

Phylogenetic Nomenclature and the PhyloCode

Kevin de Queiroz

*Department of Systematic Biology, National Museum of Natural History,
Smithsonian Institution, Washington, DC 20560-0162, U.S.A.*

Philip D. Cantino

*Department of Environmental and Plant Biology, Ohio University, Athens,
OH 45701-2979, U.S.A.*

In a recent paper Forey (2001; BZN 58: 81-96) provided a description of the draft Phylogenetic Code of Biological Nomenclature (PhyloCode; <http://www.ohiou.edu/phylocode/>), followed by a largely negative commentary. Several of Forey's criticisms of the system of phylogenetic nomenclature embodied in the PhyloCode stem from misunderstandings about that system, and several confuse taxonomic with nomenclatural issues. In fact, the PhyloCode would regulate the naming of taxa and the subsequent application of taxon names in ways that are thoroughly consistent with the taxonomic approach that he advocates. In this essay, we comment upon some aspects of Forey's description of the draft PhyloCode, and we explain why none of his criticisms represent serious problems.

Forey's Part 1 (Goals and Mechanics of the PhyloCode)

Part 1 of Forey's paper was intended to provide readers with an impartial description of the goals and mechanics of the PhyloCode. This section is largely accurate but omits some important issues, which we would like to describe, and contains some misleading statements, which we would like to clarify.

Motivation for the PhyloCode

One important topic omitted by Forey is a discussion of the pragmatic issues that motivated development of the PhyloCode. The PhyloCode is designed to make explicit the reference of taxon names to clades, and thereby bring the subsequent application of taxon names into line with contemporary (i.e. evolutionary) conceptualizations of taxa (de Queiroz & Gauthier, 1994; de Queiroz, 1997). In so doing, it simplifies the process of naming clades and thereby facilitates communication about phylogeny. The need for an effective and efficient system for naming clades is particularly urgent now, as the unprecedented progress in phylogenetics in the past decade is likely to accelerate even further in the coming years, and the current system of nomenclature, as embodied in the International Code of Zoological Nomenclature (Zoological Code) and its botanical and bacteriological counterparts, is poorly suited to govern clade names. Under the current system, authors use the same names for different clades, and different names for the same clade, even when there is no disagreement about relationships and composition (de Queiroz & Gauthier, 1994; de Queiroz, 1997). Moreover, many newly discovered clades, even well-supported ones, are currently left unnamed, at least in part because it is often difficult: (1) to name clades one at a time (in the way that species are named as they are discovered) without having to develop an entire new classification and thus change the names of

other clades (Kron, 1997; Hibbett & Donoghue, 1998), and (2) to name those clades that one wants to name without having to recognize groups that one does not want to recognize (Cantino, 2000).

The feature of the traditional system that underlies all of these problems is the link between names and ranks. Because of this link, authors who agree about the relationships and composition of clades but disagree about ranks will use different names for the same clade and the same name for different clades. Moreover, because a clade must be given a rank in order to name it, naming a newly discovered clade under the Zoological Code may require developing a new classification, which authors may be reluctant to do. The ranks of all taxa in a classification are interdependent. Therefore, depending on the availability of unoccupied ranks, naming a new clade may cause a cascade of name changes at higher or lower levels in the hierarchy when clades that include or are included within the newly discovered clade shift in rank and must therefore be renamed (Kron, 1997; Hibbett & Donoghue, 1998). Finally, because the genus rank is mandatory, and others (e.g. family) are treated by convention as though they were mandatory, naming a new clade may necessitate naming other taxa at the same rank even though one does not accept those taxa because they are paraphyletic, redundant (monotypic), or poorly supported (Cantino et al., 1999; Cantino, 2000). Under the PhyloCode, these problems do not exist because taxonomic rank has no bearing on the spelling or application of names. Instead, names are linked directly and explicitly to clades through phylogenetic definitions.

Similarities and differences between traditional (rank-based) and phylogenetic nomenclature

Another important issue not discussed by Forey concerns the fundamental similarities and differences between the PhyloCode and the Zoological Code (and the other codes of rank-based nomenclature). Regarding similarities, the PhyloCode has the same general goals as the Zoological Code, namely, the provision of rules for naming taxa and applying existing names in new taxonomic contexts so that the names of taxa, and the application of names, will be unambiguous within a given taxonomic context. In addition, the PhyloCode is like the Zoological Code in attempting to promote stability and universality in the names of taxa and the application of names, so far as that is possible given that both codes permit disagreements concerning taxonomic hypotheses. Moreover, the PhyloCode accomplishes these goals using the same general mechanisms as in the Zoological Code, that is, by establishing precedence (an order of preference) among synonyms or homonyms, which is normally based on priority of publication (seniority) but which allows for exceptions (usually through rulings by a commission or committee) in cases when using priority to determine precedence would compromise nomenclatural stability or universality.

The main difference between the PhyloCode and the Zoological Code concerns the manner in which names are linked to taxa. In both cases, names are linked to taxa using definitions, but differences between the types of definitions used under the two codes result in differences in how names are applied in new taxonomic contexts and thus which names are regarded as synonyms. (It should be noted that the definitions referred to here are statements specifying how names are to be applied, as opposed

to statements describing the characters of the taxa to which the names refer.) Forey described three categories of phylogenetic definitions (the type of definitions used in the PhyloCode), and illustrated how a particular name ('Aves') might be defined using definitions in each of the three categories (i.e. node-based, stem-based, and apomorphy-based). He did not, however, describe the rank-based definitions used in traditional nomenclature. This omission is important both because rank-based definitions, though they are the foundation of the Zoological Code and other traditional codes, are not described explicitly in those codes (instead, their use is implied by the way traditional nomenclature works), and because the difference between rank-based and phylogenetic definitions is the most fundamental difference between traditional and phylogenetic nomenclature.

