Three centuries of paradigm changes in biological classification: Is the end in sight?

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Classification has been a centerpiece of biology ever since Linnaeus, providing a framework on which existing knowledge can be organized and predictions about unknown traits can be made. But the basis of biological classification has gone through a series of upheavals over the last three centuries, from being considered a plan in the mind of the creator, to a neutral assessment of overall similarity, to a reflection of evolutionary niches, and finally to a phylogenetic mapping of the tree of life. This paper will consider this historical process, with emphasis on phylogenetic systematics (cladistics), and also consider where we might be heading in the future. It is necessary first, however, to consider the purposes of classification itself, which have not changed much over time.

KEYWORDS: cladistics, Phylocode, phylogenetic systematics, rank-free classification

PURPOSES FOR CLASSIFICATION

We need to keep firmly in mind that biological classification is a human construct, to be adopted for the uses we find most compelling in light of current understanding. Particular classifications, or general principles of classification, are not immutable or important to conserve for tradition's sake alone. Our knowledge of the biological world has changed greatly since Linnaeus, we must be free to consider changing his classification system to keep pace. Perhaps all scientists would agree in principle to this point, yet because of the weight of tradition, discussions about possible changes to the Linnaean classification rapidly become emotional, even angry (Laurin, 2008). Many systematists seem threatened to the core by any suggestion to change the classification system radically. But like any other scientific product, classification is subject to revision as knowledge increases—science should have no sacred cows. This paper will proceed in that context.

There are four general categories of desirable criteria for taxonomies (Mishler, 2000): *(1) practicality*: names should be easy to apply, stable and clear; *(2) information content*: names should index an optimal summarization of what is known about the entities being classified; *(3) predictivity*: named groups should be maximally predictive of unknown features of the entities being classified; and *(4) function in theories*: a classification should capture entities acting in, or resulting from, major natural processes. These criteria sometimes seem contradictory, for example when debates erupt between pragmatists emphasizing criterion #1 and theoreticians emphasizing criterion #4 (e.g., debates between pheneticists and cladists in the 1970s and 1980s outlined below).

Ultimately, however, these criteria should not be contradictory, and should flow from #4 to #1, in the sense that representing an important natural process in the structure of a classification will lead to high predictivity, information content, and true practicality for users of that classification. The key to "carving nature at its joints" is to find the joints first. Just as in chemistry, where the periodic table was chosen as the best way to classify elements even though it is not as practical as the simpler, earlier "Fire, Water, Earth, and Air" system, biology needed to model its primary classification system on the major natural processes affecting life. As it turns out, the overriding process turned out to be evolution.

A BRIEF HISTORY OF BIOLOGICAL CLASSIFICATION

The recognition of basic kinds of organisms, and arranging their properties into higher categories in classifications, was an ancient human imperative. All cultures have complex biological classifications, and it is extremely interesting to trace changes in these classification throughout history including the scientific era. Detailed treatments of this history include Raven & al. (1971), Mayr (1982), Dupuis (1984), Hull (1988), and Stevens (1994, 2000). I will only outline here the main historical stages.

Early folk taxonomies came out of prehistory and were oriented towards practicality and human uses of organisms (Raven & al., 1971). Organisms were grouped by their relationship with human affairs. Fine-scale groups in the hierarchy tended to compare closely with modern scientific classifications, while higher-level groups often departed radically. The first scientific revolution in biological systematics was that provided by the ancient Greeks; as in many fields of science, they justified a new logical framework within which to view the natural world. The effect of this on systematics was nicely discussed by Hull (1965): an essentialistic approach that gripped biology for 2,000 years. In this approach taxa were viewed as defined by the possession of necessary and sufficient defining traits. In the minds of taxonomists in the Christian Era, these essential characteristics were taken as evidence of the plan of creation, with the more inclusive levels in the taxonomic hierarchy being the major elements of the plan, and species the basic elements (Agassiz, 1859).

