

Definitions and Phylogenetic Nomenclature

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Recent developments in biological nomenclature suggest advantages of phylogenetic alternatives to more traditional Linnaean approaches. My aim is to discuss some fundamental aspects underlying biological nomenclature in general and phylogenetic nomenclature in particular. A basic assumption, in both traditional and phylogenetic nomenclature, is that taxon names can and should be defined. From the ontological view of individuality I question this view and argue that taxon names only refer since no defining properties are involved for particular clades. Even if we accept the idea that a taxon is a natural kind with a historical essence, and thus has defining properties, I see problems of definitions from an epistemological and inferential point of view. Our conceptualization of phylogeny is dependent on our hypotheses. Therefore, definitions based on discarded hypotheses are problematic. Instead, each new and accepted hypothesis should form the basis of our conceptualization. Another theme in this paper is what should count as the same taxon under different hypotheses. Can a phylogenetic definition guarantee that a name always refers to the same taxon under different hypotheses? I argue that this is questionable. I conclude by suggesting that we need to rethink the role of definition, sameness, and stability in nomenclature. Rethinking these concepts, I believe, will shed some new light on biological nomenclature. My conclusions strongly favor a phylogenetic approach to nomenclature but also suggest that we, besides some practical problems, still have many interesting theoretical and philosophical aspects to take into account.

Names play a prominent role both in science and life in general. Without names our ability to communicate is severely hampered. From this perspective, biological taxonomy is, perhaps, the most fundamental discipline in the biosciences because it is involved with naming biodiversity and, thus, constrains what biologists in general can talk and will think about. The names themselves function as the common currency in biological thinking. Consequently, taxon names have both a high general scientific interest as well as a more specific value for understanding and describing biodiversity.

Needless to say, biological nomenclature has a long and influential history. Linnaeus was the first to introduce a formalized approach to biological nomenclature during the 18th century with important works like *Species Plantarum* (Linnaeus 1753) and *Systema Naturae* (Linnaeus 1758). The first nomenclatural code, the Strickland Code, was published nearly 100 years later (Strickland et al. 1843), with Darwin as one of the authors, and it has been followed by more specific codes, such as the botanical code (ICBN) and the zoological code (ICZN), that are in use today. Despite many modifications, most modern approaches to biological nomenclature have their roots in the writings of Linnaeus and the notion of taxon names has remained relatively unchanged during the

last 250 years. Obviously, evolution was not in the limelight of biological thinking in the 18th century and a valid question is whether these nomenclatural approaches can be reconciled with phylogenetic theory.

In answer to this question, one can note an increased awareness in the scientific literature during the last 30 years that Linnaean based nomenclature has difficulties in conveying information about phylogeny (e.g., Griffiths 1973, 1974; de Queiroz 1992, 1994, 1997; de Queiroz and Gauthier 1990, 1992; Ereshefsky 2001; Pennisi 2001). A major concern is that the nature of the phylogenetic tree seems to be incompatible with the use of Linnaean ranks (de Queiroz and Gauthier 1990). Consequently, efforts are now underway to make phylogeny the central principle in nomenclature and to develop a rank-free system where names refer directly, and only, to clades without the detour of taxonomic ranks (e.g., de Queiroz and Gauthier 1990, 1992; Bryant 1997; Härlin 1998, 2003a, 2003b; Cantino and de Queiroz 2000; Kluge, in press; see Pleijel and Rouse 2003 for a review).

The aim of the present paper is not to review shortcomings in Linnaean-based systems (e.g., de Queiroz 1997 and Ereshefsky 2001), but instead to highlight some more general issues (e.g., definition, sameness, stability) in nomenclature. Recognizing these issues does not discourage the introduction of a phylogenetic nomenclature. On the contrary, what will emerge from the following discussion is a strong support for making phylogeny the central tenet also in nomenclature.