In contrast with phylogenetic definitions, which are based on the phylogenetic relationships of designated specifiers (e.g. 'Aves' is the name of the least inclusive clade containing (say) *Struthio camelus* and *Corvus corax*), traditional definitions are based on the ranks of taxa containing designated types. Thus, to use the same name used by Forey in his examples, 'Aves' is the name of the class containing (say) *Corvus corax*. This example is, of course, hypothetical, since the Zoological Code does not extend its principle of typification (and thus its method of definition) to names above the level of the family group. To use a real example, 'Corvidae' is the name of the family containing *Corvus*. The fundamental difference between phylogenetic and traditional definitions results in an important difference regarding the associations between names and clades. Phylogenetic definitions tie names directly to clades; in contrast, traditional definitions tie names to clades only indirectly through the ranks to which the clades are assigned. The most important consequence of this difference is that names in phylogenetic nomenclature are more strongly tied to clades than to ranks (i.e. in the face of changing taxonomic proposals), while in traditional nomenclature the reverse is true – names are more strongly tied to ranks than to clades (de Queiroz, 1997). This difference underlies both the problems with traditional nomenclature and the advantages of phylogenetic nomenclature described in the previous section.

Phylogenetic definitions and specifiers

Regarding definitions, a few statements in Forey's Part I are potentially misleading. On p. 84, Forey stated (para. 3) that specifiers (species, specimens, or apomorphies cited in a phylogenetic definition to specify the clade to which the name applies) 'serve exactly the same function as Linnaean types except their characters do not define the clade'. There are two ways in which this statement may be misleading. First, while it is true that the specifiers of phylogenetic nomenclature and the name-bearing types of traditional nomenclature both serve as reference points for the application of names, there are also differences in their functions. The most fundamental difference is that specifiers are so called because they specify the taxon to which a name refers. Thus, the specifiers of phylogenetic nomenclature are used, as parts of phylogenetic definitions, to specify particular clades. In contrast, in traditional nomenclature types do not, by themselves, specify particular taxa (clades or otherwise) because several nested taxa may contain a given type. A rank is needed to restrict the reference of the name to one of the several nested taxa containing that type, and thus, in one sense, the specifiers of traditional nomenclature are both types

and ranks. However, in another sense, traditional definitions do not really specify particular taxa (i.e. 'taxonomic taxa' in the sense of the Zoological Code—that is, taxa that are conceptualized in terms of composition, characters, or relationships, rather than solely in terms of a rank and a type), because a given name can be applied to any one of several taxa in a nested series, depending on which one is assigned the specified rank. In this sense, types are not really specifiers at all. Therefore, regardless of whether taxa are conceptualized solely in terms of ranks and types, types are not functionally equivalent to specifiers.

Another difference between types and specifiers (related to the fundamental difference described above) is that single types are used in traditional definitions while, in contrast, multiple specifiers are required in phylogenetic definitions. Furthermore, under the traditional codes, the type used to define a name in the family group provides the stem of the name of the taxon of which it is the type (e.g. Zoological Code, Article 29). In contrast, under the PhyloCode, (1) the specifiers used to define clade names need not provide the stem of the name of the specified clade (e.g. neither *Struthio camelus* nor *Corvus corax* provide the stem of the name 'Aves' in the above example), (2) one or more of the specifiers can serve this function (e.g. *Corvus corax* for 'Corvidae'; *Gallus gallus* and *Anser anser* for 'Galloanserae'), and (3) when a specifier provides the stem of a clade name, it does so regardless of rank.

An additional problem is that Forey's statement could be interpreted as implying that the characters of types define clade names while those of specifiers do not. In fact, the characters of neither types nor specifier species or specimens define the names of clades. In the case of types, a clade name is defined in terms of the rank of the group that contains the type, rather than the characters of the type (e.g. Corvidae = the family containing *Corvus*). In the case of specifier species or specimens, a clade name is defined in terms of the relationships of the specifiers, rather than their characters (e.g. Corvidae = the least inclusive clade containing (say) *Corvus corax* and *Platylophus galericulatus*). The only characters that are used to define clade names are specifier apomorphies, which are used in apomorphy-based phylogenetic definitions (e.g. Diapsida = the clade stemming from (say) the first amniote to evolve two temporal fenestrae homologous with those in *Sphenodon punctatus*) but not in the rank-based definitions of traditional nomenclature. Of course, regardless of whether one adopts traditional or phylogenetic nomenclature (and regardless of the type of phylogenetic definition used), the relationships and composition of taxa are inferred using characters. This, however, is a taxonomic rather than a nomenclatural issue.

Compositional changes and nomenclatural stability

Although Forey's Part 1 was intended to be impartial in its portrayal of the PhyloCode, a subtle bias was introduced through his choice of examples (see particularly his Fig. 2), all of which concern taxa ranked above the level of the family group. The names of such taxa are not defined (i.e. according to rank and type) and, for the most part, are not regulated by the Zoological Code. Consequently, Forey implicitly contrasted the ramifications of the PhyloCode not with those of the Zoological Code but with the more or less total nomenclatural freedom that would exist in the absence of any code. Most of the rank-based problems cited above, which come into play when taxon names are defined according to rank and type, do not

apply to the names of zoological taxa at ranks above the family group, where the principle of typification does not extend. As a result, readers of Forey's paper who might not like the changes in taxon composition that occur when names are applied in the context of different phylogenetic hypotheses under the PhyloCode (Forey's Fig. 2) might overlook the fact that similar changes in taxon composition occur under the traditional codes (de Queiroz, 1997). Changing ideas about phylogeny cause changes in the hypothesized composition of taxa under both systems, but under the Zoological Code, unlike the PhyloCode, additional instability in the names of clades and the membership of taxa results from changes in rank (i.e. through 'lumping' and 'splitting') even when ideas about phylogeny are stable (de Queiroz, 1996, 1997; Bryant & Cantino, in press). Furthermore, with regard to zoological names above the level of the family group, the PhyloCode will increase nomenclatural stability. Currently, no code governs the definition and application of these names, and thus, there is nothing to prevent the capricious renaming of clades – that is, the replacement of existing names with unnecessary substitute names.

