

Jake Alexander

BSc Applied Biology

Imperial College of Science, Technology and Medicine

8th April, 2002

**The future of biological taxonomy? Does the
PhyloCode offer a viable alternative to
traditional Linnaean taxonomy?**

CONTENTS

I. Introduction	3
II. The Linnaean Hierarchy	5
(1) Theoretical basis and development	5
(2) Criticisms of Linnaean taxonomy	7
(3) Nomenclatural instability and the problems of rank	12
III. Phylogenetic Nomenclature and the <i>PhyloCode</i>	15
(1) Principles and motivation	15
(2) Phylogenetic definitions of taxon names	17
IV. Analysis of PN and the <i>PhyloCode</i>	21
(1) Stability	21
(2) Apomorphy-based definitions and clarity	28
(3) Theoretical considerations	30
V. The Purpose of Nomenclature	32
VI. Conclusions	35
VII. Acknowledgements	36
VIII. References	36

I. INTRODUCTION

When Carl Linnaeus devised the binomial system of nomenclature as a shorthand for referring to species of plants, he founded a new era in biological nomenclature and taxonomy which has been increasingly modified and formalised in the various biological Codes of nomenclature up to the present day. However, the organisation of life into the hierarchical ranks with which we are familiar according to the principles of logical division in order to describe the diversity of God's creation was not an innovation conceived by Linnaeus, but rather a process accepted by contemporary thought. What is surprising to some authors (e.g. de Queiroz & Gauthier, 1992) is that a system rooted in creationism survived the Darwinian revolution in biological thinking and is still in use today. Campaigners for a complementary revolution in taxonomy object to the supposedly "essentialist" nature of the Linnaean system, which they see as an inappropriate theoretical foundation for taxonomy. However, that it has survived bears testament to the utilitarian nature of Linnaean taxonomy rather than its theoretical basis, and serves to illustrate an important point; that naming organisms is a practical exercise which must be done in a way that maximises the efficiency of communication between all those who use taxon names.

However, it is widely accepted by biologists that nomenclature should be based on empirical knowledge (Langer, 2001). Since the acceptance of the theory of evolution it has been understood that organisms are related by genealogy rather than the potentially superficial similarity of their morphological characters. With this belief, systematists have attempted to construct classifications within the framework of Linnaean taxonomy that reflect phylogenetic hypotheses, but as we shall see this is not always appropriate. Various modifications to the Linnaean system have been proposed since the prevalence of cladistics, for example the annotated Linnaean system of Wiley (1979), but these have failed to gain general acceptance, perhaps because they do not offer a more practical system than that currently in use. However, the development of ideas of phylogenetic nomenclature (PN), condensed and formalised into the draft *PhyloCode*, now present a real alternative to traditional nomenclature.

The motivation behind phylogenetic nomenclature stems from the understanding that species are related genealogically and can be represented by the terminals on a cladogram, linked by common ancestors at its nodes. Because cladograms reflect "real" patterns in nature, the only true taxa are thus believed to be species and monophyletic clades. This concept is not new (see de Queiroz & Gauthier, 1990 and references therein), but in a series of papers de Queiroz and Gauthier (1990, 1992, 1994) introduced the idea of defining names of taxa based entirely on phylogenetic hypotheses (phylogenetic nomenclature). This culminated in the publication of the *PhyloCode* on the internet (Cantino & de Queiroz, 2000). The *PhyloCode* is currently in a draft form, but outlines principles, rules, recommendations and examples for the naming of clades using PN, for the registration of phylogenetically defined names and for the governance of a phylogenetic system of nomenclature. The present draft concerns only the naming of clades, but a future draft for species names is anticipated. Although it is stated that the *PhyloCode* can be applied concurrently with the existing biological codes, it is the aspiration of its authors that it should become their replacement.

From a theoretical perspective, PN rejects what it perceives as “essentialism” within traditional nomenclature and the delimitation of taxa based on character traits. Instead, it recognises taxa as named clades or species related on the basis of common descent. In so doing, PN makes the jump that the modifiers of Linnaean taxonomy have been reluctant to take and steps beyond the manipulation of traditional nomenclature to fit a cladistic framework. It is the clean break from the perceived "burden" of traditional nomenclature that makes the *PhyloCode* so attractive to its advocates (Langer, 2001). However, although “phylogeny is real, classifications are not” (Benton, 2000:634), and the assumption that taxonomies should reflect lineages should perhaps not be taken for granted. Indeed, if the purpose of taxonomy is to communicate the greatest information on biodiversity patterns then traditional taxonomy is perhaps more appropriate than phylogenetic taxonomy (McNeil, 2000). The nested hierarchy and nomenclatural customs of the traditional system promote the communication of general information about the diversity of taxa which would be lost under the *PhyloCode*. The purpose of taxonomy and the balance between theoretical and pragmatic considerations is at the heart of the debate over the *PhyloCode*.

The above are more philosophical issues. Perhaps of more real concern to biologists and those who use classifications are the practical nomenclatural issues, which have provoked the fiercest debate. Authors of the *PhyloCode* claim that it promotes stability, clarity and universality within nomenclature (Cantino & de Queiroz, 2000), but its opponents use examples to show that the reverse is true (e.g. Benton, 2000; Nixon & Carpenter, 2000; Forey, 2001a). We shall examine the principles and problems of traditional Linnaean taxonomy to understand why supporters of PN feel it needs replacing. We shall then examine the principles and practicalities of the proposed *PhyloCode*, enabling us to objectively judge whether the *PhyloCode* presents a practical and, crucially, better alternative to the current system.

II. THE LINNAEAN HIERARCHY

(1) Theoretical basis and development

Carl Linnaeus is viewed today as the father of taxonomy, the man who created order out of the chaos of pre-eighteenth century biological nomenclature. In pre-Linnaean nomenclature organisms were usually given long Latin polynomials which summarised their essence as well as specific characteristics. In his *Species Plantarum* (1753) Linnaeus compiled a catalogue of all known plants, naming individual species by their *nomen specificum legitimum* but also simplifying this with his own *nomen triviale*. These trivial names are the binomials we are so familiar with today. They summarised the essence of a species (the generic component, or *character naturalis*) and indicated how it differs from other species with the same essence (the specific component, or *differentia*). In addition to grouping species into genera, Linnaeus formalised the organisation of genera into orders, orders into classes and classes into kingdoms. Contemporary belief held that all aspects of the natural world could be classified by some form of logical division (Ereshefsky, 2001); Linnaeus was not the first to classify life according to this method. However, his hierarchical system of arranging species into categorical ranks of increasing inclusiveness and naming species with Latin binomials was rapidly accepted due to its simplicity and practicality.

As a member of the creationist society of the eighteenth century, Linnaeus would have observed the organisms around him as products of God's hand, divisible into kinds united by kind-specific essences (Ereshefsky, 2001). It was believed by some that the method of Aristotelian logical division provided the key for understanding how organisms were organised. Philosophy is not the subject of this essay, but an introduction to the principles underlying Linnaean taxonomy is important as their incongruity with modern evolutionary thought provides the basis for the opposition to traditional taxonomy.

Linnaeus used reproductive characters of plants as the essences uniting species within a genus. This is because the reproductive organs ensure the continuation of the kind and because they provide a large number of individual characters for use in differentiating genera. Species were differentiated based on characters which preserved the individual, namely vegetative and nutritional characters. As the genus provided the essence of each species, Linnaeus believed genera to be the more important taxa (Ereshefsky, 2001). He recognised that higher taxa were "less real" than genera, as they were delimited largely as *aides memoires* to indicate the position of a genus within a kingdom. Indeed, it was Linnaeus' aspiration that a biologist should memorise the position of every species within each kingdom, and the binomial was in part designed to facilitate this. He was able to justify this aspiration by his belief in the fixity of species and that, he believed, the discovery of all species was nearing completion (Ereshefsky, 2001).

With the birth of evolutionary thought came the rejection of creationism and the notion that species were fixed entities. Although related taxa do share similar characters, this is a result of common descent (except in the case of convergent evolution) and the true nature of relationships between taxa is now accepted to be genealogical rather than "essential". Thus the theoretical foundation for Linnaeus' categorical ranks is outdated. However, the nested hierarchy of taxa is a feature of Linnaean taxonomy compatible with phylogenetic thinking, and indeed was used by Darwin as evidence for common descent (de Queiroz & Gauthier, 1992). This may help explain its persistence. It should be noted that Linnaeus may have been aware of the limitations of using logical division to classify biological entities, and indeed of the use of his sexual system in delimiting plant genera – sexual characters do not

dominate his animal classifications (Winsor, 2001). It is nevertheless the case that his divisions are based on degrees of morphological similarity, and it is with this that the supporters of PN find fault.

With the rapid expansion in the discovery of new species from the New World after the death of Linnaeus came a proliferation of names. In order to manage the confusion, botanists, zoologists and bacteriologists developed Codes to outline rules for the naming and description of organisms with the primary aim of providing a unique Latin binomial for every species (Winston, 1999). These are the International Code of Botanical Nomenclature (ICBN), the International Code of Zoological Nomenclature (ICZN) and the International Code of Nomenclature for Bacteria (ICNB). The codes established the principle of priority to resolve cases of synonymy in nomenclature, whereby the first published name of a taxon is applied. This was later followed by the concept of typification to unambiguously link a name to a type-specimen or type-taxon. This was designed to promote stability in nomenclature and provide an objective basis for the application of names, making biology a “repeatable science” (Knapp, 2000). The issue of nomenclatural stability is central to the current debate and will be considered in detail below.

