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On the lack of good scientific reasons for the growing phylogeny/classification gap

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Abstract

An increasing number of phylogenetic analyses is no longer translated into classifications. The resulting phylogeny/classification gap is undesirable because the precise transmission of phylogenetic insights depends on the frequent revision of Linnaean names. The move away from classifying has numerous correlates. These include: an expanded pool of researchers who are able to produce phylogenetic estimates, a mismatch between the properties of molecular phylogenies and the requirements for verbal Linnaean definitions, the emphasis of statistical representations over the creation and evaluation of scientific terms, and a partial disconnect between the processes of nomenclature and taxonomy. The "taxonomic concept" approach allows systematists to express their varying perspectives with a high precision and can therefore help reduce the aforementioned gap. The phylogeny/classification link must persist in order to ensure community-wide access to, and continued testing of, the products of systematic research.

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Recently Professor Joseph Felsenstein published two review pieces on the history of different systematic schools (Felsenstein, 2001, 2004). The first article focused on the struggle of likelihood methods to become established as a widespread tool for phylogenetic inference. The second is a chapter in *Inferring Phylogenies*. It offers a valuable perspective on the emergence of algorithmic methods and a critique of philosophical arguments for "non-statistical" parsimony. In the conclusion of each piece the author also commented on the increasing irrelevance of the theory and practice of classification in the overall historical scheme. My purpose here is to analyze the *reasons* for the phylogeny/classification gap. I will suggest that none of them is convincing enough to promote the gap's growth.

Felsenstein (2001, p. 467) first writes: "The focus of systematics has shifted massively away from classification: it is the phylogenies that are central, and it is nearly irrelevant how they are then used in taxonomy." He later elaborates (Felsenstein, 2004, p. 145): "The delimitation of higher taxa is no longer a major task of systematics, as the availability of estimates of the phylogeny removes the need to use these classifications. Thus the outcome of the wars over classification matters less and less. A phylogenetic systematist and an evolutionary systematist may make very different classifications, while inferring much the same phylogeny. If it is the phylogeny that gets used by other biologists, their differences about how to classify may not be important. I have consequently announced that I have founded the fourth great school of classification, the It-Doesn't-Matter-Very-Much school. Actually, systematists 'voted with their feet' to establish this school, long before I announced its existence." Felsenstein twice calls upon historians and philosophers of science to acknowledge these changes. He finally adds in response to a review (http://evolution.genetics.washington.edu/book/reviews.html): "Systematists get so worked up declaiming the centrality of classification in systematics that I have argued the opposite. Well, we'll see what things look like a few years from now."

The above statements may seem true but nevertheless remain somewhat incomprehensible. In modern

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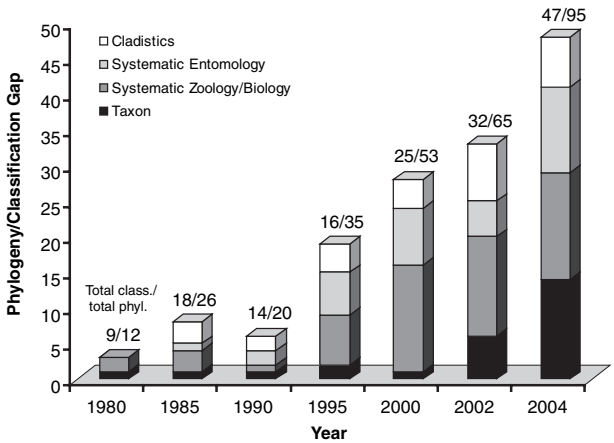

Fig. 1. Stacked column graph resulting from a subjective attempt to quantify the growing phylogeny/classification gap. Four high-profile systematics journals were analyzed for the years 1980, 1985, 1990, 1995, 2000, 2002, and 2004. All empirical articles presenting significant and new phylogenetic estimates were examined (total = 306 articles). A *subset* of the total which *also* contained new names, or explicit taxonomic rearrangements and redefinitions of names, or at least new (if only reconfirming) taxonomic summaries, were judged to represent "new classifications" (161 articles). On the other hand, articles ending mainly with elaborations on the monophyly and non-monophyly of select lineages, or tentative and ambiguous taxonomic assessments, or explicit recommendations to conduct more inclusive analyses, were judged "purely phylogenetic" (145 articles). The phylogeny/classification gap is obtained by subtracting the number of "classifying" articles from the annual total. The ratio of classifications/phylogenies per year is listed on top of each column. See Wheeler (2004) for additional relevant information.

systematics there is indeed a negative correlation of more statistical phylogenetics with less classification and nomenclature (Fig. 1). But, even if it is real and ongoing, why in general should systematists *endorse* the latter trend?