Such a view, which reached its culmination in the work of Linnaeus, became untenable as the wealth of biological diversity became known due to the explorations of the 18th and 19th centuries. It became clear that any and all characters can vary within a named group, and thus the use of defining characters became an obvious problem when a group of plants that clearly belonged together was threatened because variation was discovered in an essential character. This set the stage for the second revolution in the history of systematics, the development of the Natural System in the late 1700s and early 1800s (as discussed by Stevens, 2000). In this approach taxa were recognized by overall resemblance in many characters, which were often chosen for their "importance" in the biology of the group in question. It is important to note that this revolution in systematics preceded the Darwinian revolution, and in fact was prime evidence for Darwin to present in favor of evolution in the *Origin*. Several of Darwin's friends and correspondents such as Hooker and Gray were architects of the natural system. As has been noted by many (e.g., De Queiroz, 1988), the Darwinian revolution had no fundamental impact on systematics. The switch to the natural system had already happened. After Darwin the language systematists used became evolutionary—instead of similarities being part of a creator's plan they were now said to be inherited from common ancestors—but systematists's fundamental concepts and approaches remained the same: grouping by over-all resemblance.

This same approach was made more efficient by the advent of computerized algorithms in biology in the late 1950s and 1960s, as the numerical phenetics school developed (Sneath & Sokal, 1962). As discussed elsewhere in this volume (Jensen), numerical pheneticists developed methods for objectively grouping organisms by overall similarity in all descriptors. No fundamental change in underlying paradigms occurred, but rather a technological advance that made it possible to apply the Natural System repeatably and with many characteristics. There was no intent to apply a historical concept of homology, or to interpret the phenetic clusters as lineages (Sneath & Sokal, 1973). Pheneticists strongly emphasized the practicality criterion (#1, above). The supposedly theory-free nature of the endeavor was viewed as an advantage over a competing approach that developed from the Modern Synthesis of the 1940's, evolutionary systematics.

Evolutionary systematists, led by Ernst Mayr (1942), also used overall resemblance, but emphasizing selected characters considered of adaptive importance in the group under study. These characters often involved reproductive or ecologically important features, selected by the systematist based on his or her deep experience with the group. This approach differed from the numerical phenetics approach in a number of ways, particularly its rejection of objectivity and its overt use of a historical homology concept in choosing characters. Interestingly, however, despite these differences which were over-emphasized by extremely polemical writing in *Systematic Zoology* in the 1960s and 1970s (e.g., Mayr, 1965), neither approach resulted in a major conceptual change in systematics that could be considered a scientific revolution. Systematists of both these schools were still following a Natural System approach conceptually, in that they were using overall similarity.

A scientific revolution (in the Kuhnian sense of a change in the underlying conceptual paradigm; Kuhn, 1970) took place in the 1960s to 1980s through the work of Willi Hennig and other phylogenetic systematists (*cladists*; Hennig 1965, 1966; Nelson, 1973; Wiley, 1981; Patterson, 1982; Farris, 1983; Kluge, 1989). This advance finally connected the Darwinian Revolution to systematics (De Queiroz, 1988). The fundamental conceptual advance was rejecting the use of overall similarity in favor of what Hennig called special similarity—distinguishing between shared derived similarities (*synapomorphies*) that are indicators of shared ancestry at some level in the tree of life, and shared primitive similarities (*symplesiomorphies*) that are not indicators of shared ancestry (Sober, 1988). Hennigians recognized that the fundamental organizing principle for biological classification should be phylogeny: descent with modification punctuated occasionally by branching of lineages. They restricted the use of the formal Linnaean system to hypothesized *monophyletic groups* (i.e., groups composed of all and only descendants of a common ancestor), as evidence by synapomorphies. Following criterion #4 discussed above, the fact that living things are related to each other in a single enormous tree of life provides the ideal way for a phylogenetic classification to summarize known data about attributes of organisms and to predict unknown attributes. Monophyletic groups provide a conceptual framework, a roadmap, for interpreting biological information of all kinds.

To summarize this section, while there have been a number of technological advances, including world travel, the microscope, computer algorithms, and DNA sequence data, there have only been three scientific revolutions in the Kuhnian sense (Kuhn, 1970) in the history of systematics. I argue that only on three widely separated occasions did the fundamental conceptual basis and methodology for systematics change. One was in the introduction of logical criteria to taxonomy by the ancient Greeks, the second was the development of the Natural System, and the third was the adoption of truly phylogenetic systematics.