(2) Criticisms of Linnaean taxonomy

The principle concern of opponents to the traditional system is that it is "non-evolutionary". It is now generally accepted that organisms are fundamentally related by genealogy, rather than by potentially superficial shared character traits. However, the organisation of the Linnaean hierarchy was not designed with common descent as the *a priori* assumption and consequently is unable to fully reflect genealogical relationships in its classifications. Some critics of the *PhyloCode* argue that classifications are tools designed for their utility to maximise information content and communication, and that annealing them to phylogeny is not appropriate (e.g. Benton, 2000). However, it is the case that the majority of taxonomists aim to make their classifications mirror phylogeny, for example by making clades correspond to Linnaean categories and by the exclusion of paraphyletic taxa. We shall examine how the supposedly "non-evolutionary" nature of the Linnaean hierarchy makes it unsuited

to naming taxa in a phylogenetic context, and discuss how this results in nomenclatural instability and ambiguity.

The incongruity between the "essentialist" basis of the Linnaean hierarchy and the more modern concept of relationship through common descent has been discussed and need not be elaborated. However, the traditional system remains, with every organism being arranged into mandatory categories of increasing inclusiveness to form a complete hierarchy. Although the concept of a nested hierarchy of taxa is compatible with an evolutionary perspective, since clades are themselves parts of more inclusive clades, phylogenetic taxa (monophyletic clades) form a "truncated hierarchy" (de Queiroz & Gauthier, 1992). Thus, although descendants are placed at different distances from an ancestor in a cladogram, the system of mandatory categories, by assigning every organism, extant or extinct, to each and every Linnaean category, imposes equal distance upon them. This approach is fundamentally non-evolutionary because it classifies life in a static framework without the provision that taxa evolve from each other. (This is seen as the essentialist and creationist legacy of the Linnaean system.) For example, an ancestral species, represented by a node on a cladogram, is not part of a clade less inclusive than the one which stems from it. Although it shares apomorphies unique to that clade, it has none of those which discriminate the clade's subgroups. Thus it is impossible to insert an ancestral species into any of the existing subgroups, and likewise it cannot be assigned to any rank lower than the clade which stems from it; recognising it at all categorical levels implies the presence of clades which do not exist (de Queiroz & Gauthier, 1992) (see Fig. 1(a)). Defenders of the traditional system would argue that it is practically impossible to identify ancestors, since this can only be done based on apomorphies an organism lacks rather than those it possesses. Therefore the Linnaean framework is inappropriate for classifying potentially ancestral species.

The imposition of mandatory categories is also a meaningless exercise in reference to fossil and monotypic taxa. Because phylogenies are asymmetrical, either naturally or due to extinction, species may be assigned to a hierarchy of ranks containing no other taxa but themselves (Fig. 1(b)). For example, as we are the only extant representatives of our family, the names Hominidae, *Homo* and *sapiens* all imply the same thing, and so Hominidae and *Homo* are redundant ranks (Forey, 2001a). Delimiting a taxon as a

named clade using PN makes implicit reference to all included taxa whether extinct or extant, known or unknown (de Queiroz & Gauthier, 1992). Therefore, de Queiroz and Gauthier (1992) suggest that the problem of redundant ranks only arises if taxon membership is restricted to extant organisms. Thus Hominidae is no longer monotypic when one considers extinct Hominids.

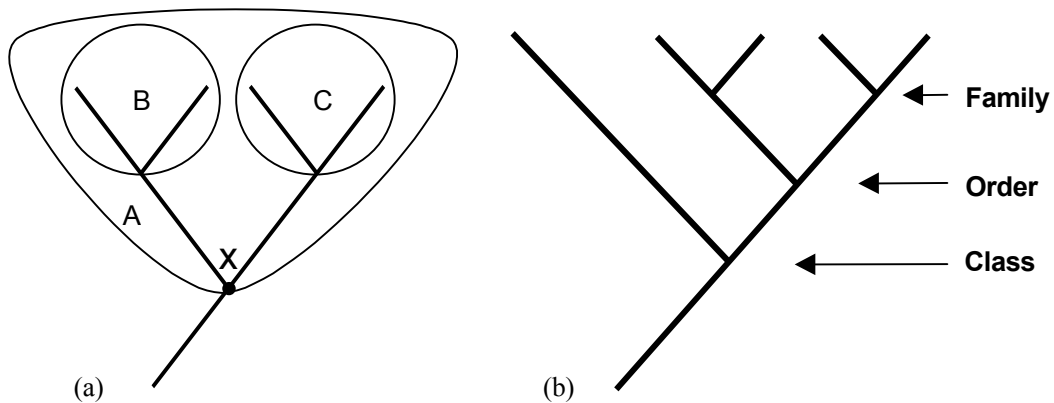


Fig. 1. Problems with mandatory categories. (a) The common ancestor (x) of clade A cannot be assigned to either of the clade's subgroups, B or C, and recognising it at the categorical level of B and C implies the presence of a sub-clade which doesn't exist. (b) The taxon represented by the terminal on the left is monotypic. Recognising it at all three categorical levels results in the family and order ranks becoming redundant.

Similarly, the assignment of newly discovered fossil taxa to each Linnaean category creates redundant ranks, as other members of those ranks may be unknown or indeed may never have existed. In order to tackle this problem, the rank of “plesion” (for plesiomorphic sister taxon) was created for fossil taxa, to allow fossils to be inserted into classifications without making assumptions about their Linnaean rank (Patterson & Rosen, 1977). For example, in the following classification (after Patterson & Rosen, 1977:163) plesions appear at ranks equivalent to super-cohort and family level (* indicates extinct taxa):

plesion * *Tharsis dubius*
 SUPERCOHORT Osteoglossomorpha
 ORDER Osteoglossiformes
 SUBORDER Osteoglossoidei
 SUBORDER Notopteroidei
 SUPERFAMILY Hiodontoidea
 plesion * *Lycoperidae*
 FAMILY Hiodontidae
 SUPERFAMILY Notopteroidea.

Ereshefsky (2001) believes that the creation of this essentially rankless category, along with other attempts to bring the current system in line with phylogenetic thinking, only serves to make traditional taxonomy “less Linnaean” and uses this as justification to abandon the Linnaean system altogether in favour of something more appropriate.

The perceived problems associated with mandatory categories discussed above stem from the subjective and arbitrary nature of the categories themselves. Assigning a taxon to a particular rank assumes a level of morphological divergence in amount and kind (Forey, 2001a). Thus within a particular classification the hierarchy of ranks represents relative levels of morphological divergence. However, just as it is impossible to quantify how much diversity is contained within a particular rank, so it is impossible to assume that the amount of diversity within two taxa of the same rank is equivalent in any meaningful way. Therefore the assignment of ranks to taxa is potentially misleading, as those unfamiliar with its arbitrary nature may assume that taxa of the same rank are comparable. Having said this, the relative diversity encompassed by Linnaean ranks, whilst not quantifiable, is considered useful in comparative biology, as for example family or generic counts may be used by ecologists to construct diversity indices (Forey, 2001a).

Because the decision to assign taxa to a particular rank is subjective and based on an observed level of morphological divergence, Linnaean taxonomy may contradict phylogeny in that taxa of the same rank may be nested within each other (de Queiroz & Gauthier, 1992). In other words, it may result in the recognition of paraphyletic taxa, which exclude one or more clades nested within them. This is perceived to be unacceptable, since assigning taxa the same rank assumes that they are mutually exclusive. For example, designating Reptilia and Aves with class status does not recognise the fact that the latter is nested within the former. It also stems from a belief that the only true taxa are monophyletic (de Queiroz & Gauthier, 1990). Despite this, the ability of phylogenetic nomenclature to recognise paraphyletic taxa through exclusion clauses in phylogenetic definitions is quoted as an advantage of that system (see "Theoretical considerations" below).

In an attempt to eliminate paraphyletic taxa from classifications, systematists adopt the practices of “lumping” and “splitting” taxa to make names refer to monophyletic groups. In the case of lumping, a paraphyletic family, for example, and nested monophyletic family are united to form a single monophyletic family (Fig. 2(c)). When splitting, the paraphyletic family is divided to create two or more monophyletic families (Fig. 2(d)). Although motivated by phylogenetic concerns, de Queiroz and Gauthier (1994:30) find issue with these practices on the grounds that “[a]s singular phylogenetic entities (clades), taxa are not things that taxonomists can unite or divide, but only things that they can discover and name”. The splitting or lumping of taxa in association with a particular rank is just as arbitrary as the assignment of the rank in the first place. These processes are purely matters of taxonomic opinion, whilst the taxa (clades) themselves have an innate existence regardless of what rank we wish to assign them.

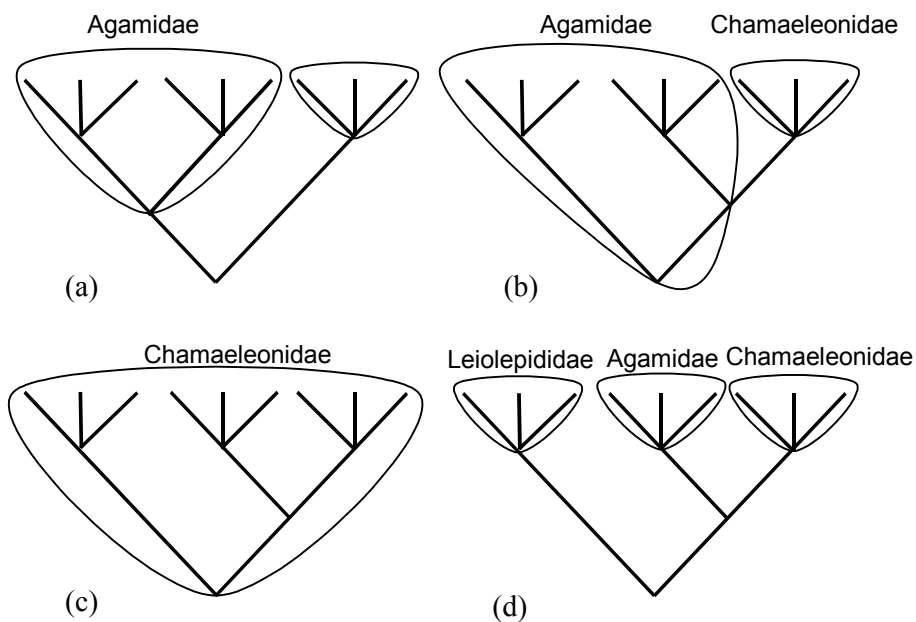


Fig. 2. Lumping and splitting. Phylogenetic revision shows that two originally monophyletic families (a) are in fact paraphyletic (b). Paraphyletic taxa can be eliminated by "lumping" (c), in which case the single inclusive taxon takes the oldest family name (Chamaeleonidae), or by "splitting" (d), where the subordinate clades are assigned family status and a new family name (Leiolepididae) must be coined (after de Queiroz & Gauthier, 1994).