The view that classifications matter less and less is neither isolated nor trivially wrong. I wish to make three points about this view, each of them aimed at a wider audience. I will start by asking to what extent the assessment that phylogenies are replacing classifications is actually true.

Are phylogenies replacing classifications?

The inference of phylogenies is central nowadays to systematic research. The products of modern phylogenetic analyses are highly regarded within the community. "Tree thinking" (O'Hara, 1997) is also starting to predominate in certain areas of comparative evolutionary or ecological research. Felsenstein adequately describes these developments. But by supplementing a traditional classification with a more precise estimate of phylogeny, one has not yet "removed the need to use" any or all parts of that classification. In the vast majority of cases, the more recent phylogenetic analyses are properly considered *revisions* of pre-existing hypotheses (however coarse) about the relationships among taxa and the evolutionary histories of character traits. Moreover, as a result of the partial interdependence of the activities of classifying and naming in systematics, the older classifications were translated into Linnaean names. Rather than rendering the traditional names and their associated information contents (such as types) superfluous, most analyses actually have to rely on these elements in order to convey their phylogenetic message. Without the names originating from previous classifications, the new tree estimates would remain incomprehensible to us. As Ronquist (2004, p. 767) put it: "I do not think we will ever see papers with titles like 'The biology of <insert tree drawing here>.'" A more proper term for the relationship among the new phylogenies and older classifications would thus be *refinement,* not replacement. The need to use the older elements continues.

Even when phylogenetic estimates represent significant improvements over existing classifications, which they do frequently, it is unclear how widely these results are acknowledged and used in other biological disciplines. Researchers who make routine use of the new estimates tend to operate within the phylobiological community. They access the primary literature and therefore understand how the contents of certain classifications and names have been revised in light of recent phylogenetic insights. Yet a much broader section of biology will likely remain uninformed. In the typical non-systematic verbal exchange, research article, or textbook it is still customary to refer to taxa by their names instead of tree representations. The "average" non-systematist is prepared to learn the meanings of names as they were specified in traditional classifications and subsequently adopted in the identification literature. The rapidly developing field of biodiversity informatics, a major research tool for ecologists and conservation scientists (Bisby, 2000), is largely unaffected by the phylogenetics trend, relying instead on Linnaean classification and nomenclature. The most important on-line repositories for systematic information cannot capture the new estimates. The *Index Kewensis*, the *Zoological Record*, the Global Biodiversity Information Facility and nearly all of its provider databases, and even GenBank are among these essential yet "non-phylogenetic" services. While the move towards directly representing phylogenies is highly desirable, everyday access to systematic information is still made possible through traditional classifications.

In summary, phylogenetic estimates are not replacing classifications but are at best refining the meanings of previously used names. Their overall impact is more restricted than Felsenstein describes. Several major biological disciplines remain untouched by the new

insights. They are not helped by the aforementioned trend (Wheeler, 2004).

Why not classify?

If the communication of new phylogenetic insights relies on pre-existing classifications then why would anyone "vote" for ending this cycle? I now review a number of reasons why classifications are perceived as increasingly irrelevant.

The democratization of phylogenetics

The increasing accessibility of molecular techniques and data has broadened the pool of researchers who produce phylogenetic estimates. Many among them are neither personally motivated nor employed to contribute to the 250-year-old legacy of classifying and naming taxa. Felsenstein (2001, p. 466) writes about developments in the 1970s: "At the same time numerical criteria were gaining ground in the new field of molecular evolution. Molecular evolutionists were not interested in philosophical frameworks or issues of how to classify. They were more pragmatic and eclectic."

