

PHYLOGENETIC TAXONOMY*

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Our classifications will come to be, as far as they can be so made, genealogies The rules for classifying will no doubt become simpler when we have a definite object in view. (Darwin 1859, p. 486)

The doctrine of evolution is not something that can be grafted, so to speak, onto the Linnaean system of classification. (Woodger 1952, p. 19)

INTRODUCTION

During the century following the publication of Darwin's (24) *Origin of Species*, biological taxonomy waited for the revolution that should have followed upon acceptance of an evolutionary world view. Although the principle of common descent gained wide acceptance early in that era, it assumed a largely superficial role in taxonomy (131). Pre-existing taxonomies were explained as the result of evolution (16, 86, 124, 128), and evolutionary interpretations were given to long-standing taxonomic practices (111), but the principle of descent did not become a central tenet from which taxonomic principles and methods were derived (111, 115).

In the middle of the twentieth century, the late Willi Hennig outlined an approach (57–59) that represented a fundamental shift in outlook concerning the role of the concept of evolution in taxonomy, and which engendered significant changes in that discipline (see 3, 29, 30, 97, 133, and references therein). By deriving the principles and methods of his approach from the tenet of common descent, Hennig granted the concept of evolution a position

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therein). By deriving the principles and methods of his approach from the tenet of common descent, Hennig granted the concept of evolution a position of central importance in taxonomy (114). The revolution initiated by Hennig is now well underway in systematic analysis, the field concerned with methods for estimating phylogenetic relationships (reviewed in 37, 129). But the same cannot be said about taxonomy proper, the discipline concerned with methods for communicating the results of systematic analysis. At the present time, biologists still have not developed a phylogenetic system of taxonomy. Hennig's distinction between monophyly and paraphyly was a crucial first step, but there is more to a phylogenetic system of taxonomy than the precept that all taxa must be monophyletic.

There is, after all, an important distinction between a phylogenetic taxonomy—an arrangement of names all of which refer to monophyletic taxa—and a phylogenetic *system* of taxonomy—a unified body of principles and conventions governing the use of those names. In order for a taxonomic system to be truly phylogenetic, its various principles and rules must be formulated in terms of the central tenet of evolution. It is this common evolutionary context that unifies the various principles and rules into a coherent system. But the concept of evolution still has not been granted such a central role in taxonomy. This is exemplified by the continued use of the Linnaean system, a taxonomic system based on a pre-Darwinian world view.

Even in taxonomies adopting Hennig's principle of monophyly, the Linnaean system generally has been taken for granted, and then modified or elaborated to accommodate the representation of phylogenetic relationships. Perhaps the most explicit example of this approach is Wiley's (132, 133) "annotated Linnaean system" (see also 20, 23, 30, 98). It is doubtful, however, that ad hoc modification of a body of conventions based on a pre-Darwinian world view is the most effective way to develop a phylogenetic system of taxonomy. Indeed, this preference for ad hoc modification, rather than reorganization starting from evolutionary first principles, demonstrates the resistance of biological taxonomy to the Darwinian Revolution. As long as this situation persists, a truly phylogenetic system is unlikely to be achieved.

Here we adopt an alternative approach intended to further the development of a phylogenetic system of taxonomy. Instead of taking the Linnaean system as a given and modifying it to facilitate the representation of phylogenetic relationships, we take the goal of representing phylogenetic relationships as primary. From this perspective, we outline the basic framework of a phylogenetic system of taxonomy by reformulating various taxonomic principles and rules in terms of the first principle of common descent. Some of the principles and rules of the phylogenetic system have already been formulated, and some current taxonomic practices are compatible with them. Nevertheless, there are important differences between the principles and rules

of the phylogenetic system and those developed around the Linnaean system as formalized in the various codes of biological nomenclature (69–71). We emphasize some of these differences in order to illustrate the fundamental shift in both perspective and practice represented by a phylogenetic system of taxonomy.

BASIC TERMS, GENERAL PERSPECTIVE, AND SCOPE

In order to avoid ambiguity and misinterpretation, it is necessary to define some basic terms used throughout this paper. Our use of these terms differs in subtle ways from the same or similar terms as they are used by other authors. Some of these definitions have been stated above but are reiterated here for emphasis.