PHYLOGENETIC NOMENCLATURE

In the early 1990's de Queiroz and Gauthier (1990, 1992, 1994) proposed a method for making phylogeny the central component in biological nomenclature. These papers have received a relatively large amount of attention, both positive (e.g., Sundberg and Pleijel 1994; Schander and Thollesson 1995; Cantino et al. 1997; Ereshefsky 2001; Härlin 1998, 2003a, 2003b; Pleijel and Rouse 2003; Pleijel and Härlin 2004) and negative (e.g., Lidén and Oxelman 1996; Dominguez and Wheeler 1997; Nixon and Carpenter 2000; Benton 2000; Keller et al. 2003). A set of rules aimed at disciplining phylogenetic nomenclature, i.e., the PhyloCode (Cantino and de Queiroz 2000), is now present as a draft version on the web <<http://www.ohiou.edu/phylocode>>. According to de Queiroz (1997), phylogenetic nomenclature is the logical extension of the Darwinian revolution that previously has taken place in the discussions on the ontology of taxa (e.g., Ghiselin 1966, 1974, 1997; Hull 1978; Frost and Kluge 1994) and in the developments of phylogenetic inference that begun with Hennig (1966). This is what O'Hara (1988) calls tree thinking.

A modern, but traditional, system that has its roots in the writings of Linnaeus strives to achieve nomenclatural stability by utilizing types and ranks. Within such a system the name is connected to the type and a particular rank while the circumscription is made in order to demarcate one taxon from another. By tradition, morphological characters have played an important role in circumscriptions. The idea is to somehow maintain stability when adopting a new hypothesis by letting the name refer to the "same" taxon with regard to its content (i.e., terminal taxa and similar morphology) (see also Bryant and Cantino 2002). De Queiroz and Gauthier (1990) instead suggested a rank-free system where the taxon name was attached directly to a clade by a phylogenetic definition (be it node-, stem-, or apomorphy-based) that includes two or more specifiers (Cantino and de Queiroz 2000) but makes no reference to types or taxonomic rank. As a consequence, when adopting a new phylogenetic hypothesis, nomenclatural stability is provided by the phylogenetic definition referring to the same ancestor irrespective of the hypotheses. Phylogeny does, indeed, become the central principle of nomenclature, but is the phylogenetic approach without problems? Let us take a look at some potential issues.

Definitions

The explicit nature of phylogenetic definitions highlights some fundamental problems with any nomenclatural system that attempts to fit historical entities like clades. The problems of definition, sameness, and stability that I will discuss below are thus not restricted to the phylogenetic approach. Any system based on definitions (i.e., also Linnaean-based methods) suffers from similar problems (Härlin 1998; Härlin and Sundberg 1998; see also Moore 1998, 2003; Kluge, in press).

Whether definitions are applicable or not depends on the ontology of taxa. If taxa are considered to be ontological individuals, i.e., spatio-temporally restricted particulars whose existence are due to the contingent nature of evolution, then no defining properties are available (e.g., Ghiselin 1966, 1995, 1997; Härlin 1998; Härlin and Sundberg 1998; Keller et al. 2003; Kluge, in press). Names of individuals are proper and just refer to the referent through an initial ostensive connection (Ghiselin 1997) and a causal chain of reference (Kripke 1980; Evans 1982; Devitt and Sterelny 1999). That is, the name is transmitted, beginning with the ostensive attachment, from sender to receiver through history — history shapes the connection between the name and the named thing. However, from an ontological point of view, taxa need to be natural kinds (e.g., Mahner and Bunge 1997; Griffiths 1999) in order for definitions to be applicable (but see de Queiroz 1992, 1995). Natural kinds, unlike particulars, are unrestricted in time and space and, thus, have defining properties; either as shared organismal features (Mahner and Bunge 1997) or as particular common descents, historical essences in the words of Griffiths (1999). Hence, from a philosophical point of view there seems to be an inconsistency in connecting a definitional approach of nomenclature with the individuality thesis of taxa (Härlin 1998; Härlin and Sundberg 1998; Keller et al. 2003; Kluge, in press). An ontology of taxa as individuals, which seems appropriate in an evolutionary paradigm, requires a purely referential approach to nomenclature (Härlin 1998; Härlin and Sundberg 1998; see below for further discussion). On the other hand, one might argue that a tree-based approach to nomenclature (like above) is applicable irrespective of the ontology of taxa as long as one is aware of the different assumptions and implications involved — the ontology of taxa constrains explanations and predictions (Pleijel and Härlin 2004).