In a more heterogeneous demographic of researchers who construct phylogenies, many are able to *reuse* established names and meanings in order to convey their interests and results. Until this dependency breaks down they may thrive while maintaining their personal indifference towards classifying. To do so they must focus on taxa which already have a sufficiently adequate set of names.

The limits of verbal classification systems

A further reason not to classify is perhaps more fundamental. Modern analytical packages allow researchers to extract phylogenetic signals from molecular data whose properties are difficult to translate into words. I have suggested this elsewhere (Franz, 2005) and will keep the discussion brief.

A plausible explanation for why we can recognize the extant members of million-year-old lineages as such is the presence of causal mechanisms that have upheld several (though typically not all) of their distinctive features over time. Angiosperms can be characterized by their triploid endosperm and spiders have silk-producing spinnerets. In part the meanings of their names are thereby fixed as well. Suppose these structures or their molecular homologs had not evolved at all after coming into existence. In that case there would be no additional properties and no subordinate lineages to classify in reference to them. On the other hand, certain aspects of the pheno- and genotype of angiosperms and spiders probably evolved too rapidly to yield reliable phylogenetic estimates. The challenge is to observe traits evolving at intermediate velocities, since their existence plays an essential role in our recognition and labeling of species and higher-level taxa (Boyd, 1999).

New tools to infer molecular phylogenies are reaching beyond the limits for verbal diagnoses of taxa. High rates of saturation combined with a paucity of character states restrict our ability to create property-referencing labels. Homology assessments must be presented with probability values and are best displayed visually (Pagel et al., 2004). Molecular phylogeneticists may understand *that* a lineage is monophyletic but should have difficulties describing *why* (other than mentioning support values). When property-based definitions are unavailable, the only remaining alternative to name and define a lineage is by ostension, i.e. by "pointing" at all of its sub-elements. This option is not favored by the Linnaean system where names are defined by individual types plus a diagnosis.

Molecular phylogeneticists must often be discouraged to name taxa based solely on ostensive definitions, particularly if the support for a lineage is weak and there is no possibility to compare the insights to other information expressible in words. This is part of the reason why the age-old systematic objective of classifying evolved into testing of monophyly, or simply, inference of phylogeny.

The emphasis of statistics over language

The increasing irrelevance of classifications is also partly explained by a general trend in science towards valuing experimental, statistical analyses more highly than "purely descriptive" research. The trend is deeply rooted and far reaching (Cleland, 2002). Its inherent misconceptions and effects on systematics have been treated at length by Wheeler (2004). In the end, systematists who publish extensive statistical analyses have been effective in positioning their products. Those working on classifications need to understand the value of having adequate names well enough to regain vital ground.

The reliability of the meanings of scientific terms is not something one can assess early on or ignore after a while (Quine, 1969; Boyd, 1991; Lipton, 1993). Rather, useful terms must be improved and poor choices eliminated. Scientists can never afford to concede the objective of a close mapping of names and knowledge. Much intellectual work is invested into the dubbing and definition of a reliable scientific term, and the names of species or higher-level taxa are no exception. Yet the more effectively they accommodate a range of ecological observations and evolutionary theories, the easier it may be to underestimate their value. They just seem to "work". Most scientists can import such terms into their areas of inquiry without much reflection. Felsenstein's

(2004, pp. 145–146) discussion illustrates this point succinctly. He first seems to approve of the increasing irrelevance of classifications in systematics, but then immediately uses that argument to *redefine* and *rename* a number of terms for the systematic schools under review. In short, scientists will rightly care about names whose meanings reflect their research insights and agendas.

The need for a more precise language

My last point is a mixture of controversy and promise. A number of phylogeneticists are becoming dissatisfied with the Linnaean system of nomenclature (Cantino et al., 1999; Hebert et al., 2003). Their motivations are varied, and some solutions likely premature (Nixon and Carpenter, 2000; Will and Rubinoff, 2004). Still, it appears as though the traditional process of classifying taxa must evolve in order to meet today's challenges. Fewer and fewer phylogenetic results are translated into proper Linnaean names and definitions. Those who mainly use the latter might be misled into thinking that systematics has reached consensus when the opposite is true. On the other hand, most users would appreciate even greater naming stability, or at least more transparency about the dynamics of defining names over time.