Phylogenetic taxonomy is the branch of *phylogenetic systematics* concerned with the representation—rather than the reconstruction or estimation—of phylogenetic relationships. The objective of phylogenetic taxonomy is to represent relationships of common descent using a system of names. A *phylogenetic taxonomy* is a particular system of names representing the entities that derive their existence from a particular set of phylogenetic relationships. Finally, a *phylogenetic system of taxonomy* (as contrasted with the *Linnaean system* or the *current taxonomic system*) is a body of principles and rules governing taxonomic practice, the components of which are unified by their relation to the central tenet of evolutionary descent.

The purpose of any taxonomy is communication, which implies that taxonomies contain some kind of information. The information contained in a phylogenetic taxonomy is information about phylogeny, that is, about common descent (20, 36, 59). That information is conveyed in two ways, through taxon names and their graphic arrangement, as in a branching diagram or an indented list. In order for a taxonomy to convey information most effectively, the meanings of taxon names should be stable, universal, and unambiguous (e.g. 23, 65, 69, 71, 76, 85, 87, 130, 133). Promoting these qualities is one of the primary purposes of a taxonomic system. In the case of a phylogenetic system of taxonomy, the rules should be designed to promote stable, universal, and unambiguous meanings of taxon names with regard to what they signify about common ancestry.

We limit our discussion to the principles and rules governing the taxonomy of monophyletic taxa (*sensu* Hennig). We do not reiterate arguments about monophyly and paraphyly here; they have received due consideration elsewhere (e.g. 3, 5, 9, 10, 12, 13, 20, 25, 30, 58, 59, 61, 95, 97, 99, 109, 111, 117, 133). Furthermore, populations of interbreeding organisms are not the subject of this paper; they are members of a fundamentally different category of biological entities than monophyletic taxa.

TAXA

Taxa are named entities, generally named groups of organisms. Under traditional interpretations, organisms belong to taxa because they possess certain characters (organismal traits). By contrast, taxa in phylogenetic taxonomy are historical entities (50, 133) resulting from the process of common evolutionary descent. This implies that taxa are composite wholes or systems (e.g. 46–50, 55, 59, 61, 66, 104, 111–114, 137) composed at one organizational level of organisms as their component parts. Therefore, organisms are parts of taxa not because they possess certain characters, but because of their particular phylogenetic relationships (59, 114, 116, 132, 134, 136).

Taxa as systems of common descent are unified by their common evolutionary history. For this reason, their organisms (parts) are not necessarily continuous with one another at any given time, although they exhibit historical continuity through lines of descent (47, 133). Neither is a phylogenetic taxon composed only of those organisms that are currently alive or are recognized as belonging to it. Because of its historical nature, a phylogenetic taxon is composed of *all* the organisms exhibiting the appropriate relationships of common descent, whether those organisms are living or dead, known or unknown (3, 59, 113, 114).

The nature of phylogenetic taxa was clarified by Hennig (e.g. 58, 59, 61), who restricted the concept of monophyly to complete systems of common ancestry—entities each consisting of an ancestor and all of its descendants—that is, clades. By deriving his concept of taxa from the principle of descent, Hennig took an important step in the development of a phylogenetic system of taxonomy. For our discussion, what is significant is that *the taxa of concern in a phylogenetic system are named clades* (46, 59). Consequently, *taxon names are the names of clades*, which convey information about the existence of monophyletic entities, and the nomenclatural aspect of phylogenetic taxonomy is concerned specifically with the naming of clades, or *clade nomenclature*. This perspective makes for a more straightforward terminology than that currently adopted, for example, by the *International Commission on Zoological Nomenclature* (ICZN) (Table 1). Despite the undeniable importance of Hennig's insight, the principle of monophyly is only one component of a phylogenetic system of taxonomy.

NESTED HIERARCHY

One component of the Linnaean system that is compatible with a phylogenetic system of taxonomy is the nested, hierarchical arrangement of taxa. Perhaps this feature accounts for the persistence of the Linnaean system well into the

Table 1 Comparison of terminology in the Linnaean and phylogenetic systems. Quotations are from the International Code of Zoological Nomenclature (1985).