THE TRIUMPH OF PHYLOGENETIC CLASSIFICATION

Why is it that phylogenetic classification carried the day, and virtually all systematists (at least the younger generations) are now Hennigian phylogenetic systematists? It stems from the natural biological answer to criterion #4 above—divergent evolution is the single most powerful and general process underlying biological diversity. The major outcome of the evolutionary process is the production of an ever-branching phylogenetic tree of life, through vertical descent with modification along the branches (although some horizontal transfer among branches occurs also!). This results in life being organized as a hierarchy of nested monophyletic groups (clades), that bear homologous characteristics at each level. Since the most effective and natural classification systems are those that capture entities resulting from processes generating the things being classified, most systematists now feel that the general biological classification system should be used to reflect this tree of life. However, there still remains considerable controversy about how exactly to do this, which I will address below.

Phylogenetic taxa are truly "natural" in the sense of being the result of the evolutionary process. Natural selection might under some extreme conditions cause distantly related organisms to become very similar to each other. But such similarity will not be across the board, but rather in the suite of attributes being influenced by convergent selection (e.g., a hummingbird pollination syndrome, thorns, or succulence). Across the board, detailed matching in apparent apomorphies is more likely to be due to descent (homology) than common environment (analogy). This is true for either morphological or molecular data (Donoghue & Sanderson, 1992); contrary to common perceptions, our recent, rapid progress in understanding relationships in plants is due as much to the new cladistic methods of analyzing data as to new sources of molecular data.

The phylogenetics revolution has improved research in all areas of biology, well beyond classification. Phylogenies provide a conceptual framework for studying biological variation in an astounding array of features (e.g., Donoghue, 1989; Wanntorp & al., 1990; Brooks & Mclennan, 1991; Harvey & Pagel, 1991). They allow scientists to make predictions about species and their properties that are of biogeographical, ecological, physiological, behavioral, developmental, or genomic significance. Phylogenies are useful for summarizing all information known about biodiversity and predicting currently unknown properties of organisms. This predictive power has in turn proven useful in such areas as prospecting for novel chemicals and medicines, guiding genomic/biotechnology studies, evaluating potential cures for diseases or control measures for pests, and deciding on conservation priorities. New comparative phylogenetic methods are being proposed at an ever-increasing rate (e.g., Felsenstein, 1985; Maddison, 2000).

Yet despite the triumph of the principles of phylogenetic classification in general, and the development of associated phylogenetic methods that have revolutionized comparative biology, all is not calm and clear at present. Controversy remains in several areas, and I would like to discuss two of the most important debates, both of which encapsulate the playing out of threads that lead from the 20th century debates discussed above. Since the Hennigian revolution, the general goals of systematics have been clear: reconstruct well-supported monophyletic groups and reflect them in classifications. Nonetheless, there remains considerable controversy over methods for reconstructing phylogenetic trees, as well as how precisely to name them.

BUILDING PHYLOGENETIC TREES

The phylogenetics revolution was derived from at least three different sources. One was the comparative morphological approach and distinction between apomorphy and plesiomorphy pioneered by Hennig. A second source was derived from some aspects of numerical phenetics by the application of computer algorithms to phylogenetics (e.g., Farris, 1970). A third source was from population genetics, a concern with the descent of genes and statistical frameworks (e.g., Felsenstein, 1981). Each brought unique contributions to the mix, which acquired a sort of hybrid vigor, yet also considerable contradictions and difficulties in communication.

There remain two basic approaches to tree building: *(1)* Distance-based approaches, such as UPGMA and neighbor-joining, are still used widely in molecular studies by non-systematists. These approaches build trees using a derived distance matrix without reference back to the individual character evidence. They are slowly falling out of favor, as not being phylogenetic, nor as accurate (Huelsenbeck, 1995) so will not be discussed further here. *(2)* Character-based approaches such as parsimony, weighted parsimony, maximum likelihood, and Bayesian inference are favored by most systematists. These approaches build trees using individual hypotheses of homology (characters) directly in tree-building. All are based on an underlying model of evolution, but differ in complexity of their model.