It is precisely this subjectivity, coupled with certain features of Linnaean taxonomic procedure governed by the biological Codes, which leads to much nomenclatural instability and ambiguity. It is appropriate to mention here that for the advocates of phylogenetic nomenclature, the stability of a name is considered in terms of its

orthography and reference to a particular clade. Opponents see stability in terms of the content of a named group (Langer, 2001). The differences between the two approaches will be examined in later sections (see "Stability" below).

(3) Nomenclatural instability and the problems of rank

The principle pragmatic concern with the traditional system is that in its failure to fully divorce nomenclature from taxonomy it creates unnecessary nomenclatural instability as a result of changes in taxon rank. The intrinsic link between taxonomy and nomenclature in the traditional system is made explicit in the association of a name and its designated rank by rank-specific suffixes. For example, the ICBN specifies that family names have the suffix *-aceae*, subfamilies *-oideae* and so on. Instability arises because the concepts of synonymy and priority place more importance on the association between a name and a rank than between a name and a clade (de Queiroz & Gauthier, 1992; 1994). Phylogenetic nomenclature is designed to promote nomenclatural stability by eliminating any rank significance contained in taxon names, and thus ensure that a name refers to the same clade regardless of taxonomic revisions by lumping and splitting (de Queiroz & Gauthier, 2001).

Take again the example in Fig. 2. After the revision of an earlier hypothesis (Fig. 2a) of the relationships between Agamidae and Chamaeleonidae, Agamidae is shown to be paraphyletic (Fig. 2b). If the paraphyletic taxon is split (Fig. 2(d)), the name "Agamidae" now refers to a less inclusive group and a new name, "Leiolepididae", must be coined for the other new family. In this case, the "evolutionary meaning" of the name "Agamidae" has been changed from designating a more-inclusive paraphyletic taxon to a less-inclusive monophyletic taxon. In addition, the "evolutionary taxa" (clades) now referred to as Agamidae and Leiolepididae have changed their names, all as a result of an arbitrary taxonomic decision and with no change in the phylogenetic relationships of the less-inclusive taxa (de Queiroz & Gauthier, 1994). If lumping taxa (Fig. 2(c)), taxon names again "change their evolutionary meanings, while evolutionary taxa either change or lose their names" (de Queiroz & Gauthier, 1994:27). This is because uniting Agamidae and Chamaeleonidae into one family throws the two names into synonymy. The principle of priority as directed in the biological Codes dictates that the oldest of the two names

in connection with a particular rank is the correct name, and so the more inclusive clade is named “Chamaeleonidae”. As a result, the name “Chamaeleonidae” has changed its evolutionary meaning by designating a more inclusive clade, and the taxon previously referred to as “Chamaeleonidae” must now be renamed. This is presented as evidence of nomenclatural instability.

It is the concept of synonymy based on categorical ranks to which de Queiroz and Gauthier object. In the last example, the most inclusive clade was lumped into a single family and so took the name “Chamaeleonidae” because that was the oldest family name of the two. This happened despite the fact that the name “Chamaeleonidae” already referred to a subgroup of the clade. This serves to illustrate that under traditional nomenclature, the association between a name and a rank is more important than its association with a particular taxon (clade) (de Queiroz & Gauthier, 1992). This is seen as non-phylogenetic and results in nomenclatural instability as a result of arbitrary, subjective decisions.

Although it may be useful to convey information about the taxonomic placement of a taxon, contained in its rank-specific suffix, at the same time as communicating its name, this convention leads to unnecessary instability during taxonomic revision. If the rank of a particular taxon is changed, then so too is the spelling of its name to make the name and rank agree, despite the fact that the name still refers to the same group. Differences in opinion over the ranking of a taxon thus mean that taxonomists use different names to refer to the same group, even though they may be in complete agreement over the phylogenetic relationships of the group. Not only is this seen as unstable, but it hinders one of the principle aims of the nomenclatural codes, to facilitate communication by the universal usage of names.

In addition, this practice makes it difficult to insert new taxa into classifications. If all conventional categorical ranks have been filled, to accommodate a new taxon within a classification one must either use an unconventional rank (e.g. super-sub-family) or else change the status of superior or subordinate taxa, entailing a cascade of name changes (de Queiroz & Gauthier, 1992). It is feared that in order to minimise disturbance, many taxonomists may delay publication of new clades until they have developed a complete classification, and so taxonomy may lag behind phylogenetic

knowledge (Cantino & de Queiroz, 2000). All this instability is purely a result of taxonomic opinion regarding the assignment of rank, which is itself unnecessary in a phylogenetic context. In an attempt to accommodate the diversity of life discovered since the time of Linnaeus, taxonomists have been forced to create sixteen new categorical ranks (Ereshefsky, 2001). This proliferation of ranks is considered undesirable (e.g. Ereshefsky, 2001; de Queiroz & Gauthier, 1992), perhaps for practical reasons, and indicates how insufficient the traditional system is at reflecting fine levels of phylogenetic definition. Clearly to classify every level of inclusiveness on the tree of life with a categorical rank would be practically impossible.

Symptomatic of the theoretical and pragmatic problems with the Linnaean system as a whole is the convention of naming species with Latin binomials. Ancestors of monophyletic higher taxa are not themselves part of monophyletic genera (de Queiroz & Gauthier, 1992) (see discussion of Fig. 1(a) above). Aside from this theoretical consideration are the practical problems that arise when species are reassigned to different genera. Every time this happens a species must change the generic component (and sometimes the specific component) of its name due merely to differences in taxonomic opinion. For example, in the Strobilantheae one author (Bremekamp, 1944) delimited 54 distinct genera whilst another (Anderson, 1867) recognised only four. The result is a long list of synonyms for what both consider to be the same species. Again, it is the custom of linking taxonomy with nomenclature that results in this unnecessary nomenclatural instability. Although the current draft of the *PhyloCode* is only concerned with the naming of clades, the issue of species names in phylogenetic nomenclature is under discussion and proposals can be found in Cantino *et al.* (1999).

The importance of rank association when resolving synonymies points to the fact that in effect taxon names are defined on ranks and nomenclatural types (de Queiroz & Gauthier, 1994). Returning again to Fig. 2(d), the decision as to which of the two clades from the split paraphyletic group should retain the name “Agamidae” is based on which contains the type genus *Agama*. Thus the definition of “Agamidae” is in effect “the family containing the type genus *Agama*”. Although Ereshefsky (2001) praises this ostensive definition as a departure from essentialism, de Queiroz and Gauthier (1994) criticise it as “non-evolutionary”. All three point to the fact that this

form of definition does not provide sufficient conditions for the application of a name, and consequently that name's definition becomes ambiguous. They argue that only by defining names based on a system of phylogenetic nomenclature can one achieve nomenclatural stability, clarity and universality.

III. PHYLOGENETIC NOMENCLATURE AND THE *PHYLOCODE*

(1) Principles and Motivation

Criticism of the Linnaean hierarchy rest upon the preface that it is “non-evolutionary” and generates unnecessary nomenclatural instability. The assignment of taxa to all categorical ranks within the hierarchy is seen as problematic, since it imposes equal distance upon organisms which in reality (i.e. in a phylogeny) are placed at different distances from a common ancestor. In particular, this system fails to classify ancestors in an evolutionary meaningful way, since ancestors of a monophyletic clade cannot be placed into a category less inclusive than the taxon which stems from it. Similarly, fossil outgroups cannot be meaningfully assigned to a category any less inclusive than the Recent ingroup taxon without creating redundant ranks.

The merger of taxonomy and nomenclature and the importance attached to taxonomic rank under the current system is also perceived to be the root cause of nomenclatural instability. The significance of rank-specific suffixes means that differences in opinion over the rank of a taxon results in different people using different names for what they agree to be the same clade. Thus, not only are taxon names *unstable*, but their use is not *universal*. Application of the principle of priority when resolving problems of synonymy after taxonomic revision results in the association between a name and a categorical rank being more important than its association with a particular clade. This leads to instability in terms of taxon content. Taxon names are thus effectively defined in terms of rank and type, which makes the reference of a name to a particular taxon *ambiguous*.

The authors of the *PhyloCode* and supporters of phylogenetic nomenclature feel that defining names with phylogenetic definitions will promote “clarity ” (*PhyloCode* Principle 2), “uniqueness” (Principle 3), and “stability” (Principle 4) in nomenclature

(see Box 1). Unlike the Linnaean system, phylogenetic nomenclature is evolutionary in that it has the concept of common descent as its central tenet; “[t]he PhyloCode is concerned with the naming of taxa and the application of taxon names within a phylogenetic context” (Cantino & de Queiroz, 2000: Principle 5) (see Box 1). The use of phylogenetic definitions, described below, makes it suitable for naming clades, which in the eyes of PN represent the only true taxa. Basing nomenclature in an “appropriate theoretical context” (de Queiroz & Gauthier, 1992:472) and removing mandatory categories solves the conceptual problem of naming ancestral species and their unequally spaced descendants.