The primary function of taxon names

Forey's discussion (p. 85) of PhyloCode Principle 1 suggests a misunderstanding of its intent. Principle 1 states that '*the primary purpose of taxon names is to provide a means of referring to taxa, as opposed to indicating their characters, relationships, or membership*'. This statement is adapted from item 1 in the Preamble of the International Code of Botanical Nomenclature. Its purpose is to describe the principle that although taxon names often describe the characters (e.g. Gnathostomata = jaw mouth), relationships (e.g. *Paradipsosaurus* = near *Dipsosaurus*), or membership (e.g. Galloanserae = Galliformes plus Anseriformes) of the taxa to which they refer, conveying such information is a secondary function of taxon names; the primary function is to supply a means of referring to taxa. Consequently, the PhyloCode does not permit rejection of a name simply because the name does not accurately describe the characters, relationships, or composition of the taxon to which it refers. The same is true under the Zoological Code (see Article 18). Thus, *Paradipsosaurus* is still the valid name of a taxon, even though that taxon is no longer thought to be closely related to *Dipsosaurus* (Estes, 1983).

It appears that Forey misinterpreted Principle 1 by confusing taxonomic and nomenclatural issues. He quoted that principle in three successive paragraphs (p. 85) to point out three different properties of phylogenetic nomenclature: (1) that '*a shift in taxon membership with changing ideas of phylogeny is perfectly acceptable to the PhyloCode*'; (2) that '*ideas of relationships can vary substantially . . . but . . . there will always be some position . . . on a phylogeny where [a name] will apply*'; and (3) '*a name is applied to a phylogeny without reference to why that phylogeny should have been chosen*'. Forey described these properties as if they were undesirable, but all three are also properties of traditional nomenclature (or at least have analogs therein). Thus, in traditional nomenclature: (1) changes in taxon membership often result from changing ideas about phylogeny; (2) ideas about relationships can vary substantially, but certain names will always apply to some taxon, and (3) names can be applied in the context of a taxonomic proposal without reference to the justification for adopting that proposal. All of these properties, which are common to both traditional and phylogenetic nomenclature, are related to the basic principle that

nomenclatural codes do not infringe upon taxonomic judgement but only regulate the application of names (Zoological Code, Principles 1 and 2; PhyloCode, Principle 6). These properties are neither unique to phylogenetic nomenclature nor problematical.

Synonymy

Another point of confusion in Forey's Part 1 concerns synonymy. Forey stated (p. 87) that under the PhyloCode '*With regard to synonymy there is the possibility of two names specifying the same taxon but since they may be defined in different ways (e.g. stem- and node-based) they may both be valid*'. To support this conclusion, Forey cited PhyloCode Note 14.1.2, which reads: '*Node-based, apomorphy-based, and stem-based definitions (Note 9.4.1) usually designate different clades, although they may be nested clades that differ only slightly in inclusiveness. Therefore names based on two or more of these different kinds of definitions are usually not synonyms*'. The qualifier 'usually' was included to cover the rare possibility that names defined using different kinds of phylogenetic definitions might refer to the same clade (e.g. if the apomorphy specified in an apomorphy-based definition originated (or became fixed) at precisely the same moment as the divergence (from its sister lineage) of the stem lineage specified by a stem-based definition). However, in this rare event, the names in question would be synonyms despite their being based on different types of definitions (such 'hetero-definitional synonyms' are analogous to names that the Zoological Code terms 'subjective synonyms' in that the conclusion that they refer to the same taxon depends on a taxonomic judgement). According to the PhyloCode (Principle 3 and Article 14.2), if two names denote the same taxon, then they are synonyms and cannot both be valid (in the terminology of the Zoological Code = 'accepted' in the terminology of the PhyloCode). Thus, although Forey is correct in pointing out that names defined using different types of phylogenetic definitions can sometimes refer to the same taxon, he is incorrect in stating that more than one such name can be valid.

Forey's Part 2 (Commentary)

The second part of Forey's essay is explicitly critical of phylogenetic nomenclature and the PhyloCode. Forey's criticisms, however, either misrepresent the PhyloCode or are no more problematical for phylogenetic nomenclature than for its traditional counterpart. In this section, we address each of Forey's criticisms and show that phylogenetic nomenclature stands up to every one.

Taxonomic ranks

In the introduction to his commentary (pp. 88–89), Forey incorrectly implied that phylogenetic nomenclature and the PhyloCode require the abolition of taxonomic ranks. Although it is true that some advocates of phylogenetic nomenclature favor the abolition of ranks and that the nomenclatural system described by the PhyloCode is rankless (Article 3.1), adoption of phylogenetic nomenclature and the PhyloCode does not require the elimination of ranks. The statement that the system of nomenclature is rankless does not mean that taxa cannot be assigned to ranks (de Queiroz, 1997); instead, it means only that '*assignment of a categorical rank (e.g. genus, family, etc.) is not part of the formal naming process and has no bearing on the spelling or application of taxon names*' (Article 3.1). In other words, if a name refers

to a clade, then changing the rank of that clade does not cause a change in its name (de Queiroz, 1997). Under the traditional system, changing the rank of a taxon from family to subfamily, for example, requires a change in the name of that taxon (e.g. from 'Corvidae' to 'Corvinae'). Under the PhyloCode, the same change in rank would not result in a name change. In any case, the PhyloCode does not prohibit the use of ranks, and therefore, Forey's concerns about its effect on the assessment of biodiversity are unfounded. Biologists will still be able to rank taxa, if they so desire, and thus to count numbers of taxa at particular ranks.

On the other hand, there are problems with these simple counts of equally ranked taxa. For one thing, such counts generally do not distinguish between monophyletic and paraphyletic taxa (Smith & Patterson, 1988; Smith, 1994). Moreover, it is widely acknowledged that taxa of the same rank generally are not comparable with respect to any biologically significant property, such as age, number of species, or disparity (Hennig, 1966; Mayr, 1969; Mayr & Ashlock, 1991), and that rank assignment is largely subjective, varying from one taxonomist to another (Simpson, 1961; Mayr & Ashlock, 1991). The PhyloCode's de-emphasis on ranks permits (without requiring) the abandonment of ranks and thus encourages biologists to develop more meaningful ways of assessing diversity. One obvious possibility is to count numbers of species (i.e. separately evolving lineages). Another possibility is to count the number of mutually exclusive clades possessing properties that are relevant to the question being addressed. For example, one might count the (minimum or maximum) number of non-nested clades that originated or became extinct in a particular time period, or the number that are characterized by organisms exhibiting different natural history strategies with regard to reproduction (e.g. oviparous, viviparous), feeding (e.g. carnivorous, herbivorous), metabolism (e.g. ectothermic, endothermic), etc. To assess overall similarity or disparity, multivariate measures can be used (e.g. Foote, 1995) rather than using subjectively assigned ranks. And, in biodiversity inventories, organisms that cannot be assigned to a species can still be assigned to more inclusive clades, regardless of whether those clades are ranked. In short, the PhyloCode's de-emphasis on ranks, rather than hindering studies of biodiversity, might actually contribute to the development of improved methods for such studies.