However, setting the ontological issue aside, there are also epistemological problems of definitions when applied in phylogenetic inference. By epistemology I mean the process of phylogenetic inference and the hypotheses that it generates. As biologists interested in phylogeny we try to infer history. Our main problem is that history cannot be directly observed — we have to rely on indirect evidence from extant and fossil specimens. Consequently we are left with hypotheses of history rather than the “real” history. Most efforts in nomenclature, be they Linnaean or phylogenetic, aim at attaching names on reality. For instance, the phylogenetic nomenclature underlying the PhyloCode uses definitions (like “Mammalia” being defined as the least inclusive clade comprising Monotremata and Eutheria) and claims that the common descent of a clade makes taxa sharing that descent logically and necessary parts of that clade (de Queiroz 1992, 1995; but see Ghiselin 1995; Härlin and Sundberg 1998); a natural kind perspective of taxa (e.g., Griffiths 1999) that echoes individuality! Furthermore, the names and definitions primarily refer to real ancestors and not hypotheses. Nevertheless, a definition (like the one of “Mammalia” above) rests on a purely inferential foundation and only makes sense within the context where it was originated (see below). This system, introduced by de Queiroz and Gauthier (1990) and labeled the phylogenetic system of definition (PSD) by Härlin (1998), also suggests that, once a taxon is conceptualized, the definitional approach refers to reality by navigation through possible hypotheses via an autopilot — the initial definition. In other words, phylogenetic definitions of taxon names suggest (1) involvement

of logical and necessary properties; (2) that a definition is erected once — no redefinitions allowed; (3) that the definition determine the inclusiveness of a taxon name in each successive hypothesis; and (4) that sameness is achieved through reference to the same real ancestor/ancestry across hypotheses.

However, at the interface between real history and observation we have the hypotheses of evolutionary history. And, these hypotheses form our conceptualization of history. Consider the example in Figure 1. Observations on extant specimens have led to a hypothesis of five different species (A, B, C, D, and E).

Based on a phylogenetic analysis we have reached a hypothesis of their phylogenetic relationships as depicted in the right hand tree. This tree structure, in turn, leads us to attach a name *alpha* to the ABC clade. The tree structure, the hypothesis of evolutionary history, thus, provides us with a particular conceptualization of history that we for some reason find important enough to name. According to the PSD approach we also attach a phylogenetic definition to the name. Such a definition could take the form “the least inclusive clade comprising A and C” and involves a subjective choice of specifiers like A and C. Again, the tree structure is most likely also to determine the choice of specifiers. Two important points should be made here. First, to what history the name refers may (is likely to) differ between hypothesis (right hand tree) and reality (left hand tree). Reality will always be cast in the shadow, somehow as in Plato’s cave metaphor. Accordingly, there will often be a discrepancy between what history the name refers to within a hypothesis and what history it may refer to in reality — a discrepancy over which we do not have any control. In other words, a name (and its definition) may imply different histories in hypotheses and reality. The impossibility to ascertain the true evolutionary history suggests that it might be beneficial to attach names to phylogenetic hypotheses only. After all, hypotheses provide us with our conceptualization of history and play the leading role in all parts of biology (Fig.2). Second, the subjective choice of specifiers plays a decisive role in the interpretation of taxon names under revised phylogenetic hypotheses (Fig. 3). That is, the choice of specifiers shapes our conceptualization of reality — it determines what we will think and talk about (Figs. 2 and 3). Inasmuch as a strict definition-

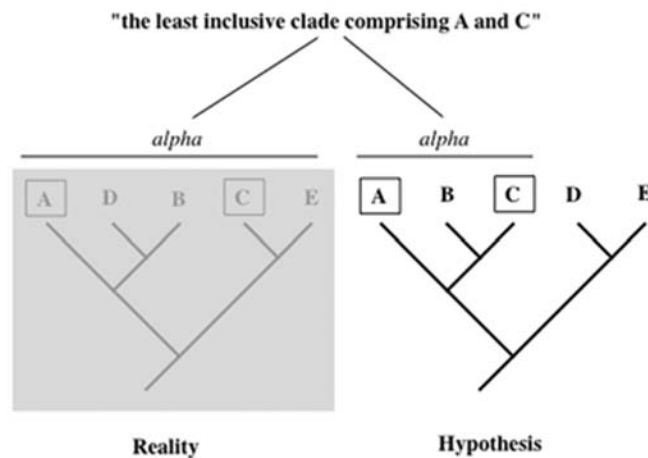


FIGURE 1. The phylogenetic hypothesis (right hand tree) provides the impetus for naming. It also forms the basis for picking specifiers and designing phylogenetic definitions. It is likely that that a taxon name refers differently in reality (left hand tree). This incongruence is out of our control and a reason why names and reference are better restricted to hypotheses only. Specifiers are marked with squares.