Box 1. PhyloCode Principles (Cantino & de Queiroz, 2000)

1. Reference. The primary purpose of taxon names is to provide a means of referring to taxa, as opposed to indicating their characters, relationships, or membership.
2. Clarity. Taxon names should be unambiguous in their designation of particular taxa. Nomenclatural clarity is achieved through explicit definitions.
3. Uniqueness. To promote clarity, each taxon should have only one accepted name, and each accepted name should refer to only one taxon.
4. Stability. The names of taxa should not change over time. As a corollary, it must be possible to name newly discovered taxa without changing the names of previously discovered taxa.
5. Phylogenetic context. The PhyloCode is concerned with the naming of taxa and the application of taxon names within a phylogenetic context.
6. The PhyloCode permits freedom of taxonomic opinion with regard to hypotheses about relationships; it only concerns how names are to be applied within the context of a given phylogenetic hypothesis.

Another fundamental feature of PN is that it is rankless. That is to say, “assignment of a categorical rank [...] is not part of any formal naming process and has no bearing on the spelling or application of taxon names” (Cantino & de Queiroz, 2000: Article 3.1). Herein lies a significant advantage of PN, as it achieves the separation of taxonomy and nomenclature by removing the significance of rank or other associations from names, and so prevents nomenclatural instability for purely taxonomic reasons. This is encompassed by Principle 1 of the *PhyloCode*, which states that “[t]he primary purpose of taxon names is to provide a means of referring to taxa, as opposed to

indicating their *characters, relationships, or membership*” (Cantino & de Queiroz, 2000, my italics) (see Box 1). In particular, this prevents instability in the spelling of taxon names due to differences in opinion over a taxon’s rank. At the same time, it removes the subjective element from nomenclature, since under the *PhyloCode* taxonomic disagreements are a result of different phylogenetic hypotheses, which are objective, rather than subjective opinions of rank assignment. Due to this nomenclatural stability, once coined a name refers to a taxon regardless of its content (see "Phylogenetic definitions of taxon names" below). This permits taxonomists a “freedom of taxonomic opinion” as it allows differences in hypotheses about relationships to be expressed in reference to a particular taxon (Principle 6).

The loss of rank associations from names makes the process of classification much easier because it removes the need to apply rank to a taxon at the same time as a name. For instance, one may name clades individually in isolation from a classification, or name a taxon without the need to also name its sister group (de Queiroz & Cantino, 2001). A clade may thus be easily inserted into an existing classification without entailing a cascade of name changes when the insertion means that existing clades must change their rank.

A further difference between PN and traditional nomenclature lies in the concepts of synonymy and priority. Under traditional nomenclature, names are synonymous if they are based on the same nomenclatural type, or on different types considered to belong to the same taxon at a particular rank (see "Criticisms of Linnaean taxonomy" above). This is considered "non-evolutionary" as it places more importance on ranks and types than on clades. Similarly, a name is given priority based on its first use in association with a particular rank. Under PN, names are synonymous only if they refer to the same clade, and a name is given priority on its first use in association with a particular clade. This puts these concepts into an evolutionary perspective.

(2) Phylogenetic Definitions of Taxon Names

According to de Queiroz and Gauthier (1994:28), definitions are “the foundation of biological nomenclature” and the key to nomenclatural stability, clarity and universality. Phylogenetic definitions rest on the principle that as genealogical

relationships define taxa, so the only true taxa are monophyletic clades, which can be defined by a reference to common ancestry. There are three classes of phylogenetic definition, each with at least two “specifiers” and a relational phrase (de Queiroz & Gauthier, 1990; Cantino, 1999).

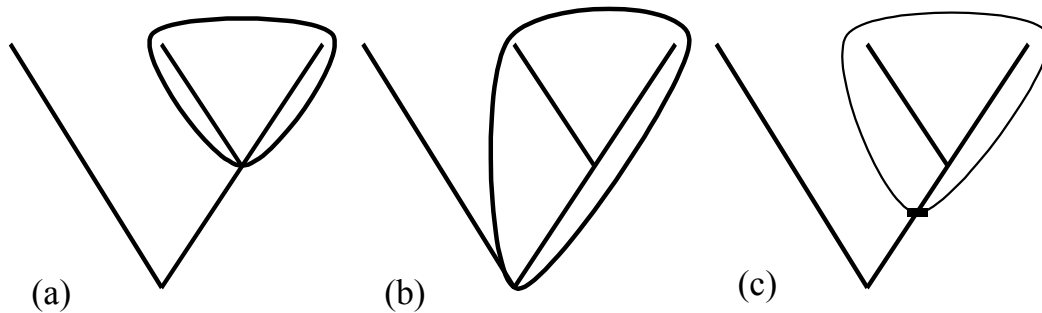


Fig. 3. The three classes of phylogenetic definition: (a) node-based, (b) stem-based and (c) apomorphy-based (see text for details).

A node-based definition defines a clade stemming from the most recent common ancestor of two or more specifiers (Fig. 3(a)). In this case both specifiers are included in the taxon. For example, Aves may be defined as “the clade stemming from the most recent common ancestor of *Struthio camelus* and *Passer domesticus*”, or, without reference to an ancestor, “the least inclusive clade containing *Struthio camelus* and *Passer domesticus*” (de Queiroz & Gauthier, 1994; Forey, 2001). A stem-based definition defines a clade containing all species more closely related to one specifier than another (Fig. 3(b)). Again, more than two specifiers may be used, but some are included in the clade and the others are excluded. For example, Aves may be redefined as “the clade consisting of *Struthio camelus* and all species sharing a more recent common ancestor with *Struthio camelus* than with *Crocodylus niloticus*”, or “the least inclusive clade containing *Struthio camelus* but not *Crocodylus niloticus*” (Forey, 2001a). Finally, an apomorphy-based definition defines the clade stemming from the first ancestor to possess a specified character (Fig. 3(c)). In this case there is one character specifier and one or more organismal specifiers. For example, Aves may also be defined as “the clade stemming from the first species to possess the character *feathers* synapomorphic with those in *Struthio camelus*” or “the clade diagnosed by *feathers* homologous with those in *Struthio camelus*” (Forey, 2001a).

The use of apomorphy-based definitions has come under most criticism and will be discussed in the next section. Suggestions have been made as to the application of the other two. De Queiroz and Gauthier (1992) propose that node-based definitions are best applied to crown clades. Crown clades consist of the latest common ancestor of all living members of a group plus its extinct and extant descendants, the immediate outgroup of which is extinct (Serenó, 1999) (Fig. 4(a)). Their rationale is that fossil outgroups are often ignored and that associating commonly used names with crown groups through node-based definitions would be most useful to the majority of biologists and best reflect the original usage of a name. In addition, the use of node-based definitions prevents making unsupported generalisations about the characters of extinct outgroups and allows the maximum number of inferences to be made about the characters of extinct ingroups from their living relatives. According to Sereno (1999), these arguments show a "lack of general rationale", and he demonstrates how stem-based definitions may be applied to crown taxa, and may indeed be preferable if the basal ingroup relationships are uncertain. A discussion of how the careful application of definitions may help stabilise taxon content is given in the next section.

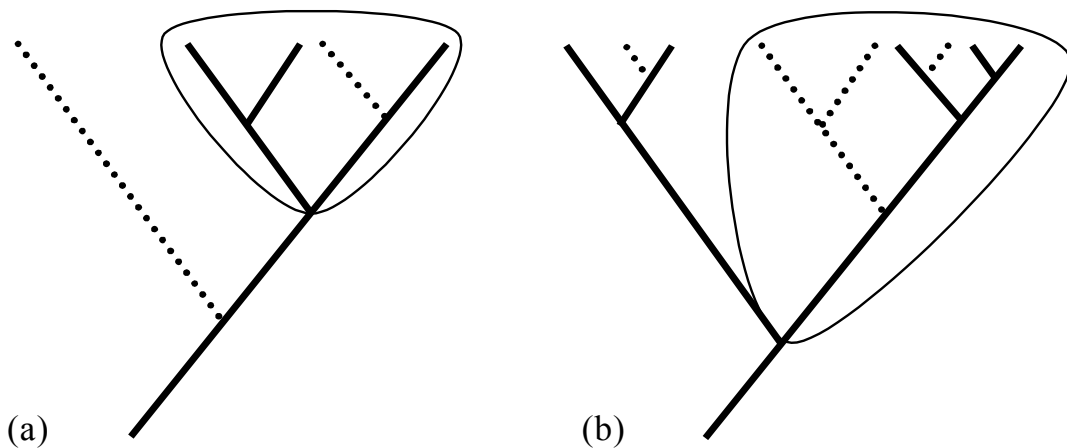


Fig. 4. A crown taxon (a) is a living species, or clade that can be defined by living species, whose immediate outgroup is extinct. A total taxon (b) consists of a crown clade plus all immediate outgroups more closely related to that crown than another. Solid lines represent extant taxa, dotted lines represent extinct taxa (after Sereno, 1999).

The stated need to associate common names with crown taxa is not necessarily justifiable. The original intent of a name is ambiguous since when names were founded they contained no relational phrase to indicate potential membership. Therefore, just because names may have been coined for extant representatives of a group does not mean that subsequently discovered fossil outgroups should be

excluded. Since names are usually associated with characters, the inclusion of fossil outgroups displaying those characters may best represent common usage (Sereno, 1999). Thus, by this rationale *Archaeopteryx* should be included in Aves because it possesses feathers.