Annotated Linnaean systems

Because ranking is often associated with the recognition of paraphyletic taxa, Forey himself has 'some sympathy' (p. 89) for the development of rank-free approaches. On the other hand, he believes that 'there are ways around the problem which do not involve the adoption of a PhyloCode' (p. 89, para. 2), specifically 'the annotated Linnaean system' (p. 89) developed by authors such as Nelson (1973), Patterson & Rosen (1977), and Wiley (1979). Forey's statements are misleading on several counts, which (in addition to resting on the incorrect premise that phylogenetic nomenclature prohibits the use of ranks) result from his not distinguishing consistently between taxonomy and nomenclature. First, although it is true that paraphyletic taxa can be eliminated and the relationships of monophyletic taxa can be conveyed using annotated Linnaean systems, these are taxonomic solutions that are logically and pragmatically separate from the nomenclatural problems that the PhyloCode is designed to solve. Rather than being designed to convey the relationships of monophyletic taxa (clades), the PhyloCode is designed to prevent

unnecessary changes in the associations between taxon names and clades that result under the Zoological Code from changes in taxonomic ranks. This nomenclatural problem is not addressed by the annotated Linnaean system advocated by Forey, which consists of conventions – such as phyletic sequencing (Nelson, 1973) and the plesion category (Patterson & Rosen, 1977) – designed to reduce the proliferation of taxonomic ranks, as well as other conventions for representing polytomies, uncertain placement within a larger clade, non-monophyletic groups, ancestors, taxa of hybrid origin, and distinctiveness (Wiley, 1979, 1981). Most of these conventions are taxonomic rather than nomenclatural in nature and are compatible with both traditional and phylogenetic nomenclature. In any case, they do not solve the problem of rank changes causing name changes.

It is worth pointing out that several of the conventions of the annotated Linnaean system advocated by Forey de-emphasize the use and importance of ranks and might therefore be considered to anticipate the development of phylogenetic nomenclature in this regard (de Queiroz, 1997). For example, the sequencing convention (Nelson, 1974) uses the sequence of taxon names in a list, rather than ranks, to convey information about relationships. Similarly, the plesion, a category used for extinct taxa regardless of their position in the taxonomic hierarchy, is basically a rankless category. It might even be argued that the plesion category is incompatible with traditional nomenclature, given that it is rankless and that ranks are necessary for traditional nomenclature. In short, the conventions advocated by Forey do not constitute an alternative to the PhyloCode; instead, most are taxonomic conventions the use of which is entirely compatible with phylogenetic nomenclature.

Types and specifiers

Forey argued (p. 89) that there is no fundamental difference between the specifiers of the PhyloCode and the name-bearing types of traditional nomenclature and that the replacement of types by specifiers in the PhyloCode is therefore unnecessary. As explained above (*see Phylogenetic definitions and specifiers*), types and specifiers have both similarities and differences, though the concept of a specifier is more general than the concept of a type. Thus, specifiers include not only specimens and taxa, but also apomorphies in phylogenetic nomenclature and ranks in traditional nomenclature. Some other differences are as follows. (1) Although both specifiers and types serve as reference points for the application of names, the use of multiple reference points (specifiers) is necessary in phylogenetic nomenclature because a single specimen or subordinate taxon cannot unambiguously specify a clade in the way that a single type can unambiguously specify a ranked taxon. (2) Types are necessarily included within the taxon whose name they are used to define, while in stem-based phylogenetic definitions, some specifiers (called 'external specifiers' in the PhyloCode) are necessarily excluded from the specified clade (as noted by Forey on p. 84). (3) In contrast with the rule of the Zoological Code that the name of a taxon in the family group must be formed from the stem of the name of the type genus, the PhyloCode does not require that the name of a clade be formed from the stem of the name of one of the specifiers used to define that name. Given these differences between types and specifiers, introduction of the new term 'specifier(s)' in the PhyloCode is appropriate.

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When to name

Forey made much of the statement in the PhyloCode Preface that '*Criteria that influence the decision whether to name a clade include level of support, phenotypic distinctiveness, economic importance, etc.*'. He referred (p. 90) to this as a 'recommendation' of the PhyloCode and concluded that '*advocates of phylogenetic taxonomy really do not have any more precise reasons for naming a group than do followers of Linnaean Taxonomy and to include advice in the PhyloCode registers a precision which is both unnecessary and undesirable*'. This criticism is misdirected. For one thing, advocates of phylogenetic nomenclature do not claim to have more precise or objective reasons for naming taxa than do practitioners of traditional nomenclature. Such decisions are taxonomic, not nomenclatural, and therefore are beyond the scope of both the PhyloCode and the Zoological Code. Moreover, contrary to Forey's assertion, the PhyloCode does not include advice about when to name a clade. The statement that he quoted is in the Preface, and although there are many formal recommendations in the PhyloCode itself, this is not one of them. It was included in the Preface simply to elaborate on the preceding statement that not all clades need be named. Furthermore, it is difficult to see how the statement itself, which lists only very general criteria and ends in 'etc.', conveys an unwarranted level of precision. It should be apparent from both the context and the wording that none of the cited criteria is definitive, and that the list is not exhaustive. The listed criteria are simply examples of criteria that would generally be considered when one is deciding whether to name a clade.