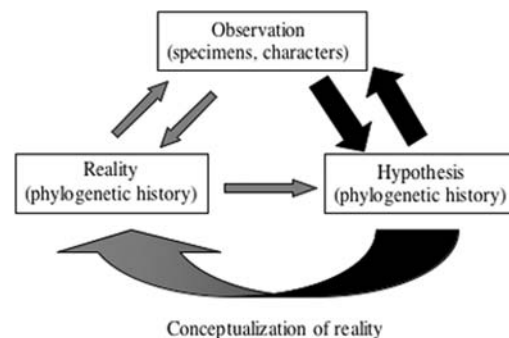


FIGURE 2. Flow diagram illustrating the central role played by the phylogenetic hypothesis and how it conceptualizes our view of phylogenetic reality.

al approach, like the PSD, does not allow for modifications in reference and/or choice of specifiers when a new hypothesis is preferred it leans heavily on the initial and subjective choice of specifiers and type of definition. It seems as if subjectivity is introduced, but not nursed.

Sameness

Connected to the issue of definition is the problem of sameness and stability. What should count as the same taxon under two successive hypotheses? In the Linnaean-based methods, nomenclatural stability equals sameness of content, and this goal is tentatively obtained by means of type and rank association. The PSD aims at another sameness, in the sense that a taxon name always refers to the same ancestor and that the phylogenetic definition with its specifiers is the tool to be used to achieve this sameness/stability. De Queiroz (1997) has clearly demonstrated that rank based systems, like the Linnaean one, suffers from instability in both name and taxon content. Similarly, sameness problems of the name "Mammalia" have been highlighted by Rowe and Gauthier (1992). My point here, however, is that phylogenetic definitions do not necessarily solve problems of sameness. As hinted in the previous lines, there are many possible kinds of sameness. Content in terms of terminal taxa (and/or internal lineages), ancestor (as in a particular point in history), and ancestry (as in the entire relational history of a clade) are all possible candidates for a concept of sameness (Härlin 1998; 2003b). Bryant and Cantino (2002) suggested that proponents of traditional nomenclature tend to emphasize the importance of taxonomic content while proponents of a PSD emphasize the importance of reference to the same ancestor. In a sense this is true, but it represents an oversimplified view of evolutionary history (Härlin 2003b) because all of these aspects are tightly intertwined and, thus, not easily, or perhaps not even possible, to separate. Strictly focusing on content is unfortunate as this restricts terminal taxa to atemporal entities, which these are not. Strictly focusing on ancestors is equally unfortunate since terminal taxa are their ancestors and vice versa (Lidén 1990), i.e., terminals are their ancestors albeit at a later point in time. Focusing on the entire ancestry of a clade puts the relational history of lineages (both terminal and internal) in focus, which is a very strict view of sameness. Arguing for sameness in terms of content is an ahistoric approach. Arguing for