However, all authors agree that stem-based definitions must be applied to total taxa (Fig. 4(b)). A total taxon consists of a crown clade plus all extinct outgroups more closely related to it than any other crown (Sereno, 1999). Only a stem-based definition will include all potential extinct outgroups up to the common ancestor with the sister total taxon (Sereno, 1999). The use of stem-based definitions to define taxa also has uses in comparative biology. The two total taxa stemming from a common ancestor are sister taxa and are thus comparable in terms of time-related phenomena such as lineage diversity. Linnaean sister taxa are not comparable in this way as they are not based on phylogeny, and neither are crown clades since they may have a different time of origin (de Queiroz & Gauthier, 1992).

The role of "specifiers" in PN bears similarities and differences with "types" of traditional nomenclature. Both are used as ostensive reference points for the application of a name, and the characters of the reference taxa in no way define the taxon being named (except in the case of the character reference in an apomorphy-based definition). However, de Queiroz and Gauthier (2001) stress that whereas specifiers specify a particular clade, types do not. A given taxon may be used as the type for several nested taxa, and only in conjunction with a rank does it specify the application of a name. For instance, "Agamidae = the *family* containing *Agama*". However, the specifiers alone in PN allow the isolation of only one taxon (clade) as they unambiguously pinpoint a single common ancestor. Since the application of Linnaean rank is subjective, and a given rank with its associated type may be applied to any clade in a series of nested clades, de Queiroz and Cantino (2001) suggest that types are not specifiers at all, in that they do not uniquely indicate a clade, but may relate to different clades after taxonomic revision.

Phylogenetic nomenclature clarifies the distinction between the definition and diagnosis of taxa. Under the traditional system this is far from clear, and the two terms may be used interchangeably (Winston, 1999). Although it has been stated that

Linnaean definitions are "character-based", a list of apomorphies is a diagnosis to identify members of a taxon rather than a definition. Thus de Queiroz and Gauthier (1992, 1994) and Lee (2000) point to the fact that under traditional nomenclature names are defined in terms of ranks and types. Under phylogenetic nomenclature, definitions are clear relational statements that specify the content of a taxon, whilst diagnoses are separate statements listing apomorphies identifiable in the common ancestor (Serenó, 1999). Apomorphy-based phylogenetic definitions are an intermediate state, in that they include a diagnostic phrase within the definition.

It is proposed that a phylogenetic definition promotes nomenclatural clarity as it unambiguously pinpoints a common ancestor on a phylogeny. The definition of a taxon as the clade stemming from that ancestor is explicit, and the content of the taxon as all known and unknown, extant and extinct species in the clade is also precise. Similarly, phylogenetic definitions clarify the diagnosis of members of a clade by shared apomorphies present in the common ancestor (Serenó, 1999). They enhance nomenclatural stability since a name will always apply to a clade somewhere on the tree of life in the face of any taxonomic revision. The disassociation of names and rank also prevents any change in the spelling of names due to taxonomic revisions. As a result of this stability and clarity, it is hoped that the use of PN makes the application of a name universal (de Queiroz & Gauthier, 1994). Furthermore, this explicitness is objective and removes the "inscrutability" of authority judgements by which taxa are defined under traditional taxonomy (Langer, 2001). However, there has been considerable opposition to PN and the *PhyloCode* expressed in the literature, and in the next section we shall examine how stable, clear and universal PN is in practice.

IV. ANALYSIS OF PN AND THE *PHYLOCODE*

(1) Stability

One of the principle claims of the *PhyloCode* is that it increases nomenclatural stability by preventing "unnecessary changes in the associations between taxon names and clades that result under the Zoological Code from changes in taxonomic ranks" (de Queiroz & Cantino, 2001:261). However, critics have produced many examples to

demonstrate how PN generates considerable instability (e.g. Forey, 2001; Nixon and Carpenter, 2000). Both sides are correct in their claims, because they rest on a different interpretation of the word "stability". For proponents of PN, stability is measured in terms of the way names are spelled and in terms of the integrity of the definition itself. This is achieved by divorcing names from rank associations and so completely separating the processes of nomenclature and taxonomy. The desired result is a name that, once coined, never changes its spelling nor changes its phylogenetic definition. However, to achieve this nomenclatural stability one must sacrifice stability in terms of the content of the named taxon. That a named taxon may drastically change in inclusiveness as a result of phylogenetic revisions is freely accepted by authors of the *PhyloCode*, and is justified on the grounds that taxon circumscription is a taxonomic issue and as such should not affect nomenclature.

However, this concept of stability is not acceptable to *PhyloCode* critics, who dismiss it as "metaphysical" (Nixon & Carpenter, 2000). Indeed, Langer (2001) points out that definitions are always stable because they "say nothing empirical" (Ghiselin, 1966 quoted in Langer, 2001) about the content of taxa without a classification hypothesis. Thus one must assess the "stability in practice" of a system of nomenclature (Benton, 2000), and this can only be measured in terms of taxon circumscription. If the content of a named taxon changes with every phylogenetic revision, then the taxon can hardly be considered to be stable. We shall lay de Queiroz and Gauthiers' concept of nomenclatural stability to one side, and rather consider stability according to Nixon & Carpenter, measured by "the correspondence between the composition of groups and the names applied" (2000:315) in order to assess the "stability in practice" of PN.

It is accepted that the content of taxa will change when newly discovered taxa are inserted into them, or if sub-clades or species are moved in or out in the light of new research. Such changes are common in taxonomy and reflect an increase in knowledge. However, under PN the content of taxa may change due to phylogenetic rearrangements within them and the association between a name and a group may easily be broken. This does not happen under traditional nomenclature where a name retains its association with a particular group irrespective of phylogenetic rearrangements within it, unless the type is relocated. Under PN, if phylogenetic rearrangements cause specifiers to be relocated relative to the basal dichotomy, then

the specifiers will identify a different common ancestor. As a result a less or more inclusive clade is defined. If a specifier is moved to the opposite side of the basal dichotomy the name will be applied to a less inclusive taxon, and sub-taxa originally intended to be included within that name will be excluded. If a specifier is relocated outside of the basal dichotomy, a more inclusive group is defined, and taxa intended to be excluded are now included in a name.

De Queiroz and Gauthier (1992, 1994) argue that instability arises in the traditional system when taxa change their rank as a result of subjective taxonomic decisions, despite the fact that the same clade is being pointed at (see "Criticisms of Linnaean taxonomy" above). However, under PN a parallel, though inverse situation arises. If the relationships of basal ingroups or outgroups of a taxon change such that the specifiers now circumscribe a more or less inclusive clade, the taxon itself changes (in terms of its content), despite the fact that the same name is applied. For example, a name "X" is coined for the taxon (A(B(CD))) and defined as "the least inclusive clade containing A + D". New data shows that although A, B, C and D still form a monophyletic clade, B is in fact the sister of (A(CD)). Under the rules of PN, taxon X now contains only A, C and D. To de Queiroz and Gauthier this is acceptable, since taxa change their content as a result of taxonomic revisions all the time, and the name and definition remains unaltered. However, to a traditional taxonomist this would not be acceptable. The monophyletic clade containing A, B, C and D still exists and all four share the synapomorphies unique to that clade. To change the circumscription of X based on a change in phylogenetic hypothesis is consequently inappropriate, deviates from what is understood by the original application of the name and does not increase stability.

To take a real example, de Queiroz and Gauthier (1994:30) defined Mammalia as "the clade stemming from the most recent common ancestor of monotremes and therians". Under an initial hypothesis (Fig. 5(a)), this definition includes multituberculates in Mammalia, but after reappraisal of the evidence multituberculates is shown to be the sister group of monotremes and eutherians (Fig. 5(b)) and so the phylogenetic definition now excludes them from Mammalia. Under Principle 6 of the *PhyloCode* the exclusion of multituberculates in this case demonstrates "freedom of taxonomic opinion" and the separation of nomenclature from taxonomy. However, Nixon and

Carpenter (2000) object to this because the original intent was to include multituberculates in "Mammalia", and it should not be excluded merely as a result of an internal rearrangement within the clade. Such instability would not occur under the traditional system, where taxa are defined by shared synapomorphies.

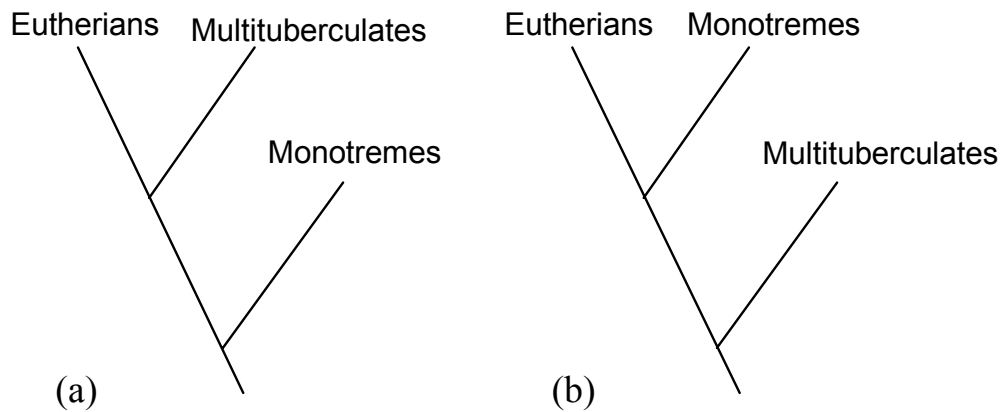


Fig. 5. Two hypothesised relationships of some mammals (after Nixon & Carpenter, 2000)

Consider the example provided by Forey (2001a) (Fig. 6), which presents three different validly published hypotheses for the placement of the coelacanth relative to other vertebrates. De Queiroz and Cantino (2001), in their response to Forey's paper, remark that this example introduces a "subtle bias", since it concerns names ranked above the family level. As such names are not defined nor regulated by the traditional Codes, they are therefore not subject to the rank-based problems which the *PhyloCode* is designed to eliminate. However, the example serves only to illustrate the changes in inclusiveness of names under different phylogenetic hypotheses which apply at any taxonomic level.