Parsimony has the simplest model; it assumes that all characters and all character state changes are similar enough in their probability of change to be equally weighted. The basic assumption is that an apparent homology is more likely to be due to true homology than to homoplasy, unless evidence to the contrary exists, i.e., a plurality of apparent homologies showing a different pattern (Funk & Brooks, 1990). This assumption of equal weighting is very robust, when rates of change of characters are low, but it has been shown to be misleading in some cases. Parsimony can lead to mistaken reconstructions under extreme circumstances of asymmetric probabilities of change among branches on a tree (the famous Felsenstein Zone; Felsenstein, 1978; Albert & al. 1992). In such cases simple parsimony can be modified using more complicated models of change, i.e., characterizing differential probabilities of changes in different classes of characters or character-states. This can be carried out by weighted parsimony or maximum likelihood approaches (including Bayesian analysis). These more complicated approaches can be misleading also, however, if their models do not match reality closely enough (Siddall, 1998; Sanderson & Kim, 2000).

Thus there has been much ink spilled over which character-based approach is best, in what situation. My own current feeling is that these debates are overblown, for several reasons. The simulation studies that have identified situations where different model-based methods depart from the truth use admittedly extreme datasets with very high rates of change. Empirically, most real datasets give nearly identical results over a broad range of model choices. The more slowly the characters change, relative to the rate at which lineages branch, the more identical are the results between simple parsimony and complicated ML analyses (Albert & al., 1992, 1993). Therefore, given how easy it is to generate comparative molecular data these days, it is probably not worth attempting to extend the utility of a given set of data by selecting complex models. A better approach is to set aside data that are unsuitable because of evolutionary rates that are too fast for the question at hand, and look for more suitable data. Characters can and should be chosen for their suitability as markers at a particular depth in history: ease of homologizing and correct rate of change (Mishler, 2005).

The primary importance of the data matrix has been ignored in much of this controversy over tree building. The process of phylogenetic analysis per se inherently consists of two phases: first a data matrix is assembled, then a phylogenetic tree is inferred from that matrix. One could easily argue that the first phase of phylogenetic analysis is the most important phase; the tree is basically just a different way of presenting the data matrix with no value added. All the phylogenetic information content is in the data matrix. Yet paradoxically, by far the largest effort in phylogenetic theory has been directed at the second phase of analysis, the question of how to turn a data matrix into a tree. The future focus for improving phylogenetic tree building will need to be more careful choice and analysis of potential characters for particular questions (Mishler, 2005). New sources of data coming from complete genome sequences of an increasing number of organisms will facilitate this process in the future.

RANK-FREE PHYLOGENETIC TAXONOMY

Many phylogenetic systematists are resigned to applying the existing codes of nomenclature to name monophyletic groups, but several problems have become apparent. For one thing, there are not nearly enough ranks to suffice in classifying the tree of life, with its millions of branches (Laurin, 2005). This has lead to the widespread use of unranked, informal names in recent systematic studies, but these names are problematical for the reasons that led to having a code of nomenclature in the first place: the application of such informal names is unclear from study to study and the informal name of a clade can change since there is no principle of priority.

A further problem is that the need to maintain the hierarchy of the ranks under the current codes often leads to instability (i.e., names being changed without good reason) in cases of improved understanding of phylogenetic relationships. For example, if new studies show that one group currently regarded as a family is nested inside of another family, the younger family name must be dropped since one family can't be inside another (Judd & al., 1994). It would be better for the sake of users who know these groups if both names could be retained, with the added recognition that one is nested inside the other. In a rank-free classification a clade would retain its name regardless of where new knowledge might change its phylogenetic position, thus increasing nomenclatorial stability.

The two most important problems with the current codes of nomenclature that employ taxonomic ranks are different from the above, however, and these are the two I will emphasize below: *(1)* the impossibility of precisely specifying which clade is being named using only one type specimen (Ereshefsky, 2002), and *(2)* the incomparability of taxonomic ranks under a phylogenetic worldview (Laurin, 2005, 2008). Arguably, both of these problems stem from the pre-evolutionary origin of the current codes; the ranks made sense when biological classification was regarded as a reflection of a divine hierarchy, but do not make sense when biological classification is regarded as a reflection of a dynamic evolutionary process.

It has become clear that the current codes don't lend themselves well to naming monophyletic groups unequivocally, primarily because there is only one type specimen. The type belongs to the monophyletic group, certainly, but it is not clear how far back in time the named group is supposed by its author to extend. Tying a monophyletic group to one type is like navigating using only one beacon; triangulation with several beacons is needed to fix your position precisely. Similarly, the developing Phylocode (Cantino & De Queiroz, 2007) uses several specifiers to fix the name of a clade precisely. There are three ways of defining a name under the Phylocode: node-based, stem-based, or apomorphy-based (De Queiroz & Gaultier, 1992; Cantino & al., 2007), all of which use multiple specifiers.