In this context, Forey's criticisms of the specific criteria lose their force. The PhyloCode is entirely neutral regarding the various measures of support that he lists (number of synapomorphies, Bremer support, bootstrap proportions, etc.); what is considered an adequate level of support is a taxonomic issue that is to be decided by the individual systematist. The same holds for levels of phenotypic distinctiveness and economic importance. Incidentally, Forey's point that the criterion of phenotypic distinctiveness implicitly advocates use of apomorphy-based definitions but that '*apomorphy-based naming is less favoured than the other two [kinds of] definitions*' (p. 90) is both questionable and irrelevant. For one thing, at least some PhyloCode proponents have argued for the use of apomorphy-based definitions (e.g. Pleijel, 1999; Lee, 2001; see also Gauthier & de Queiroz, 2001). Moreover, regardless of the types of phylogenetic definitions favored by individual systematists; there is nothing in the PhyloCode indicating that one kind of definition is preferred over others.

Compositional stability

In his section entitled '*How to name*', Forey first argued (p. 91) that phylogenetic nomenclature is '*curiously illogical*' in attempting to choose definitions that will promote stability in the composition of taxa given that '*taxonomic content is not the primary purpose of Phylogenetic Nomenclature (PhyloCode, Division 1. Principles)*'. His argument, however, is based on his misinterpretation of PhyloCode Principle 1 (see *The primary function of taxon names*), which does not state that compositional stability is unimportant but only that the primary purpose of taxon names is to refer to taxa rather than to describe (i.e. through the meanings of the words from which the name is formed) their composition (or characters or relationships). Forey then

correctly noted that stability in taxon composition will depend on the stability of the phylogenetic hypothesis, but then he reiterated his irrelevant complaint that '*Phylogenetic Nomenclature is mute in offering guidelines since there are no agreed criteria [for assessing support]*', concluding (again correctly) that although the name itself may remain stable, the composition of the taxon to which it refers '*may be decidedly unstable*'. As we argued above (see *When to name*), the issue of support is a taxonomic rather than a nomenclatural issue. In addition, neither traditional nor phylogenetic nomenclature can guarantee compositional stability. On the other hand, under phylogenetic nomenclature, changes in taxon composition result *only* from changes in hypotheses about phylogenetic relationships, while under traditional nomenclature, such changes can result *both* from changes in phylogenetic hypotheses *and* from changes in rank assignments, and the latter can occur even when ideas about phylogenetic relationships remain unchanged (de Queiroz, 1997). Moreover, phylogenetic definitions can be worded so as to limit potential changes in taxon composition (see PhyloCode Article 11.9), an option that is unavailable under the Zoological Code. Thus, far from highlighting shortcomings of phylogenetic nomenclature, the issue of compositional stability reveals significant advantages of that approach.

Nomenclatural stability

Later in his section titled '*How to name*', Forey argued (p. 91) that PhyloCode rules regarding conservation can lead to instability in names (as opposed to taxon composition). In his hypothetical example, identical definitions are given to the names 'Sarcopterygii' and 'Gnathostomata', followed by conservation of 'Sarcopterygii' and redefinition of 'Gnathostomata', so that the application of the name 'Gnathostomata' is unstable. This example is flawed in several ways. First, under the PhyloCode, the establishment of different names with identical definitions will be very unlikely to occur because all names and their definitions will be registered (see Article 8). The implementation of the PhyloCode will coincide with the establishment of a registration database, which will be accessible through the Internet. In addition to providing a useful entry to the literature relevant to particular names, this database will make it very easy for authors to avoid accidentally publishing homodefinitive synonyms (i.e. the sort in Forey's example) and homonyms. An author who proposed to give the name 'Sarcopterygii' the same definition that had previously been published for 'Gnathostomata' would have to register the name and definition, and the registration number would have to be included in the publication, in order for the name to be established under the PhyloCode (i.e. be 'available' in the terminology of the Zoological Code). If a definition submitted for registration were identical to one that had previously been registered, the submitting author would be notified (see PhyloCode Appendix A). It is very unlikely that the author would then proceed to publish that definition, knowing that it could never be accepted (i.e. be 'valid' in the terminology of the Zoological Code) unless it were conserved by the International Committee on Phylogenetic Nomenclature (ICPN).

On the other hand, suppose that the earliest phylogenetic definition of the name 'Gnathostomata' (e.g. the least inclusive clade containing the specifiers coelacanth and frog, symbolized 'clade (coelacanth + frog)' though under the PhyloCode one would use scientific names of species for the specifiers) were highly inconsistent with

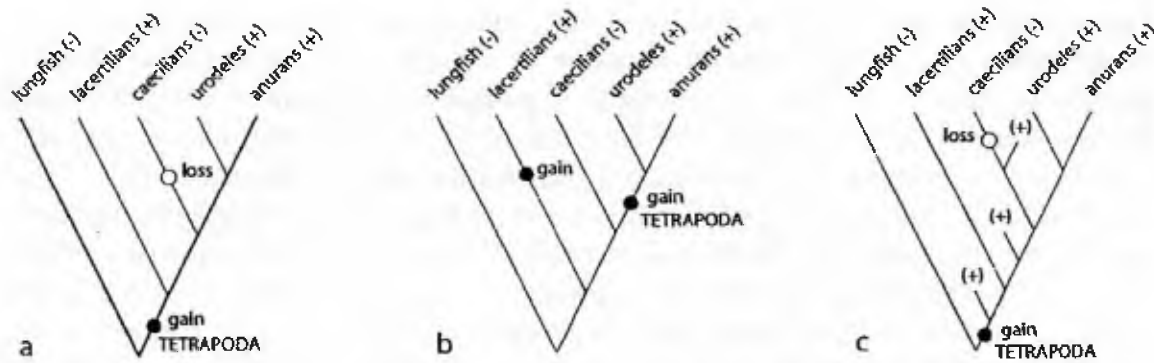


Figure 1. Alternative equally parsimonious character optimisations and their bearing on an apomorphy-based phylogenetic definition. In this example, the name 'Tetrapoda' is defined as referring to the clade of all animals with fingers and toes homologous (synapomorphic) with those in *Rana esculenta* (a member of the group anurans). Plus ('+') and minus ('-') signs indicate the presence and absence of the character, respectively. (a) Under the accelerated transformation optimisation procedure, the name 'Tetrapoda' refers to a clade that includes anurans, urodeles, caecilians and lacertilians. (b) Under the delayed transformation optimisation procedure, the name 'Tetrapoda' refers to a clade that includes anurans and urodeles but not lacertilians and caecilians. (c) When additional taxa are taken into consideration (short branches with plus ('+') signs indicating the possession of finger and toes), only a single most parsimonious optimisation exists (i.e. under both accelerated and delayed transformation) and the name 'Tetrapoda' refers to a clade that includes anurans, urodeles, caecilians, lacertilians and various other taxa.