Suppose that the name "Sarcopterygii" had been coined for the taxon presented in Fig. 6(a). If the coelacanth, a specifier for the phylogenetically defined Sarcopterygii, is relocated to a more nested position in the phylogeny (Fig. 6(c)), then Sarcopterygii denotes a less inclusive group than that in Fig. 6(a). As a result of a change in phylogenetic hypothesis, the application of the name has changed from its original intent. Furthermore, this example demonstrates that under PN the hierarchical relationships of names may reverse. In Fig. 6(a) Choanata is a less inclusive group than Sarcopterygii, whilst in Fig. 6(c) the reverse is true (Forey, 2001a). This could be

confusing for all users of names and represents a fundamental instability in the system.

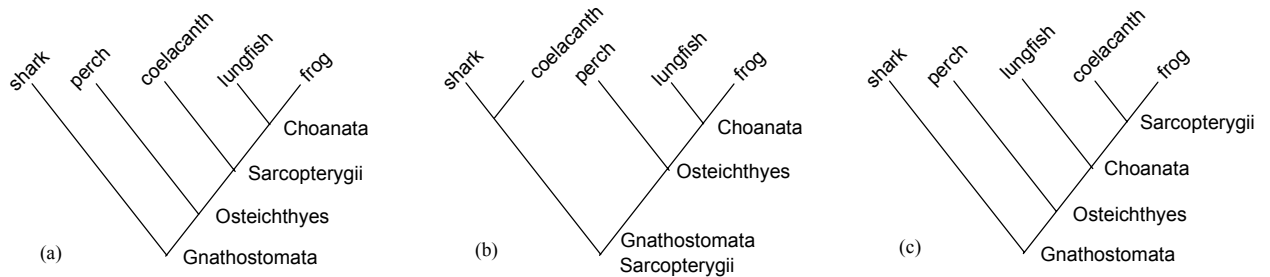
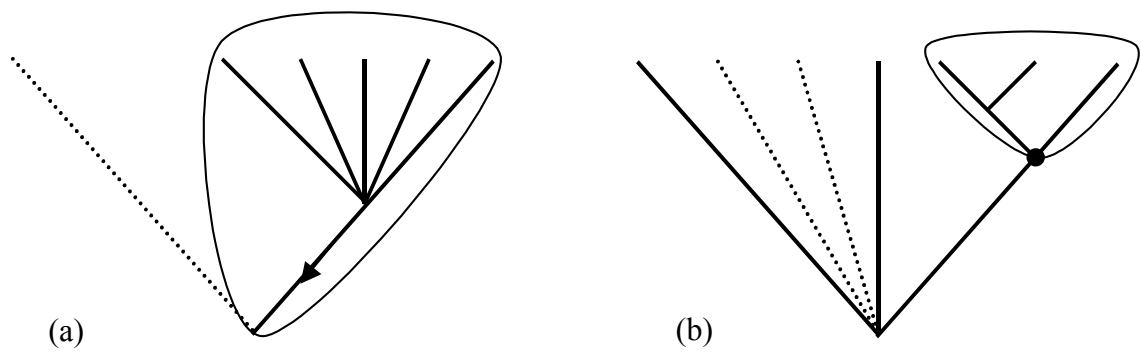


Fig. 6. Changes in the inclusiveness and relative hierarchical relationships of phylogenetically defined names in the face of phylogenetic revisions. (a)-(c) are three validly published hypotheses of relationships amongst vertebrates. Sarcopterygii is defined as "the least inclusive clade containing the coelacanth and the frog" and Choanata as "the most inclusive clade containing the lungfish and the frog" (adapted from Forey, 2001a).

If the coelacanth is moved to a more basal position in the phylogeny (Fig. 6(b)), then Sarcopterygii denotes a more inclusive group than that in Fig. 6(a). Moreover, the name denotes a clade which has already been named, Gnathostomata, and so these names become synonymous. One must be suppressed, and the clade originally called "Sarcopterygii" but lacking the coelacanth must now be renamed. This form of nomenclatural instability is precisely that abhorred by de Queiroz and Gauthier (1994) (see Fig. 2). They claim that in "situations involving either lumping or splitting, taxon names change their evolutionary meaning, while evolutionary taxa either change or lose their names" (1994:27). Although the relocation of the coelacanth in this example is a very different matter from the lumping or splitting of taxa, the nomenclatural consequences are similar. Despite the fact that the phylogenetic definition of Sarcopterygii remains the same, its "evolutionary meaning" in the sense of the group it was coined to denote has changed to a more inclusive clade. The same thing happens in taxonomic lumping when a name is inflated to encompass a larger clade. At the same time, the "evolutionary taxon" that was called Sarcopterygii, but no longer contains the coelacanth, has lost its name in the same way that the small clade once called "Chamaeleonidae" loses its name when Chamaeleonidae and Agamidae are lumped (Fig. 2(c)).

The objection of de Queiroz and Gauthier (1994) to lumping and splitting is hard to fathom when one applies the rules of PN to their own examples. Returning once more to Fig. 2, consider the initial instance where both Agamidae and Chamaeleonidae are monophyletic (Fig. 2(a)). Under PN, Agamidae could be defined as the least inclusive clade containing a representative from each branch of the basal dichotomy. If Agamidae is subsequently demonstrated to be paraphyletic (Fig. 2(b)), then by definition the name applies to the most inclusive clade (Fig. 2(c)). The consequence is the same as lumping, although the most inclusive clade is now called Agamidae not Chamaeleonidae - the taxa have been implicitly lumped. Clearly there is a difference, in that the nested clade Chamaeleonidae maintains its name and spelling (this is nomenclatural stability). However, de Queiroz and Gauthier (1994:27) object to lumping and splitting because "names change their associations from one clade or ancestor to another". Exactly the same thing happens with PN. In both applications of the name "Sarcopterygii" discussed above (Figs. 6(a) and (b)) it is possible to imagine that the name refers to the same clade or ancestor. This is because in the definition "the clade stemming from the common ancestor of the coelacanth and the frog", the "common ancestor" is not a fixed point but can change with phylogenetic hypotheses. However, this perspective is clouded by "metaphysical correctness" (Nixon and Carpenter, 2000), and in practical terms the ancestor referred to in Fig. 6(a) is clearly not the same as that in Fig. 6(b).

Sereno (1999) has suggested various ways in which the stability in content of phylogenetic definitions may be improved. As mentioned above, he disputes the claim of de Queiroz and Gauthier (1992) that crown groups are best defined using node-based definitions. If the basal ingroup relationships of a crown group are uncertain (Fig. 7(a)), then relocation of those branches during phylogenetic revisions will cause instability in content if the taxon is defined with a node-based definition. In these circumstances, the use of a stem-based definition would promote stability because it is based on reference to an outgroup. Therefore, rearrangement of branches within the clade would have no bearing on the circumscription of the taxon, unless the ingroup specifier is moved to a more basal position than the outgroup specifier. Conversely, if the outgroup relationships of a crown clade are uncertain, then the stability of the group is best served by using a node-based definition (Fig. 7(b)).



Other proposals for increasing stability relate to reference taxa. Because an alternative common ancestor can only be identified when one of two specifiers is moved to the opposite side or outside of the basal dichotomy, one may select reference taxa that are less likely to be moved in this way. For example, it is harder to relocate nested taxa in this way because they share more synapomorphies which place them at a greater distance from the common ancestor. The use of nested reference taxa also reduces internal inconsistencies and instability that can arise from the use of maximally inclusive reference taxa (see Sereno, 1999).

Sereno (1999) also suggests the use of well-known taxa as specifiers, since these are more likely to retain their phylogenetic integrity. Poorly-known taxa with missing data entries in phylogenetic analyses cause poor resolution as they may generate numerous equally parsimonious trees. They are therefore much more likely to cause instability in the light of phylogenetic revisions. This may be so, but many definitions may rest on a reference to fossil taxa, which are notorious for their unstable phylogenetic placement due to often poor preservation and ambiguous character states (Nixon and Carpenter, 2000; Forey, 2001b). In these instances, traditional character-based definitions would be better at retaining the original intent of a name in the face of phylogenetic revisions.

The use of multiple reference taxa has also been suggested as a means of increasing the stability of taxa under certain circumstances (Sereno, 1999). In the case of a stem-

based definition, if the basal outgroup relationships of a clade are uncertain then selecting multiple outgroup reference taxa will conserve the content of the taxon under any outgroup rearrangement (Fig. 7(b)). Regarding node-based definitions, the selection of specifiers from all ambiguous branches will conserve the content of the taxon under any internal rearrangement if the ingroup relationships are unresolved (see Fig. 7(a)). Taking this to the extreme would involve listing all taxa included in a clade as specifiers. However, in this case the relocation of any specifier outside of the clade would cause an inflation of the name. This is seen as a fundamental instability in the system (Nixon & Carpenter, 2000). Obviously a middle ground would need to be struck, but there are few proposals in the literature on this issue.

(2) Apomorphy-based definitions and clarity

It is difficult to dispute the claims of clarity in phylogenetic definitions. No matter how unstable the content of a taxon may be, its circumscription under PN remains unambiguous. However, although this may be true for node- and stem-based definitions, the same can not be claimed for apomorphy-based definitions. Apomorphy-based definitions have been criticised because the placement of characters on a cladogram is open to ambiguity (Sereno, 1999; Forey, 2001), which Sereno (1999:335) believes "should not be extended to taxonomic definitions". De Queiroz and Cantino (2001:265) accept that ambiguity poses a problem "concerning inferences about the composition of a taxon", but insist that this is a taxonomic not a nomenclatural issue.