Concept	Term	
	ICZN (1985)	Phylogenetic System
"any taxonomic unit . . . whether named or not"	taxon	clade
a named taxonomic unit	taxon	taxon
"a nomenclatural concept denoted by an available name . . . but having no defined taxonomic boundaries"	nominal taxon	—
"A taxon . . . including whatever nominal taxa and individuals a zoologist at any time considers it to contain in his or her endeavour to define the boundaries of a zoological taxon"	taxonomic taxon	hypothesized content (approximately)
"The word or words by which . . . something is known"	name	name

era dominated by an evolutionary world view, for it can be deduced from the principle of common descent that phylogeny also forms a nested hierarchy of clades (24). According to Stevens (128), the nested, hierarchical structure of pre-Darwinian taxonomies may have hindered the development of phylogenetic taxonomy. Darwin used the nested, hierarchical structure of existing taxonomies as evidence supporting the theory of descent, which seemed to imply that these taxonomies were already phylogenetic.

The nested hierarchical structure of various pre-Darwinian taxonomies, however, does not have the same underlying basis as that of phylogenetic taxonomies. Humans commonly erect nested groups through a mental process of categorization in order to organize information (126), thus producing an arrangement similar in gross structure to the pattern of relationships resulting from common descent (59, 114). In most non-evolutionary taxonomies, however, taxa are treated either implicitly or explicitly as if they are abstract classes based on shared organismal traits (23, 46, 126). Consequently, the nested, hierarchical organization of such taxonomies reflects logical relationships among the abstract classes. In contrast, the nested hierarchical structure of phylogenetic taxonomies represents genealogical relationships among clades.

In any case, a hierarchical, nonoverlapping taxonomy is suited to the representation of phylogenetic relationships, although cases involving reticulate evolution require special conventions (98, 132, 133). Nested, hierarchical relationships among taxa are commonly represented by branching or Venn diagrams or by indented or sequenced lists. The arrangement of the names conveys information about the relationships of clades to one another, and in so doing it conveys information about the hypothesized content of taxa. Although nested, hierarchical arrangements of taxa are compatible with, and

perhaps even integral to, a phylogenetic system of taxonomy, other conventions of the current taxonomic system are not.

LINNAEAN CATEGORIES

In the Linnaean system, a familiar set of categories (kingdom, phylum, class, etc) is used to convey information about the relative positions of taxa (i.e. rank) in the taxonomic hierarchy. Although Linnaean categories can be used for this purpose in phylogenetic taxonomies, they are unnecessary for conveying such information. If used only to represent relative position in a hierarchy, the Linnaean categories contain no information about common ancestry that is not present in a branching diagram or an indented list of names. Concomitantly, if used in conjunction with indentation or a branching diagram, the information provided by the categories is redundant. Moreover, the categorical assignments of taxa are, by themselves, insufficient to specify relationships. In order to determine the relationships among taxa from their categorical assignments, one must first know whether the taxa in question are interested or mutually exclusive. For example, simply knowing that one taxon is a family and another is an order does not indicate whether that family is nested within that order.

Traditional and Hennigian Approaches to Categorical Assignment

The traditional manner in which taxa were assigned to Linnaean categories was incompatible with phylogenetic taxonomy in that it often caused taxonomies to contradict phylogenetic relationships (133). Categories were assigned on the basis of the degree of distinctiveness or the importance attributed to certain characters (e.g. 85, 87). Because the taxonomic hierarchy is one of nested, mutually exclusive taxa, a conflict arose between the use of Linnaean categories for reflecting distinctiveness versus their use for reflecting common ancestry. For example, the mutually exclusive relationship implied by assigning Pongidae and Hominidae to the same Linnaean category (family) contradicts the nested relationship of the hominid clade within the clade stemming from the most recent common ancestor of the various pongids.

