



Point of view

Misunderstandings about the phylogenetic approach to biological nomenclature: a reply to Lidén and Oxelman

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Although adoption of an explicitly phylogenetic perspective has had profound effects on both methods of systematic analysis (e.g., synapomorphy) and concepts of taxa (e.g., monophyly), it has, until recently, had little effect on the principles and rules of biological nomenclature. This situation is now changing as several authors have started to develop and put into use a system of nomenclature based on phylogenetic principles (e.g., de Queiroz & Gauthier 1990, 1992, 1994; de Queiroz 1992, 1994, 1995a, 1995b; Bryant 1994, 1996; Sundberg & Pleijel 1994; Schander & Thollesson 1995; Holtz 1996; Lee 1996a; Wyss & Meng 1996; Cantino *et al.* 1997). It was probably inevitable that this new approach would eventually be criticized by authors defending the traditional system of nomenclature, a system based on the taxonomic categories of Linnaeus. Lidén & Oxelman (1996) have recently taken up the defense of the traditional approach; however, many of their criticisms of the phylogenetic alternative are inaccurate or misleading. My purpose in this response is to call attention to errors and misunderstandings in their critique so that the debate about the phylogenetic approach to biological nomenclature can be based on its properties, the advantages of which are properly open to debate, rather than on misconceptions. Some of these points have also been addressed by Lee (1996b).

Phylogenetic systematics and the traditional nomenclatural system

According to Lidén and Oxelman, advocates of the phylogenetic approach claim that the traditional nomenclatural system “fails to accomplish the goals of phylogenetic systematics” (p. 183). This characterization is not entirely accurate. The statement made by de Queiroz and Gauthier (e.g., 1994) is that the traditional nomenclatural system fails to accomplish its own stated goals in the context of a phylogenetic concept of (higher) taxa. Lidén and Oxelman explicitly endorse a phylogenetic concept of taxa when they consider taxa equivalent to named clades, and they acknowledge that under the traditional system

the same name can be used by different authors for clades of different inclusiveness. In other words, they admit that the traditional system permits ambiguity and instability in the phylogenetic meanings of taxon names. This is the sense in which the traditional system of nomenclature fails to accomplish its own stated goals.

Lidén and Oxelman’s misunderstanding seems to result from confusing the goals of nomenclatural systems with the goals of phylogenetic systematics. The goals of phylogenetic systematics are, to summarize Lidén and Oxelman’s position, to reconstruct phylogeny and to represent phylogenetic relationships by naming clades (monophyletic entities). In contrast, some primary goals of traditional systems of nomenclature are to promote nomenclatural explicitness, universality, and stability (e.g., ICBN 1985; IMS 1992; IBC 1994). Although the traditional nomenclatural system can accommodate the tenet that taxon names must be applied only to clades, it is quite another matter whether the associations between taxon names and clades under that system are explicit, universal, and stable. Lidén and Oxelman admit that they are not, in the sense that different authors can apply the same name to different clades. Thus, there is little basis for their statements that the traditional system “works admirably well” (p. 183) and that it “will favour stability” (p. 184).

Definitions, types, and changing ideas about relationships

Lidén and Oxelman discuss the use of types in the definitions employed by traditional and phylogenetic systems, criticizing the solution to the problem of ambiguity and instability that follows directly from the use of phylogenetic definitions. According to Lidén and Oxelman, the phylogenetic approach may force renaming of well supported and familiar clades if our ideas about intra-taxon relationships change. They then note Schander and Thollesson’s (1995) suggestion to avoid reference to taxa with uncertain relationships in formal definitions, but they dismiss it as overly optimistic. In so doing, Lidén and Oxelman confuse related but distinct problems.

Schander and Thollesson's recommendation is one example of a general class of solutions that can be formulated in the context of phylogenetic definitions to prevent certain nomenclatural consequences of changing ideas about relationships. Contrary to the opinion of Lidén and Oxelman, the problem with Schander and Thollesson's recommendation is not that it is overly optimistic, but that it is designed to solve a somewhat different problem than the one with which Lidén and Oxelman are concerned. Schander and Thollesson's recommendation is designed to deal with uncertainty about whether a particular terminal taxon (designated *incertae sedis* in the terminology of Wiley 1981) is a member of a larger clade. If the name of the larger clade is defined with reference to such a taxon, and if the phylogenetic position of that taxon is later found to be outside of the larger clade, then the name in question may end up referring to a more inclusive clade than was originally intended (Schander & Thollesson 1995).

