

Hennig W. 1966. *Phylogenetic systematics*. Urbana, IL: University of Illinois Press.

Hillis DM, Moritz C, Mable BK. 1996. *Molecular systematics*, 2nd edn. Sunderland, MA: Sinauer.

Ho SYW, Phillips MJ. 2009. Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Systematic Biology* **58:** 367–380.

Ho SYW, Phillips MJ, Cooper A, Drummond AJ. 2005. Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. *Molecular Biology and Evolution* **22:** 1561–1568.

Johns GC, Avise JC. 1998. A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome *b* gene. *Molecular Biology and Evolution* **15:** 1481–1490.

Kumar S. 2005. Molecular clocks: four decades of evolution. *Nature Review Genetics* **6:** 654–662.

Kumar S, Hedges SB. 1998. A molecular timescale for vertebrate evolution. *Nature* **392:** 917–920.

Laurin M. 2008. The splendid isolation of biological nomenclature. *Zoologica Scripta* **35:** 223–233.

Lee MSY, Skinner Q. 2007. Stability, ranks, and the PhyloCode. *Acta Paleontologica Polonica* **52:** 643–650.

Li W-H. 1997. *Molecular evolution*. Sunderland, MA: Sinauer.

Linnaeus C. 1758. *Systema naturae*. Stockholm: Laurentius Galvius.

Marjanović D, Laurin M. 2007. Fossils, molecules, divergence times, and the origin of lissamphibians. *Systematic Biology* **56:** 369–388.

Minelli A. 2000. The ranks and the names of species and higher taxa, or a dangerous inertia in the language of natural history. In: Ghiselin MT, Leviton AE, eds. *Cultures and institutions of natural history: essays in the philosophy of sciences*. San Francisco, CA: California Academy of Sciences, 339–351.

Moritz C, Cicero C. 2004. DNA barcoding: promise and pitfalls. *PLoS Biology* **2:** 1529–1531.

Nei M, Kumar S. 2000. *Molecular evolution and phylogenetics*. New York, NY: Oxford University Press.

Padial JM, Miralles A, De la Riva I, Vences M. 2010. The integrative future of taxonomy. *Frontiers in Zoolology* **7:** 16–30.

Polaszek A, Wilson EO. 2005. Sense and stability in animal names. *Trends in Ecology and Evolution* **20:** 421–422.

Pulquério MJF, Nichols RA. 2006. Dates from the molecular clock: how wrong can we be? *Trends in Ecology and Evolution* **22:** 180–184.

Purvis A, Gittleman JL, Brooks T, eds. 2005. *Phylogeny and conservation*. New York, NY: Cambridge University Press.

de Queiroz K. 2006. The PhyloCode and the distinction between taxonomy and nomenclature. *Systematic Biology* **55:** 160–162.

de Queiroz K. 2007. Toward an integrated system of clade names. *Systematic Biology* **56:** 956–974.

de Queiroz K, Gauthier J. 1990. Phylogeny as a central principle in taxonomy phylogenetic definitions of taxon names. *Systematic Biology* **39:** 307–322.

de Queiroz K, Gauthier J. 1992. Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* **23:** 449–480.

de Queiroz K, Gauthier J. 1994. Toward a phylogenetic system of biological nomenclature. *Trends in Ecology and Evolution* **9:** 27–31.

Rand DM. 1994. Thermal habit, metabolic rate, and the evolution of mitochondrial DNA. *Trends in Ecology and Evolution* **9:** 125–131.

Stoeckle M. 2003. Taxonomy, DNA and the bar code of life. *BioScience* **53:** 796–797.

Wilson EO, ed. 1988. *Biodiversity*. Washington, DC: National Academy Press.

Zuckerkandl E, Pauling L. 1965. Evolutionary divergence and convergence of proteins. In: Bryson V, Vogel HJ, eds. *Evolving genes and proteins*. New York, NY: Academic Press, 97–166.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. References from which published estimates of evolutionary dates of origin for genus-level taxa in the various vertebrate groups (and also decapods) were extracted.