prevailing use and ended up referring to a taxon that had traditionally been called 'Sarcopterygii' (as in Forey's hypothetical example). Under these circumstances, an author might purposely publish the same definition (i.e. clade (coelacanth + frog)) for the name 'Sarcopterygii' and then apply for conservation. If the ICPN agreed that stability would be promoted by conserving Sarcopterygii = clade (coelacanth + frog) over Gnathostomata = clade (coelacanth + frog), it would formally suppress the latter name-definition combination, and, as Forey stated, 'Gnathostomata' could then be redefined (e.g. as clade (shark + frog)). In Forey's view, 'this is hardly stability' (p. 91). On the contrary, permitting redefinition of taxon names following suppression enhances stability in that it permits their continued use in a manner consistent with prevailing use. Otherwise, a well known name such as 'Gnathostomata' might have to be abandoned simply because the first definition published for it was inappropriate.

Supposed problems with apomorphy-based definitions

Forey suggested that linking a name with a statement about phylogeny causes difficulties for phylogenetic nomenclature – in particular, with apomorphy-based definitions – because it 'leads into theories of homology' (p. 91), or more specifically, because 'characters [apomorphies] are homologies and homologies are theories' (p. 92). To illustrate the supposed problem, he used as an example the name 'Tetrapoda' defined as 'the clade consisting of all those animals with fingers and toes homologous with those in *Rana esculenta*'. He noted that under certain phylogenetic hypotheses the evolution of this character (fingers and toes) is ambiguous (see Fig. 1, which corresponds to Forey's Fig. 4). It might have originated in the common ancestor of amniotes (represented by lacertilians) and amphibians (represented by caecilians, urodeles, and anurans), with subsequent loss in the caecilians; this result is obtained under accelerated transformation optimisation (Fig. 1a, or Forey's

Fig. 4a). Alternatively, fingers and toes might have originated separately in amniotes (lacertilians) and in the common ancestor of urodeles and anurans, so that the absence of fingers and toes in caecilians is primary; this result is obtained under delayed transformation optimization (Fig. 1b, or Forey's Fig. 4b). Forey concluded that under the second scenario (delayed transformation), the character fingers and toes is not regarded as a synapomorphy (i.e. of lacertilians and urodeles plus anurans) and therefore presumably would not be used as a specifier. On the contrary, Forey included the stipulation that the fingers and toes that specify the reference of the name 'Tetrapoda' must be homologous with those of *Rana esculenta*. Clauses of this sort are included specifically to deal with the possibility of convergent and parallel evolution (Gauthier & de Queiroz, 2001). Under this stipulation, if the fingers and toes of lacertilians are not homologous with those of urodeles and anurans (including *Rana esculenta*), then lacertilians are not part of Tetrapoda. Thus, homoplasy is not a reason to avoid the use of a character as a specifier.

On the other hand, Forey pointed out that in this example the two scenarios (i.e. those based on accelerated vs. delayed transformation procedures) are equally parsimonious. From this observation, he concluded (p. 93) that '*in order for there to be no ambiguity we need [to add] a qualifying phrase*' stipulating further that the fingers and toes are homologous with those of *Rana esculenta* '*under the optimising procedure of accelerated transformation*'. Forey's conclusion is incorrect and results from an unrealistic requirement that there be no ambiguity regarding the composition of a taxon. In this case, ambiguity results from the equally parsimonious alternative scenarios for the evolution of the character, which result in different conclusions about the composition of Tetrapoda (i.e. whether lacertilians and caecilians are part of that taxon). But contrary to Forey's view, ambiguity does not cause a problem for apomorphy-based definitions, let alone for phylogenetic nomenclature in general; instead, it only causes a problem concerning inferences about the composition of a taxon – a taxonomic problem that can exist regardless of one's preference for traditional versus phylogenetic nomenclature. In the example under consideration, there is no need to add Forey's further stipulation to the definition; all that is necessary is to accept some uncertainty about the composition of Tetrapoda (i.e. about whether lacertilians and caecilians are part of that taxon). Forey himself seems to acknowledge such uncertainty when he suggests (p. 93) the alternative qualifying clause '*under any optimising procedure*'. If 'any' here means 'any one of several', then this stipulation is undesirable in that it would lead to the conclusion that lacertilians and caecilians are part of Tetrapoda—that is, in spite of the uncertainty about the homology of lacertilian digits and whether caecilians are primarily or secondarily digitless. Alternatively, if 'any' means 'no matter which', then this statement goes without saying and leads to the same conclusion described above – namely, that it is uncertain whether lacertilians and caecilians are part of Tetrapoda. Thus, although Forey's example does illustrate a problem, that problem is a shortcoming neither of apomorphy-based definitions nor of phylogenetic nomenclature in general. Instead, it is merely the problem of inferential uncertainty – a general problem that applies to all scientific hypotheses.

Finally, as Forey pointed out, his example is highly contrived. There are, in fact, additional taxa possessing fingers and toes positioned at various points on Forey's tree (e.g. Laurin & Reisz, 1997). When these taxa are considered, there is only one

most parsimonious optimization of the character, namely, gain in a common ancestor of amphibians and amniotes with subsequent loss in caecilians (Fig. 1c). This optimisation leads to the unambiguous inference that the fingers and toes of lacertilians are homologous with those of *Rana esculenta*, that caecilians are secondarily digitless, and thus that both lacertilians and caecilians are part of Tetrapoda.

Phylogenetic nomenclature: what is to be lost and gained?