In contrast, the problem of concern to Lidén and Oxelman does not involve a case of uncertainty about whether certain terminal taxa are members of a particular larger clade (Angiospermae, in their example) but rather about the internal relationships within that clade. And in such cases, the solution is not to avoid reference to the taxa whose relationships are uncertain but rather to mention them explicitly. For example, defining "Angiospermae" as "the clade stemming from the most recent common ancestor of Ceratophyllaceae, Magnoliales, Laurales, paleoherbs, monocots, and eudicots" would prevent the unintended removal of magnoliids from Angiospermae in Lidén and Oxelman's hypothetical example (see also Lee 1996b). Wyss and Meng (1996) discuss several additional alternatives. Thus, changes in ideas about intra-taxon relationships do not pose a problem for the phylogenetic approach.

Different classes of phylogenetic definitions

Another misunderstanding of Lidén and Oxelman concerns different classes of phylogenetic definitions. Although they mention node-, stem-, and apomorphy-based definitions (p. 184), their criticisms overlook important differences between these three classes of phylogenetic definitions, treating all three as if they have the properties of node-based definitions. For example, Lidén and Oxelman seemingly consider all phylogenetic definitions to be based on two or more 'types' (taxa used as points of reference in definitions). While this is indeed true for node-based definitions (those taking the form "the taxon stemming from the most recent common ancestor of 1 and 2"), it is certainly not true for apomorphy-based definitions (those taking the form "the taxon stemming from the first ancestor of 1 to bear character a") (see also Lee 1996b). Furthermore, although stem-based definitions (those taking the form "the taxon composed of all species sharing a more recent common ancestor with 1 than with 2") refer to at least two taxa, one of those taxa is not a member of the clade whose name is being defined and hence probably should not be considered a type. Lidén and Oxelman object to the use of multiple reference points

('types') based on their supposition that this practice will result in the renaming of well-supported and familiar clades if ideas about relationships change. As I have argued in the preceding section, that supposition is erroneous.

Some of the problems that Lidén and Oxelman attribute to phylogenetic definitions are more appropriately attributed to their own oversights concerning the three classes of phylogenetic definitions. For example, they note that if the name "Agamidae" is defined as the "clade stemming from the most recent common ancestor of *Agama* and *Leiolepis*", then any newly discovered species falling outside of the node in question is not part of Agamidae—even if it shares most of the synapomorphies of that taxon. Although this conclusion does indeed follow from the node-based definition used in their example, it is irrelevant. Lidén and Oxelman's concept of the taxon Agamidae apparently is based on the possession of particular synapomorphies, and it is to be expected that a node-based definition will not adequately describe an apomorphy-based concept. An apomorphy-based definition is required. If the name Agamidae had been defined using an apomorphy-based definition, then any newly discovered species possessing the relevant apomorphy would, of course, be included in the taxon designated by that name. Stem-based definitions have similar properties.

Taxonomic categories and binomials

Lidén and Oxelman believe that adoption of a phylogenetic approach to nomenclature would require "the abandonment of ranks and binomial nomenclature" (p. 184). On the contrary, neither ranks (taxonomic categories) nor binomials would have to be abandoned (de Queiroz & Gauthier 1992; de Queiroz 1997). A consequence of the phylogenetic approach is that it would render categorical assignments irrelevant with regard to nomenclature (de Queiroz 1996, 1997), but taxonomic categories could still be used to represent hierarchical relationships. Alternatively, different representational devices—such as indentation or numerical prefixes—could be used instead. Similarly, adoption of a phylogenetic approach would not require the elimination of binomials, though it would require a different interpretation of the first of the two names making up a binomial, which would no longer be the name of a genus (Griffiths 1976; de Queiroz & Gauthier 1992). Alternatively, uninomials could be used instead (de Queiroz & Gauthier 1992). The phylogenetic approach would thus permit, rather than require, elimination of the Linnaean taxonomic categories and binomials.