Many systematists are convinced that our use of Linnaean nomenclature is a natural, working compromise. It should lead to a relatively stable system of naming that is nevertheless responsive to certain changes in taxonomic information content. Adjustments to new taxonomic insights are required in particular when the Priority among names for type specimens is involved, or when species are transferred among genera. In other cases the names will simply change their statuses or referential extensions, and only expert speakers may notice. In other words, the accepted Linnaean system produces a *partial disconnect* between the processes of nomenclature and taxonomy (Fig. 2). Although some degree of vagueness in naming is desirable, there is room for a more precise language to harvest the fruits of the abundant "non-nomenclatural" publications in systematics.

Those who are unsatisfied with the Linnaean compromise have three core options. The most radical choice is to stop applying new Linnaean names to newly perceived taxa and instead refer to them by unruled names or (usually incomprehensible) DNA base strings. Another is to define names in such a way that they are less receptive to the aforementioned changes in information content. In comparison to current practice, each of these proposals effectively weakens the link between nomenclature and taxonomy. Systematists would no longer have proper names to communicate their evolving phylogenetic insights.

A third and more promising solution *strengthens* the link between nomenclature and taxonomy. It provides a more granular and precise language for referring to the products of systematic research. This option is under

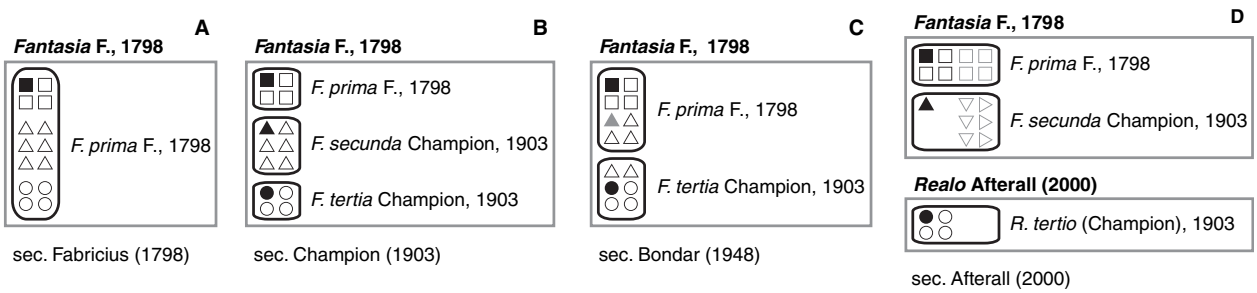

Fig. 2. Schematic illustration of the partial disconnect between Linnaean nomenclature and taxonomy over time (adapted from Kennedy et al., 2005; for a real-life example see Randall and Caldwell, 1966). Displayed is a sequence of four revisions of the hypothetical taxon *Fantasia* F., spanning from the original naming act in 1798 to the latest treatment in 2000. The individual specimens considered in each revision are represented with the symbols □, △, ○, etc. The relevant nomenclatural types for species and higher-level taxa are shown as ■, ▲, and ●. (A) In 1798 Fabricius described and named *F. prima* F. based on a set of specimens. (B) This set was reexamined by Champion in 1903 and judged to contain specimens of two additional species *F. secunda* Champion and *F. tertia* Champion, each with their respective new type. (C) In 1948 Bondar revised *Fantasia* and thereby reassigned the specimens "unevenly" to two of the three existing names. A heterotypic synonym *F. secunda* was created for *F. prima* which has priority. At the same time, a small portion of the *F. secunda* specimens (sec. Champion, 1903) was renamed as *F. tertia*. (D) Afterall publishes a revision in 2000 in which she considers *parts* of Fabricius' original material as well as newly collected specimens (marked as ▽; and ▷). The specimen circumscription of *F. prima* is now more inclusive in comparison to 1798 and 1903, and overlapping with respect to 1948. The name for *F. secunda* is resurrected to apply to Champion's type and numerous specimens not examined by the previous authors. The author proposes that the material formerly named *F. tertia* (sec. Champion, 1903) is deemed sufficiently distinctive to merit placement in a separate genus *Realo* Afterall. The epithet is changed accordingly to yield the new combination *R. tertio* Afterall. The sequence of illustrations could be modified to apply to higher-level taxa or characters instead of specimens. Tracing the meaning of the names *Fantasia, F. prima,* or *F. tertia/R. tertio* through time clarifies what Linnaean names and the Principle of Priority (typification) can and cannot achieve in terms of uniquely labeling the four authors' taxonomic perspectives. Misspelled or invalid names only add to the problem complex. The "sec." annotation may be used to refer to each unique view.