In the first two paragraphs of his section entitled '*Pain – no gain*', Forey argued (p. 93) that '*with respect to clarity and stability there may be no difference between Phylogenetic Nomenclature and Linnaean taxonomy*', and he concluded (p. 94) that the claim that the PhyloCode will improve nomenclatural clarity and stability '*is at best illusionary and at worse misleading. There is nothing to be gained*'. In support of this view, he discussed changes in the membership of Crossopterygii as hypothesized phylogenies changed through the years and concluded (p. 94) that, under either phylogenetic or traditional nomenclature, '*if we want to understand the systematic history of a particular taxon we still have to examine all of the phylogenies under which that name has been used because the name itself may be compatible with more than one phylogenetic hypothesis*'. This is certainly true, but it has nothing to do with the manner in which phylogenetic nomenclature improves clarity and stability of names – that is, by eliminating changes in the names and/or membership of clades caused solely by changes in rank. This problem and others that result from tying names to taxonomic ranks under the Zoological Code and its botanical and bacteriological counterparts are summarized briefly above and elaborated upon in the cited literature. Forey largely ignored these problems in his commentary, and he further avoided the issue by choosing examples above the rank of family group (e.g. Aves, Crossopterygii, Tetrapoda), where names are not defined under the Zoological Code (see *Compositional changes and nomenclatural stability*).

After presenting this irrelevant discussion purporting to show that nothing is to be gained from phylogenetic nomenclature, Forey asserted (p. 94) that this system will administer '*pain*' in five ways. In each case, the supposed pain is either questionable, false, exaggerated, or irrelevant. First, Forey asserted that '*new names may have to be coined for very familiar groups*'. He did not present any evidence to support this statement but instead went on to discuss a different issue – the implications of a single name being defined differently in phylogenetic versus traditional nomenclature. Contrary to Forey's assertion, adoption of phylogenetic nomenclature should rarely result in the coining of new names for very familiar taxa. Names that currently refer to clades will continue to refer to the same clades; the difference will be that the names will be defined so that their references to those clades will be direct and explicit. The primary exceptions will be names (mostly those of genera) that are used under more than one traditional code. Because the PhyloCode will apply to all organisms, it will require replacement of one member of each pair of such cross-code homonyms. For example, if the existing plant genus name *Prunella* were to be defined phylogenetically as referring to a clade of plants, then the identical existing bird genus name could not subsequently be used for a clade of birds, and the bird clade that currently bears this genus name would have to be given a different name under the PhyloCode. If this situation jeopardized a widely used genus name, its replacement could be prevented

through conservation (for further discussion see Cantino, 2000). On the other hand, names that did not previously refer to clades either would not be used or would be redefined as referring to clades. For example, the name 'Osteichthyes' – originally the name of a paraphyletic taxon – either would be avoided or it would be defined to include the subgroup (i.e. Tetrapoda) that had formerly been removed to render it paraphyletic.

Later in the same paragraph (p. 94), Forey presented an example of how phylogenetic redefinition of a name could cause confusion. However, the example he cited – Laurin's (1998) phylogenetic redefinition of the name 'Anthracosauria' so that (in the context of Laurin's proposed phylogeny) the taxon no longer included *Anthracosaurus* – would not be permitted under the PhyloCode. According to PhyloCode Article 11.8, when a clade name is a converted name derived from the stem of a genus name, the definition of the clade name must use the type species of the genus name as an internal specifier. The name 'Anthracosauria' is derived from the stem of the genus name *Anthracosaurus*; therefore, if 'Anthracosauria' is to be converted under the PhyloCode by defining it phylogenetically, Article 11.8 requires that *Anthracosaurus russelli* (the type species of *Anthracosaurus*) be used as an internal specifier. Consequently, the clade Anthracosauria would have to include *Anthracosaurus* regardless of the hypothesized phylogeny, since internal specifiers are, by definition, members of the clades whose names they are used to define. In fact, Forey cited Article 11.8 in his discussion, but he apparently misunderstood it to cover only clade names converted from preexisting genus names and not those converted from preexisting suprageneric names derived from the stems of genus names.

Second, Forey asserted (p. 94) that the PhyloCode is agnostic about characters, relationships, and membership – that is, '*precisely the . . . information which may be of importance to comparative biologists*'. He thus overlooked the fact that the Zoological Code is also agnostic about characters, relationships, and membership, which are taxonomic rather than nomenclatural concerns. In addition, contrary to Forey's assertion, the PhyloCode (like the Zoological Code) does not suggest that the retrieval of information about these properties will be either easy or difficult.

Third, Forey complained (p. 94) that under phylogenetic nomenclature, '*changing hypotheses of relationship will mean that names are used and disused according to the phylogeny in fashion at that time (in Linnaean taxonomy the name will remain the same but the membership may change)*'. Although Forey is correct in saying that some names would not be used in certain phylogenetic contexts, this situation is appropriate. If a name does not apply to any clade in the accepted phylogeny, or if it is synonymous with an earlier-published name for the same clade, then not using that name makes perfect sense. Furthermore, the accepted phylogeny, which Forey seemed to denigrate as a 'fashion', is determined by the judgement of taxonomists based on their assessments of the available evidence, just as in traditional taxonomy. Finally, Forey is incorrect in believing that in traditional taxonomy names remain the same and only membership changes. Taxon names in traditional nomenclature, just like those in phylogenetic nomenclature, are used and disused according to the taxonomic hypothesis accepted at the time. Thus, under the Zoological Code, if a name is judged to be synonymous with an earlier-published name for the same ranked taxon in the accepted taxonomy, then that name is not used as the valid name of the taxon. It should also be noted that in traditional nomenclature, the use and

disuse of names depending on precedence among competing synonyms results from changes in rank and the associated phenomena of splitting and lumping. What Forey failed to mention is that in traditional nomenclature such changes in rank can result not only from the acceptance of an alternative phylogenetic hypothesis (as in phylogenetic nomenclature) but also from phenetic considerations or even arbitrary decisions – sources of instability that do not occur in phylogenetic nomenclature.