Supposed advantages of the traditional approach

Lidén and Oxelman list what they consider three main advantages of the traditional nomenclatural system over the phylogenetic alternative. Let us consider these purported advantages in order:

A) Its ability to reflect a phylogenetic hierarchy with a series of nested ranks (taxonomic categories). As noted

above, the phylogenetic approach can also use taxonomic categories to reflect hierarchical relationships, so this hardly counts as an advantage of the traditional system. In addition, Lidén and Oxelman point out that under the phylogenetic approach the forms of taxon names (i.e., their endings) would not necessarily reflect subordination in the hierarchy (i.e., categorical assignments). They neglect to mention that this is also true under the traditional approach for names of zoological taxa above the level of the family group as well as for names of botanical taxa above the rank of family that are not based on names of genera. In any case, it is debatable whether rank-signifying endings represent a significant advantage of the traditional approach, given that hierarchical subordination can be conveyed by other means (e.g., numerical prefixes) under the phylogenetic approach. More importantly, the use of rank-signifying endings entails that categorical assignments are built-in to taxon names. As a consequence, the associations of those names with particular Linnaean categories are granted more importance than their associations with particular clades, and this is what causes ambiguity and instability under the traditional approach (de Queiroz 1997). Rather than constituting an advantage of the traditional approach, rank-signifying endings are part of its most significant disadvantage.

B) Its flexibility as to inclusiveness of a named entity at a specific rank, i.e., inclusiveness can be adjusted in accordance with tradition and convenience, should ideas about relationships change. Lidén and Oxelman consider stable names for the best supported clades desirable, but they mistakenly believe that the phylogenetic approach requires a correct and complete picture of relationships to accomplish this goal (Lee 1996b). As noted above, the phylogenetic approach includes methods for maintaining associations between names and particular sets of terminal taxa despite changing ideas about relationships. Although the phylogenetic approach cannot prevent certain kinds of ambiguity and instability, at least its difficulties in this regard result solely from differences or changes in ideas about a natural phenomenon, phylogeny. In contrast, ambiguity and instability in the traditional system can also result from differences or changes in ideas about an artificial construct, assignment of taxa to Linnaean categories. Consequently, not only does nomenclatural ambiguity and instability in the traditional system stem from ideas that are not subject to empirical evaluation, but they can also exist even when there is complete agreement about phylogenetic relationships. Much of the ambiguity and instability in the traditional system is a direct result of its flexibility in terms of the associations between taxa and taxonomic categories. Such flexibility hardly qualifies as an advantage.

C) Its strict and straightforward rules for typification. The rules for defining taxon names (typification) can be just as strict and straightforward under the phylogenetic approach. For example, a definition taking the form "the most inclusive clade containing both 1 and 2" is no less strict or straightforward than one taking the form "the taxon containing 1 that is assigned to Linnaean category A". It is true that more complicated definitions are

required to avoid unintended changes in the hypothesized composition of taxa, but this is simply the price that must be paid to make the intended meanings of taxon names unambiguous in the context of uncertain phylogenetic relationships under any nomenclatural system. The traditional approach does not solve but rather ignores this problem by retaining simple definitions and, as a consequence, tolerating ambiguity and instability in the associations between taxa and taxon names. The traditional system holds no advantage over the phylogenetic alternative in terms of definitional simplicity, and in any case, it is not at all clear that simple definitions are preferable.

Conclusions

It is ironic that Lidén and Oxelman, professed proponents of a phylogenetic approach to systematics, oppose a similar approach to nomenclature. They advocate a phylogenetic concept of taxa (p. 183), yet they are reluctant to fully embrace that concept by defining the names of taxa in an explicitly phylogenetic manner. They acknowledge that the traditional system of nomenclature promotes ambiguity and instability with regard to the associations between names and clades (p. 183), yet they consider the source of those problems, the non-phylogenetic nature of that system, a strength. Finally, they assert that the traditional system is perfectly compatible with phylogenetic systematics, yet they invoke Hennig (1966) as the authority for that discipline (p. 184). Hennig, in contrast, perceived significant incompatibilities between the traditional Linnaean approach to taxonomy and phylogenetic systematics (see especially Hennig 1969, 1981). He noted that fruitless debates about the categorical assignments of taxa often interfere with the fundamental questions of phylogenetic systematics. Moreover, he effectively rejected the traditional approach by deliberately refraining from assigning taxa to Linnaean taxonomic categories, using instead a system of numerical prefixes to convey hierarchical relationships. Contrary to the claims to Lidén and Oxelman, the traditional Linnaean approach to taxonomy and nomenclature is not particularly compatible with phylogenetic systematics. Fortunately, this problem can be solved by extending the explicitly phylogenetic approach that underlies Hennig's writings on systematics into the realm of nomenclature.

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