There are several problems with apomorphy-based definitions, which are commonly associated with traditional character-based definitions (Sereno, 1999). Characters themselves can be ambiguous if they are composed of several distinct structures. For example, a contour feather is not a single structure, but is composed of a rachis, barbs, barbules, etc.. Fossil taxa form a series in the development of a character and so display intermediate character states (Forey, 2001b). Given that the definition of a feather may be interpreted differently by different authors, its placement on a cladogram relative to taxa with intermediate "feathers" is a matter of subjective taxonomic opinion. Defining Aves as "the clade stemming from the first species to

possess feathers synapomorphic with those in *Struthio camelus*" is therefore not explicit.

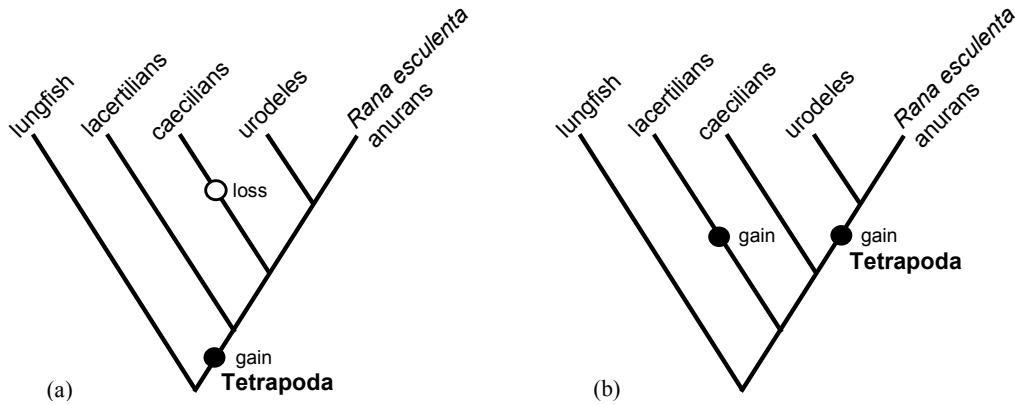


Fig. 8. Ambiguity in apomorphy-based definitions, where Tetrapoda is defined as "the clade consisting of all those animals with fingers and toes homologous with those in *Rana esculenta*". Under the optimising procedure of accelerated transformation (ACCTRAN) (a), the digits of lacertilians and other Tetrapods are homologous. Under the equally parsimonious delayed transformation (DELTRAN) procedure (b), digits in lacertilians and other Tetrapods arise by homoplasy, and so Tetrapoda denotes a less-inclusive clade (after Forey, 2001).

Another problem is that the optimisation of characters can also be ambiguous in that there may be numerous most parsimonious ways of placing a character on a tree. This may be due to a lack of data, already isolated as a particular problem for fossil taxa, or due to homoplasy. Take for example the definition of Tetrapoda as "the clade consisting of all those animals with fingers and toes homologous with those in *Rana esculenta*" (Forey, 2001a). Under the phylogenetic hypothesis presented in Fig. 8, lacertilians, urodeles and *Rana esculenta* possess these characters whilst lungfish and caecilians do not. There are two equally parsimonious ways of optimising fingers and toes onto the phylogeny, both requiring two evolutionary steps. Under accelerated transformation (ACCTRAN - Fig. 8(a)) digits are gained once and then secondarily lost in caecilians. In this case the digits of lacertilians and *Rana esculenta* are homologous and the lungfish is the outgroup of Tetrapoda. However, under delayed transformation (DELTRAN - Fig. 8(b)) digits are gained once in an ancestor of lacertilians and once in an ancestor of urodeles and *Rana esculenta*. In this instance, "fingers and toes" are homoplastic in the two groups, arising by convergent evolution, and Tetrapoda is a much less inclusive group with caecilians as the outgroup. The name "Tetrapoda" may thus apply to two nodes on the same phylogeny, requiring a qualifier such as time of origin or the optimisation procedure to determine where the

name should apply. This potential ambiguity encompassed by apomorphy-based definitions has caused them to be largely side-lined in the literature.

Despite these considerations, Lee (2000) has proposed that apomorphy-based definitions have a number of advantages over other types of definition. He argues that the single type of apomorphy-based definitions is most familiar and so most acceptable to traditional systematists, and that defining names in this way can retain the historical usage of names. He also proposes that apomorphy-based definitions are more stable than other phylogenetic definitions because they retain the association between characters and a named clade, despite changes in inclusiveness. Furthermore, an apomorphy-based definition may be applied to a group for which the phylogenetic relationships are completely unknown, since no reference is made to included or excluded taxa. In this way apomorphy-based definitions share some of the advantages of the traditional system over other phylogenetic definitions. He argues that the "Linnaean" definition of names proposed by Nixon and Carpenter (2000:306) as "the largest inclusive group bearing the designated homologies" that includes the type is in fact an apomorphy-based phylogenetic definition. Therefore, all arguments proposed by the latter in defence of traditional taxonomy are in fact supporting phylogenetic nomenclature.

(3) Theoretical Considerations

Aside from the claims for pragmatic benefits from the introduction of phylogenetic nomenclature, the *PhyloCode* has been drafted to introduce a "philosophical purity" into nomenclature (Benton, 2000). Generation of the instability discussed above is justified on the grounds that nomenclature would be placed within an "appropriate theoretical context". Opponents of PN argue that classifications are utilitarian constructs which should not be limited by this "metaphysical correctness" (Benton, 2000; Nixon & Carpenter, 2000). Nonetheless, Nixon and Carpenter (2000) return to philosophy to isolate logical inconsistencies underlying the *PhyloCode*. An underlying principle of PN is that clades are individuals and so deserve to be named. However, according to the theory of types, "no individual, or element, can be composed in part or whole by other individuals or elements *of like kind*" (Nixon & Carpenter, 2000:309). Thus a clade is not an individual as it is composed of sub-

clades, and so the whole metaphysics underlying phylogenetic nomenclature is inconsistent. Admittedly this point may be verging on the pedantic, but it does serve to illustrate that the philosophical bickering can work both ways and that a system of nomenclature should perhaps be judged more heavily on its practical merits.

Despite the assertion that all true taxa are monophyletic, de Queiroz and Gauthier (1990:311) demonstrate that phylogenetic definitions may be used to define paraphyletic or even polyphyletic taxa using exclusion clauses. For example, Reptilia may be defined as "the most recent common ancestor of Mammalia and Aves and all of its descendents *except* Mammalia and Aves". This is seen as a positive characteristic of PN, as indeed it may be, but it does display a measure of theoretical hypocrisy. Ereshefsky (2001) claims that by adding cladistic conventions to the traditional system it is made to be "less-Linnaean" and should thus be abandoned for something more naturally suitable. By this reasoning we should reject the *PhyloCode* on the grounds that in recognising paraphyletic taxa it becomes "less phylogenetic". Clearly this is nonsense. Indeed, though objectionable on theoretical grounds, the recognition of paraphyletic taxa may be desirable. One may wish to recognise the paraphyletic assemblage leading up to a crown-group that constitutes the "stem-group". A paraphyletic taxon, for example Bryophyta, may still constitute some form of meaningful group which should be recognised for the information it conveys. Furthermore, monophyly has yet to be demonstrated for large tracts of the tree of life, and failing to recognise non-monophyletic taxa would thus leave them unnamed (Forey, 2001a).

As discussed, nomenclatural instability under the *PhyloCode* is caused by changes in phylogenetic hypothesis. Herein lies another fundamental problem with PN. Just as clades are not individuals, neither are they real; at least, none of the trees presented as figures in this essay are "real", they are just hypotheses which are subject to change. The "tree of life" may be real if we accept that all life can ultimately be traced back to one origin, but we are a long way from drawing that final tree. Until that day we can never claim to "see" clades or the location of hypothetical common ancestors because they can change with every phylogenetic revision. Phylogenetic nomenclature is based on a system of hypotheses. However, characters, which are after all what allow

us to construct trees in the first place, are real and can be seen. They are therefore the best basis for classification.

V. THE PURPOSE OF NOMENCLATURE

Any system of classification finds itself caught between two potentially opposing objectives: the need to name (nomenclature) and the need to classify (taxonomy) (Winston, 1999). Ideally names should be stable and explicit, whilst classifications aim to be predictive and explanatory. However, in order for them to achieve the latter classifications must themselves evolve to incorporate our increase in knowledge. Therefore under the Linnaean system a conflict arises, as names sacrifice their orthographical stability to retain their information content. Under the proposals of the *PhyloCode*, names maintain their stability in the face of any taxonomic change because the processes of nomenclature and taxonomy are completely divorced. Names lose their association with rank and so are free to drift relative to each other in the hierarchy of taxa and may apply to clades of significantly fluctuating inclusiveness, depending on changes in phylogenetic hypothesis. In effect, "classification equals phylogeny" (Benton, 2000). Because this gain in nomenclatural stability is entirely at the expense of taxonomic information, as authors of the *PhyloCode* freely accept (e.g. de Queiroz and Cantino, 2001), the *PhyloCode* does not really represent a system of classification at all.

Although the separation of taxonomy and nomenclature is desirable to maintain stability, the purpose of nomenclature is to serve taxonomy (McNeill, 2000). Thus, if the taxonomy of a group is in flux, so too will be its nomenclature. Naming species and higher taxa is of fundamental importance, because without a way of referring to a taxon there is no way of communicating knowledge about it. An organism's name is "the key to its literature" (McNeill, 2000), and so it is important that names remain as stable as possible if they are to be used effectively. However, as well as being orthographically stable, names must be stable in terms of the taxa to which they are applied. Whilst accepting that the content of taxa will change in the light of new research and discoveries, if a name changes its content to the extent that it loses its association with the original *intent* of its application, it loses all utility. In the context

of PN this concept is "metaphysically incorrect" (Nixon & Carpenter, 2000), but it ignores the fact that classifications are tools which we use.