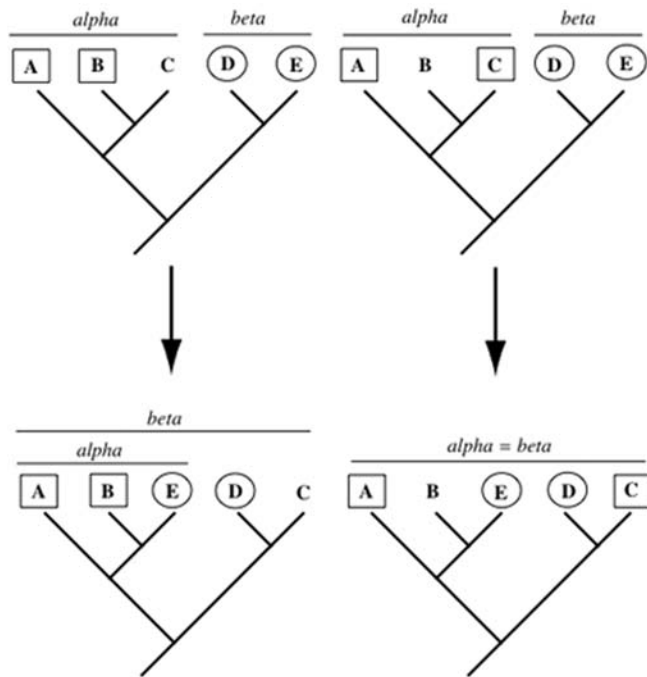


FIGURE 3. Within a definitional approach to nomenclature the acceptance of a new hypothesis comes with an automatic shift in reference. The choice of specifiers plays a crucial role in this process. Different specifiers, different reference in forthcoming hypotheses. The subjective choice of specifiers dictates our future conceptualization of reality. Specifiers for *alpha* are marked with a square and specifiers for *beta* are marked with a circle. In the left-hand trees the name *alpha* is defined as "the least inclusive clade comprising A and B," whereas in the right-hand trees as "the least inclusive clade comprising A and C". The name *beta* is defined as "the least inclusive clade comprising D and E" in both left and right-hand trees.

sameness in terms of ancestor without taking terminal taxa into account is an equally ahistoric approach. Arguing for sameness in terms of ancestry is a historic but too strict approach to sameness. My conclusion is that we need to loosen up the definitional approach and rethink the need for sameness on a case-by-case basis.

RELAXING THE DEFINITIONAL APPROACH

Arguably, the phylogenetic approach to biological nomenclature initially sketched by de Queiroz and Gauthier (1990) carries a lot of promise with it — not the least by making evolutionary history its very foundation. Still, as we have seen above it also carries some historical burden in terms of definition and the need for sameness. An effort to loosen up both the role of definition and the need for sameness across hypotheses is the phylogenetic system of reference — PSR (Härlin 1998, 1999; see also Kluge, in press). The core features of a PSR are (1) to avoid definitions since it is argued that no logical and necessary properties are involved (i.e., a particular common descent is not a defining property — taxa are individuals, not natural kinds); (2) to primarily refer to phylogenetic hypotheses; and (3) to force us to reconsider reference and specifiers with each new and accepted hypothesis.

In practice, a PSR is as phylogenetic as PSD since both aim at directly attaching names on clades. However, while a PSD has its roots in a legislative approach to nomenclature a PSR is closer to ordinary language and how names and reference evolve. The need to modify the link between the name and the named thing is common in language (Evans 1973, 1982) and also illustrates that nomenclature is meant to allow messages to be exchanged between senders and receivers. A dialogue evolves which means that an initial definition may not be enough for future communication. Forcing the taxonomist to reconsider reference and specifiers of a taxon name with each new and accepted hypothesis shifts the focus from a hidden reality to an explicit hypothesis about it. Reconsidering specifiers and reference with each new and accepted hypothesis also allows for a reinterpretation of what we mean by the same taxon. It is possible to take content, ancestor, as well as ancestry into account and to make a subjective choice of how the association between the name and the named thing should be re-established (including the possibility to change the name). Admittedly, this increases the level of subjectivity. However, once subjectivity is introduced it must be nursed in order to maintain effective communication between sender and receiver.

A phylogenetic system of reference combines the best of the Linnaean systems with the best of the PhyloCode (PSD). With the PhyloCode it shares features like being rank-free, explicitly phylogenetic, and the possibility to name parts of a tree without affecting other parts of the tree. On the other hand it allows for new circumscriptions, modifications in reference and choice of specifiers as does the Linnaean methods within their particular framework.

CONCLUSIONS AND DIRECTIONS FOR THE FUTURE

Phylogenetic nomenclature is likely here to stay. Exactly in what form is still to be settled. Any system intended for the future needs to get rid of ranks. Ranks are incompatible with phylogeny (Griffiths 1974; de Queiroz and Gauthier 1990) and also invite illegitimate, and in some areas widespread, comparisons between taxa of the “same” rank (Mishler 1999; Minelli 2000). Both PSD and PSR fulfill this requirement. These methods allow for a nomenclatural system of hierarchic and nested uninomials (or rather multinomials) that better fits a rank-free system (Härlin and Härlin 2001). A system for the future should not rest on the necessity of stability. Stability in either/or both names and content is a utopia that does not fit an evolutionary and scientific world-

view. Both names and reference should be allowed to change. That is, taxon names need not be unique — only traceable. Traceability and unequivocal communication should be the prime goals of nomenclature, not stability.

As I see it, a future system of nomenclature needs to combine the freedom of traditional Linnaean-based methods with the explicit phylogenetic operability of the PhyloCode approach. Such a system will take nomenclature to a new dimension with a focus on hypotheses and disruptiveness without losing traceability.

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