For example (see Fig. 1), a node-based name takes the form of a statement that: "I hereby name clade X that consists of specifiers A, B, and C, and all descendants of their most recent common ancestor," while a stem-based names takes the form of a statement that: "I hereby name clade X that consists of the largest clade which includes internal specifiers A, B, and C but not external specifier Z." The difference is that the former only names the node and above, while the latter names the stem below the node as well (the latter may be more stable when new fossils are discovered). But the most important feature of this approach is that the clade being named at one particular time can be clearly interpreted in the future in the face of new data. If an additional terminal group is discovered, whether fossil or living, and it nests inside clade X it is an X; if it nests outside X as previously defined it is not an X.

Ranked classifications can lead to bad science, if a user of a classification assumes that taxa at the same rank are comparable in some way (Bertrand & al., 2006). For example, ecologists often attempt to answer questions of biodiversity or assess conservation priorities by comparing numbers of species or genera present in different habitats. Paleobiologists study macroevolutionary changes in diversity by tracking the number of families through geologic time. Alpha taxonomists worry whether a new species is different enough to be a new genus or maybe even a new family. This assumption of equivalence between groups at the same rank may seem naive to any phylogenetic systematist, but it is quite understandable. If a particular rank doesn't mean anything biologically, why would systematists present them to the world? Users would feel tricked to find out ranks are only necessary because of our chosen nomenclatorial system. There are far better alternatives to assessing biodiversity, such as the Phylogenetic Diversity Index or PDI (Faith, 1992).

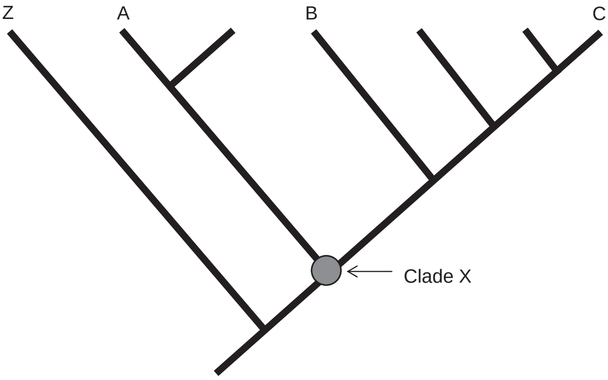

Fig. 1. An example of specifiers used in naming a clade; see text for explanation.

It is possible to jury-rig the current rank-based codes of nomenclature for use in phylogenetic systematics (e.g, Barkley & al., 2004). The current codes can certainly be tweaked to name monophyletic groups, but they are far from ideal for that purpose. For one thing, the current codes are used to name all kinds of groups, so a user has no way of easily knowing if a given taxon name is thought to be monophyletic by its author. And even if it is thought to be monophyletic, its precise limits can not be indicated with only one type specimen as discussed above. With a Phylocode-based name, the user at least knows that its author had enough evidence to hypothesize the existence of a monophyletic group, and the user can clearly test whether a new specimen is phylogenetically inside the named group, or not. Better to have a system that explicitly reflects phylogeny (the main organizing principle for biological data), than a system that can reflect anything and thus conveys nothing.

For all the reasons discussed above it is time to bite the bullet and complete a synthesis between the Darwinian Revolution and the Hennigian Revolution. Ranked classifications are a hold-over from the pre-Darwinian creationist mindset (Ereshefsky, 2002). They are not just a quaint anachronism; they are resulting in miscommunication at many levels. Completely rank-free phylogenetic classifications are far better for teaching, research, communicating with other scientists, and interfacing with the larger society. Taxonomic ranks should be abandoned, for efficient and clear representation of phylogenetic relationships, yet the retention of many unproblematic principles of the current codes of nomenclature is needed (e.g., priority, types). The developing Phylocode is an attempt to do this and codify a truly phylogenetic classification system; it will soon be published along with a companion volume serving as a new starting point (Laurin & Cantino, 2007: 114). Thus there may be another paradigm shift brewing!

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