Fourth, as Forey correctly pointed out (p. 94), the PhyloCode deals with the names of clades – that is, monophyletic groups of species. Although Forey stated that he considers the naming of clades '*a desirable endpoint*', that he '*agrees strongly that monophyletic groups are the only real biological entities worth consideration*', and that he '*would never argue for the retention of paraphyletic taxa*', he noted that '*there are vast branches of the tree of life where monophyly has yet to be demonstrated*', and that he is '*mindful of the fact that for many biologists potentially non-monophyletic groups (e.g. Bryophyta) still serve a useful purpose for their own reasons of communication*'. From these observations, he concluded that phylogenetic nomenclature will leave certain assemblages of taxa un-named and that '*we will still have to live with Linnaean names alongside PhyloCode names*'. Although these conclusions are not incorrect, they are not particularly damaging to the PhyloCode. For one thing, it is not expected that all existing names will immediately be redefined phylogenetically; instead, this process will occur piecemeal as individual systematists work on the phylogenies of particular groups and apply phylogenetic nomenclature in the context of their results. For this reason, the PhyloCode suggests conventions (Recommendation 6.1B) for distinguishing PhyloCode names from names that are not defined phylogenetically. Moreover, it is not clear that these other names must be 'Linnaean', if by that term Forey means that the names will have to be governed by one of the codes of traditional nomenclature. Instead, taxa of uncertain monophyly could be referred to using informal names or formal names that are not governed by any code (much like those of zoological taxa above the rank of superfamily). Finally, as noted above (see *Annotated Linnaean Systems*), the PhyloCode is entirely compatible with the use of taxonomic conventions (e.g. quotation marks) indicating that certain names refer to non-monophyletic taxa.

Fifth, Forey predicted (p. 95) that '*adoption of the PhyloCode can and probably would lead to a rapid inflation of names*'; he then argued that systematists would not be '*servicing the wider biological community by introducing a plethora of names, each with their own definitions which need to be understood before they can be used by others*'. The idea that explicitly phylogenetic approaches will lead to a proliferation of names is an old fear (e.g. Bock, 1977; Colless, 1977). That Forey voices this fear is ironic given his own advocacy of monophyletic taxonomies, which aligns him with a movement against which the same criticism was raised. In any case, the proliferation of taxon names is a phenomenon that has continued unabated throughout the long history of taxonomy, and it is not at all clear that this trend is caused by changing taxonomic or nomenclatural philosophies rather than simply by the inexorable accumulation of knowledge about biological diversity. Moreover, the trend itself suggests that the resulting names have been useful, which calls the premise of Forey's argument into question. That is to say, it is not at all clear that the biological community is better served by limiting the introduction of new taxon names than by allowing names to be introduced freely. Consequently, we consider it

preferable not to limit the introduction of new names from the outset, but to have a nomenclatural system that allows taxonomists to name the taxa that they want to name. Those names will then persist or not depending on whether they are actually used by biologists.

As for the need to understand the definitions of taxon names, this is hardly a disadvantage of phylogenetic nomenclature. Regardless of whether one adopts traditional or phylogenetic nomenclature, the user of a taxon name must understand what taxon it refers to in order to use the name properly. And under both systems, the application of a taxon name is something that needs to be looked up – it cannot be determined from the name itself. To look up the application of a name, most users would simply consult a comprehensive taxonomic database such as a global checklist or a regional flora or fauna. Under phylogenetic nomenclature, the authors of these authoritative works will have to delve into the systematic literature to decide which phylogenies to accept, which clades to include in their works, and which names have precedence for those clades, just as they currently (i.e. under traditional nomenclature) have to delve into the original taxonomic literature to decide which circumscriptions of families and genera to use, whether to accept lumping or splitting of particular groups by previous authors, and which names have precedence.

In summary, Forey's assertion that nothing is to be gained by adopting the PhyloCode depends on his ignoring the main advantage of phylogenetic nomenclature (i.e. the stability of its names in the face of changes in taxonomic ranks) and focusing instead on irrelevant issues (e.g. the fact that understanding the systematic history of a taxon requires examining the various phylogenies under which its name has been used). In addition, the "pain" that Forey believes will result from adoption of the PhyloCode does not exist. The specific concerns that he raised are based on (1) his incorrectly interpreting the PhyloCode (e.g. his belief that the name 'Anthracosauria' could be phylogenetically defined to exclude *Anthracosaurus*), (2) his imagining problems where none exists (e.g. his conclusion that some groups will have to remain un-named because their phylogenetic relationships are poorly understood), (3) his criticizing the PhyloCode for properties that are also shared by the Zoological Code (e.g. the facts that names are used and disused depending on the accepted taxonomic hypothesis and that the application of names must be understood before the names can be properly used), (4) his accepting questionable premises (e.g. the idea that biology is best served by limiting the introduction of new taxon names), and (5) his failing to distinguish consistently between taxonomy and nomenclature (e.g. the assertion that the PhyloCode is agnostic about characters, relationships, and membership).

Conclusion

In the conclusion of his critique, Forey asked what is to be gained by adopting the PhyloCode. The answer is a system of nomenclature that regulates the naming of taxa and the subsequent application of taxon names in a manner that is more concordant with evolutionary concepts of taxa than under the traditional rank-based codes. Such a system facilitates the naming of clades and promotes the subsequent application of their names in ways that more closely conform to the manner in which they are conceptualized. As for the alleged pains, all of those proposed by Forey are either imagined or exaggerated.

Forey ended his critique of phylogenetic nomenclature and the PhyloCode with the statement (p. 95) that '*the biological community will have to judge whether the alleged gains are worth the undoubted pain*'. The developers of the PhyloCode agree that systematists should explore the ramifications of phylogenetic nomenclature in their study groups and decide for themselves which system is preferable. Although Forey's own conclusion is that the disadvantages of the PhyloCode outweigh its advantages, examination of his specific criticisms reveals that he did not identify a single significant shortcoming of phylogenetic nomenclature relative to its traditional counterpart. Moreover, although Forey believes that nothing is to be gained by adopting the PhyloCode, he reached that conclusion by ignoring the advantages that have been proposed and discussed by previous authors. When these advantages are taken into consideration along with Forey's failure to identify any disadvantages, it seems that the balance is tilted decidedly in favor of the PhyloCode. Indeed, the greatest obstacle to the adoption of the PhyloCode is probably not any disadvantage of phylogenetic nomenclature itself but the simple inertia of tradition.

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