Although "phylogeny is real, classifications are not" (Benton, 2000). Biological classifications are human constructs designed to help us organise and understand the diversity of life we observe around us. Higher taxa are not real in any sense, but are delimited for their utility. From the examples discussed above we have demonstrated that under PN, names may lose their association with a familiar group due to phylogenetic revisions; recall the definition of Mammalia, which excludes Multituberculates under an alternative hypothesis (Fig. 5). This form of instability unnecessarily destroys what is understood by a name, and "if [classifications] lack stability and familiarity, they entirely lack utility" (Benton, 2000).

However, classifications do reflect patterns observed in nature, and these patterns arise as a result of evolution. A "natural classification" based on evolutionary relationships is much more informative than an "artificial classification" of, for example, "poisonous snakes" or "annual plants", because it draws on a much larger set of shared characters (Benton, 2000). Surely every taxonomist accepts that classifications should be constructed based on genealogical relationships?, and even staunch opponents of the *PhyloCode* recognise that monophyletic groups are "the only biological entities worth consideration" (Forey, 2001:94).

The traditional nomenclatural codes represent a compromise between this "utility-evolutionary tension" (Winston, 1999; Benton, 2000:635), whilst the *PhyloCode* does not. Although the Linnaean system may not be wholly appropriate for faithfully representing evolutionary relationships (see "Criticisms of the Linnaean Hierarchy" above), it is nonetheless satisfactory and conveys additional information to its users as well as promoting a greater "stability in practice". The addition of conventions to the original Linnaean hierarchy, such as additional ranks and the plesion category, do not diminish it, as Ereshefsky (2001) believes, but rather improves its utility and allows classifications to approximate to phylogeny without becoming a slave to it. This is appropriate, because phylogenies are hypotheses and are in constant flux. If it is deemed that a classification is significantly out of sync with a phylogenetic consensus

then taxonomic revisions, perhaps entailing nomenclatural changes, may be implemented. This is the natural consequence of an increase in knowledge.

Critics of traditional nomenclature oppose the subjectivity of authority judgements and taxonomic opinion in delimiting and diagnosing taxa. Indeed, the Codes do not officially govern the application of names above the level of genus. The registration of names under the *PhyloCode* would allow their regulation at all levels of inclusiveness and their application would be prescribed by law (Langer, 2001). However, Benton (2000) fears that this "draconian" approach will cause endless squabbling over the application of names. The very subjectivity of traditional nomenclature can be seen as an advantage. Since classifications are utilitarian, systematists can "vote with their feet" to determine the best and most acceptable application of a name. A similar flexibility in approach can be and is applied to minimise nomenclatural instability. Because classifications are utilitarian, "[n]othing in nomenclature need be sacrosanct" (McNeill, 2000:710). Thus if the application of priority is excessively disruptive, provision is made under the Codes for the conservation of widely used names.

One of the principle motivations of the *PhyloCode* is the prevention of name changes as a result of changes in taxon rank. Although the system is rankless, Cantino and de Queiroz (2001) insist that adoption of PN does not require the elimination of ranks (hierarchies are inherently ranked), merely the removal of rank associations from names. However, the coupling of taxonomic information with a name through rank-specific suffixes does have its advantages. It provides instant guidance on the placement of a taxon relative to another within a given classification, and allows us to make generalisations as to the inclusiveness of each. Also, presented with two names spelt with the same suffix, we know that the taxa are exclusive of one another. The binomial itself conveys information about relationships; if two species share the generic component of their names then we know that they are very closely related. If this information is lost, then names become abstract and meaningless without reference to a classification or cladogram.

Clearly it is not possible for every level of inclusiveness on the tree of life to be represented by a categorical rank, and so a rank based classification system will never

reflect a fine level of phylogenetic resolution. The application of rankless phylogenetic nomenclature, however, can achieve this resolution. De Queiroz and Gauthier (1992:457) argue that "given that the primary task is to represent phylogeny—and acknowledging that there are already more names than anyone can remember—then naming clades seems preferable to leaving them unnamed". But the primary task is to create a system that is utilitarian and stable in a practically, not metaphysically, meaningful way. Thus given that there are already so many names, why complicate the matter by introducing so many more? To name every clade is not serving a useful purpose.

VI. CONCLUSIONS

Objections to traditional "Linnaean" taxonomy rest on the grounds that it is "non-evolutionary" and does not classify life with the concept of common descent as it's *a priori* assumption. The imposition of mandatory ranks and the association between a name and its rank generates nomenclatural instability as a result of subjective differences in taxonomic opinion. The *PhyloCode* seeks to resolve these problems, by recognising taxa as named clades defined phylogenetically in a way that promotes stability, clarity and universality in nomenclature. By completely divorcing nomenclature from taxonomy, phylogenetic nomenclature does indeed achieve this desired stability. However, whilst the spelling of a name remains stable, its reference to an intended taxon does not except in a purely metaphysical sense. Under the *PhyloCode*, classifications simply become reflections of phylogeny, and the content of a taxon referred to by a name changes freely with every new phylogenetic hypothesis.

Opponents of the *PhyloCode* feel that the advocates of that system are missing the point. Classifications are constructed for their utility, to provide an effective way of organising and conveying information about the diversity of life. There will therefore always exist a tension between the need for nomenclatural stability against the need to encompass an increase in knowledge within classifications. Although the spelling of a name may change under the traditional system, the very subjective processes to which the *PhyloCode* authors object ensure that the application of name is consistent with its original intent. Although metaphysically incorrect, this maximises the utility value of

a classification. If we ever reach a time when we have a complete and concrete tree of life, then we could define its clades using phylogenetic nomenclature and achieve clarity and stability both in taxon name and content. However, until that day we must continue to balance theoretical desires for taxonomic purity against pragmatic considerations. Interestingly the objectives of both systems of nomenclature are the same: stability, clarity and universality. The current system has had 250 years of refinement and adaptation to develop a taxonomy that achieves these aims in a practical sense that is acceptable to its users. To replace it with a new system the inevitable (not so-) short-term problems of redefining millions of names must be justified in the long-term by a system that is better. On analysis of the case for and against implementation of the *PhyloCode*, it is hard to imagine that it presents a viable alternative to traditional taxonomy.

VII. ACKNOWLEDGEMENTS

I would like to thank Peter Forey, Mark Carine and other members of the botany department at the Natural History Museum for helpful conversations that nudged me in the right direction. I am especially grateful to Bill Baker and Dave Williams for taking the time to read a draft of this essay and for providing me with valuable comments and criticisms.

VIII. REFERENCES

Anderson, T. (1867). An enumeration of the Indian species of Acanthaceae. *Journal of the Linnean Society* 9, 425–526.

Benton, M.J. (2000). Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? *Biological Reviews* 75, 633–648.

Bremekamp, C. E. B. (1944). Materials for a monograph of the Strobilantheae (Acanthaceae). *Verhandelingen der Nederlandsche Akademie van Wetenschappen, Afdeling Natuurkunde, Tweede Sectie* 41, 1-305.

Cantino, P.D., Bryant, H.N., de Queiroz, K., Donoghue, M.J., Eriksson, T., Hillis, D.M. & Lee, M.S.Y. (1999). Species names in phylogenetic nomenclature. *Systematic Biology* 48, 709–807.

Cantino, P.D. & de Queiroz, K. (2000). *PhyloCode: a phylogenetic code of biological nomenclature*. [<http://www.ohiou.edu/phylocode/>]

De Queiroz, K. & Cantino, P.D. (2001). Phylogenetic nomenclature and the PhyloCode. *Bulletin of Zoological Nomenclature* 58(4), 254–271.

De Queiroz, K. & Gauthier, J. (1990). Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Systematic Zoology* 39(4), 307–322.

De Queiroz, K. & Gauthier, J. (1992). Phylogenetic taxonomy. *Annual Review of Ecology and Systematics* 23, 449–480.

De Queiroz, K. & Gauthier, J. (1994). Toward a phylogenetic system of biological nomenclature. *Trends in Ecology and Evolution* 9(1), 27–31.

Ereshefsky, M. (2001). *The Poverty of the Linnaean Hierarchy*. Cambridge University Press, New York.

Forey, P.L. (2001a). The PhyloCode: description and commentary. *Bulletin of Zoological Nomenclature* 58(2), 81–96.

Forey, P.L. (2001b). What's all this fuss about PhyloCode? *Palaeontological Association Newsletter* 47, 19–32.

Knapp, S. (2000). What's in a name? *Nature* 408, 33.

Langer, M.C. (2001). Linnaeus and the *PhyloCode*: where are the differences? *Taxon* 50, 1091–1095.

Lee, M.S.Y. (2001). On recent arguments for phylogenetic nomenclature. *Taxon* 50, 175–180.

Linnaeus, C. (1753). *Species Plantarum*, 2 vols., Laurentii Salvii, Holmiae.

McNeill, J. (2000). Naming the groups: developing a stable and efficient nomenclature. *Taxon* 49, 705–720.

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

Patterson, C. & Rosen, D.E. (1977). Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* 158, 81–172.

Sereno, P.C. (1999). Definitions in phylogenetic taxonomy: critique and rationale. *Systematic Biology* 48(2), 329–351.

Wiley, E.O. (1979). An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Systematic Zoology* 28, 308–337.

Winsor, M.P. (2001). Cain on Linnaeus: the scientist-historian as unanalysed entity. *Studies in the History and Philosophy of Biological & Biomedical Science* 32(2), 239–254.

Winston, J.E. (1999). *Describing Species: practical taxonomic procedure for biologists*. Columbia University Press, New York.