In an attempt to give the Linnaean categories meanings that were compatible with a phylogenetic system of taxonomy, Hennig (59) suggested that the categories be defined in terms of absolute time, and that taxa be assigned to categories on the basis of time of origin. Farris (35) advocated using time of differentiation instead of time of origin. Under either of these conventions the categories would convey information in addition to relative position in a hierarchy and thus would not be redundant if combined, for example, with indentation. Furthermore, in contrast with the traditional approach to categor-

ical assignment, taxa assigned to the same category would be equivalent in at least one important respect—a respect that would facilitate comparisons of lineage diversity and other time-related phenomena (46, 59). Despite the advantages of basing the Linnaean categories on absolute time, this convention generally has not been embraced by taxonomists (e.g. 3, 23, 30, 56, 78, 123). Instead, most phylogenetic taxonomies have used the categories only to indicate relative divergence time, which requires nothing more than assigning sister taxa to the same category (but see below).

Mandatory Categories

Although Linnaean categories can be used in ways that are consistent with a phylogenetic approach to taxonomy, certain conventions associated with them are irreconcilable with that approach. One such convention is that certain categories—kingdom, phylum/division, class, order, family, and genus—are mandatory, although this is not stated in the zoological code; that is, every named species must be assigned to a taxon at each and every one of these levels (e.g. 85, 125). The problem with this convention is most evident in the case of organisms that are parts of ancestral populations, which are not parts of clades less inclusive than the one stemming from their own population (Figure 1, left). Thus, Hennig (59) noted that the stem species of birds is to be included in the taxon Aves, but not in any of the subgroups of Aves. If

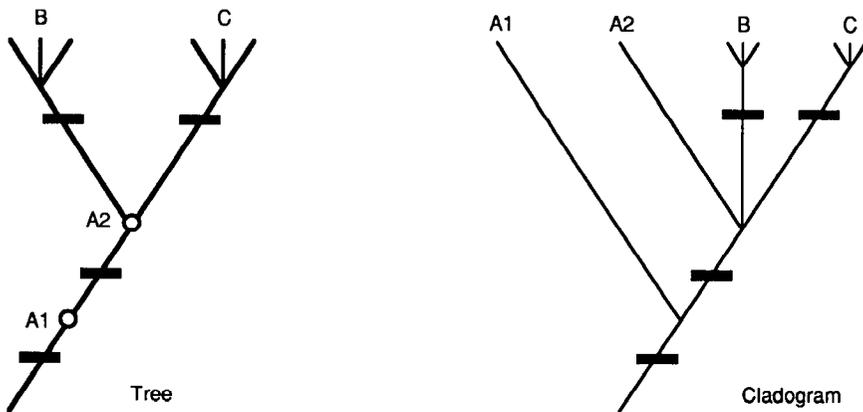


Figure 1 Ancestors cannot be assigned to monophyletic taxa less inclusive than those originating with them. *Left:* If the clade stemming from the most recent common ancestor of B and C (A2) is assigned the rank of class, then A1 and A2 are not parts of any monophyletic taxon assigned to a category of lower rank than class. *Right:* Even if no attempt is made to determine whether A1 and A2 are ancestors, they will lack the diagnostic apomorphies of subclades B and C and will not have any apomorphies unique to themselves. Consequently, they will not be referable to any taxon of lower rank than the category to which the clade stemming from the most recent common ancestor of B and C is assigned. Bars indicate apomorphies.

Aves is assigned to the class category, then the organisms in its stem species are not parts of monophyletic taxa below the class level.

The problem caused by mandatory categories is not dependent on identifying actual ancestors, the difficulty of which has been discussed by several authors (31, 35, 59, 97, 108). Ancestors, whether or not they can be identified as such, possess the derived characters of the clade originating with them but not those of any of its subgroups. Therefore, even if no attempt is made to identify ancestral organisms or populations *as ancestors*, they still will not be assignable to any of the monophyletic subgroups of the taxa originating with them (Figure 1, right). Consequently, recognizing taxa at all the mandatory categorical levels for such entities misrepresents their phylogenetic relationships by implying the existence of clades that do not, in fact, exist.

Wiley (132, 133) proposed to solve the problem posed by ancestors by assigning each ancestral species to a monotypic genus and placing the binomial in the taxonomic hierarchy in parentheses beside the name of the higher taxon stemming from it. This proposal has several problems. First, if the genus is interpreted as being equivalent to the higher taxon—suppose it is a class—then not only are the names of the genus and the class redundant, but the categories genus and class refer to the same level in the taxonomic hierarchy and thus the accepted relationship between the categories is violated. If the genus is not interpreted as being equivalent to the class, then the genus is nonmonophyletic. Moreover, Wiley's proposal does not solve the problem posed by ancestors within the context of mandatory categories, for it is, in spite of Wiley's avowed acceptance of that convention, based on an implicit rejection of mandatory categories. Continuing with the same example, the genus is not assigned to any taxon in the categories order and family.