investigation by several working groups who are developing a new generation of distributed on-line taxonomic databases (see, e.g., Kennedy et al., 2005). The real-life challenge for these information repositories is to capture more than one authoritative classification; they are built to represent the full spatial and temporal dynamic of the taxonomic *process*. It is then possible to store and reference specific updates of name definitions without discarding their predecessors. Recent efforts have been summarized under the term "taxonomic concept" approach, where taxonomic concepts are essentially placeholders for the meanings (referential extensions) of names as they are specified by a particular author in a particular publication. Such concepts are labeled with the abbreviation "sec." which stands for the Latin *secundum,* or "according to" (Berendsohn, 1995). For instance, when Keller (2000) supplemented and reanalyzed Lattke's (1994) earlier phylogenetic work on the ant tribe Ectatommini, he proposed a new tribal definition and new tribal placements for various genera. These changes were significant, yet none of them required new Linnaean names. A powerful database might store one entry of Ectatommini sec. Lattke (1994) alongside another entry of Ectatommini sec. Keller (2000). The full taxonomic definitions of the two concepts could be specified and contrasted with each other (e.g., through a set of relationship symbols and additional verbal comments; Koperski et al., 2000). Lattke's (1994) and Keller's (2000) taxonomic insights regarding the tribe Ectatommini would thereby be identified to a degree of precision that reaches beyond the limits of Linnaean names.

The particular neatness of taxonomic concepts lies in their ability to "sit on top" of our traditional system of nomenclature without altering or endangering its legacy. In many everyday situations a name in itself is precise enough to serve as a vehicle for transporting thoughts about nature among speakers. Taxonomic concepts are mainly there to label variations in name/taxon assignments to a higher degree of resolution, whenever such linguistic accuracy is needed. To function properly they will require providers and users to better describe (but not redefine) the origins and meanings of taxonomic definitions, and to honor the roles of concept authors explicitly. Such a concept approach has the potential to reduce the growing gap between nomenclature and taxonomy. It may also recruit molecular phylogeneticists whose products would otherwise be lost in the primary literature.

The phylogeny/classification link must persist

The move away from classifying is just as real as the tendency to regard the inference of phylogenies as a matter of statistics. However, in my view there are no scientifically convincing reasons why modern classificatory practice and phylogenetic inference *should* be independent of each other. According to a plausible scheme for progress, a systematist produces a phylogenetic estimate. She then define and name the obtained lineages in a way that reflects their pre-existing nomenclatural histories as well as their new insights. Subsequently the names and phylogenetic meanings are exported to the widest possible range of users, including many who operate outside of the tree-thinking phylobiological community. The users will adopt the new terms to pursue research in their own areas of expertise. To the extent that the names enable them to accommodate and confirm important observations and theories, the support for the definitions also increases. In the opposite case, or when more inclusive phylogenetic analyses lead to redefinitions, more time will pass until the names become established as reliable tools for inference throughout the biological disciplines. Why untie the phylogeny/classification link and thereby lose the aforementioned mechanisms for consilience?

I also see no substantive argument for isolating classifications from *statistical* phylogenetics. Linnaean names and definitions are readily interpreted as theories about how certain natural phenomena (homologies, species, lineages) are related to our use of language. The assumption of a correspondence is testable, and its outcome is associated with a probability that may be assessed in retrospect. In the present context there is no incompatibility between the two statements "according to the DNA substitution model this lineage is recovered with a probability of 0.90" and "based on the available data angiosperms are diagnosed by their triploid endosperm."

Statistical phylogeneticists who wish to translate their results into verbal classifications face no insurmountable obstacles. Well-established thinking in the philosophy of science indicates that the phylogeny/classification link must persist in order to ensure community-wide access to, and continued testing of, the newest products of systematic research. Practitioners need this link to be made stronger and more transparent.

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References

Berendsohn, W.G., 1995. The concept of 'potential taxa' in databases. Taxon, 44, 207–212.

Bisby, F.A., 2000. The quiet revolution: biodiversity informatics and the internet. Science, 289, 2309–2312.

Boyd, R., 1991. Confirmation, semantics, and the interpretation of scientific theories. In: Boyd, R., Gasper, P., Trout, J.D. (Eds.), The Philosophy of Science. Bradford Books, MIT Press, Cambridge, pp. 3–35.

Boyd, R., 1999. Homeostasis, species, and higher taxa. In: Wilson, R.A. (Ed.), Species: New Interdisciplinary Essays. Bradford Books, MIT Press, Cambridge, pp. 141–185.

Cantino, P.D., Bryant, H.N., de Queiroz, K., Donoghue, M.J., Eriksson, T., Hillis, D.M., Lee, M.S.Y., 1999. Species names in phylogenetic nomenclature. Syst. Biol. 48, 790–807.

Cleland, C.E., 2002. Methodological and epistemic differences between historical science and experimental science. Philos. Sci. 69, 474–496.

Felsenstein, J., 2001. The troubled growth of statistical phylogenetics. Syst. Biol. 50, 465–467.

Felsenstein, J., 2004. A digression on history and philosophy. In: Felsenstein, J. (Eds.), Inferring Phylogenies. Sinauer Associates, Sunderland, MA, pp. 123–146.

Franz, N.M., 2005. Outline of an explanatory account of cladistic practice. Biol. Phil. 20, in press.

Hebert, P.D.N., Cywinska, A., Ball, S.L., de Waard, J.R., 2003. Biological identifications through DNA barcodes. Proc. R. Soc. Lond. B, Biol. Sci. 270, 313–321.

Keller, R.A., 2000. Cladistics of the tribe Ectatommini (Hymenoptera: Formicidae): a reappraisal. Insect Syst. Evol. 31, 59–69.

Kennedy, J.B., Kukla, R., Paterson, T., 2005. Scientific names are ambiguous as identifiers for biological taxa: their context and definition are required for accurate data integration. In: Ludäscher, B., Raschid, L. (Eds.), Data Integration in the Life Sciences. Proceedings of the Second International Workshop, San Diego, CA, USA, July 20–22. DILS 2005, LNBI 3615. Springer-Verlag, Berlin, pp. 80–95.

Koperski, M., Sauer, M., Braun, W., Gradstein, S.R., 2000. Referenzliste der Moose Deutschlands. Schriftenr. Vegetationsk. 34, 1–519.

Lattke, J.E., 1994. Phylogenetic relationships and classification of ectatommine ants (Hymenoptera: Formicidae). Entomol. Scand. 25, 105–119.

Lipton, P., 1993. Is the best good enough? Proc. Arist. Soc. 93, 89–104.

Nixon, K.C., Carpenter, J.M., 2000. On the other "phylogenetic systematics". Cladistics, 16, 298–318.

O'Hara, R.J., 1997. Population thinking and tree thinking in systematics. Zool. Scripta. 26, 323–329.

Pagel, M., Meade, A., Barker, D., 2004. Bayesian estimation of ancestral character states on phylogenies. Syst. Biol. 53, 673–684.

Quine, W.V.O., 1969. Ontological Relativity and Other Essays. Columbia University Press, New York.

Randall, J.E., Caldwell, D.K., 1966. A review of the sparid fish genus *Calamus,* with descriptions of four new species. Nat. Hist. Mus. Los Ang. Cty. Sci. Bull. 2, 1–47.

Ronquist, F., 2004. A broad look at tree-building. Science, 303, 767–768.

Wheeler, Q.D., 2004. Taxonomic triage and the poverty of phylogeny. Phil. Trans. R. Soc. Lond. B, 359, 571–583.

Will, K.W., Rubinoff, D., 2004. Myth of the molecule: DNA barcodes for species cannot replace morphology for identification and classification. Cladistics, 20, 47–55.