The source of the problem, pointed out by Griffiths (54, 55, 56), is that phylogenies form truncated hierarchies, whereas the hierarchical structure of a taxonomic system with mandatory categories is not truncated. In other words, although various descendants are different distances (however measured) from the common ancestor at the base of the phylogeny, they are nevertheless forced into taxa representing all of the mandatory categories, which effectively imposes equal distances upon them. This problem applies both to ancestors and to extinct side branches relative to extant organisms, and it accounts for the supposed problem of including both fossil and Recent species in the same taxonomy (e.g. 12, 23, 59, 105). But that supposed problem is an artifact of taking the convention of obligatory Linnaean categories for granted. From the perspective of phylogenetic taxonomy, the problem is not with the systematization of fossils but with the convention of mandatory categories.

A comparable problem stems from the convention known as the principle of exhaustive subsidiary taxa (e.g. 30, 35, 125). According to that principle,

if a nonmandatory categorical level is used within any taxon, then it is used for all members of that taxon. For example, if a subgroup of a family is assigned to the subfamily category, then new taxa are customarily recognized so that all other members of the family can be assigned to some taxon of the subfamily category. In effect, this convention makes a nonmandatory category mandatory within a given part of the taxonomic hierarchy. It therefore causes the same kinds of problems discussed above. In current practice, applying the principle of exhaustive subsidiary taxa, and that of mandatory categories in general, often has an additional undesirable consequence—the recognition of new taxa for which evidence of monophyly is lacking (see 18 for discussion of an example involving genera).

Because the convention of mandatory categories is incompatible with the representation of phylogenetic relationships, a phylogenetic system of taxonomy must abandon that convention. Farris (35) has already done this in his “indented-list classifications.” Furthermore, leaving some specimens or species unassigned to taxa at particular levels in the taxonomic hierarchy is already practiced, albeit on a smaller scale, using the label “*incertae sedis*.” Although commonly followed in practice, assignment to taxa representing Linnaean categories of higher rank than genus is not an absolute requirement of any of the current codes of nomenclature (30).

Proliferation of Categories

Within the context of the Linnaean system, the discovery of new clades resulting from increasing knowledge about phylogeny led to a proliferation of taxonomic categories (e.g. 1, 11, 40, 88). Although sometimes viewed as a problem peculiar to phylogenetic taxonomy (e.g. 8, 19, 23, 64, 87), the problem exists for any approach, phylogenetic or otherwise, that attempts to reflect fine levels of systematic resolution in a taxonomy (100). More importantly, if we consider the proliferation of taxonomic categories problematical, this implies that maintaining the traditional, limited number of categories supersedes the goal of representing phylogeny. Several ad hoc modifications of the Linnaean system have been proposed as solutions to this supposed problem, for example, using the sequence of names of equally ranked taxa to convey relationships (96, 98, 132, 133), using a special category, plesion, for extinct taxa (105, see also 135), and using various combinations of prefixes to generate new categories (35). The sequencing convention might be viewed as a means of avoiding the proliferation of taxon names as well as categories. However, given that the primary task is to represent phylogeny—and acknowledging that there are already more taxon names than anyone can remember—then naming clades seems preferable to leaving them unnamed (3, 107, 135, 136).

Taxonomy Without Linnaean Categories

In light of the many problems associated with the Linnaean categories and their associated conventions (see also Binomials, Synonymy and Priority, and Redundancy), and given that the categories are neither necessary nor sufficient for conveying phylogenetic relationships, *phylogenetic taxonomy may be best served by abandoning the Linnaean categories* (see also 3, 22, 43, 54–56, 101, 136). If so, then sequencing, the plesion category, means of generating additional categories, and other ad hoc modifications of the Linnaean system designed to cope with the proliferation of categories would all be unnecessary. Eliminating the Linnaean categories is not as radical as it might seem. Systematists commonly construct taxonomies without Linnaean categories in the form of branching diagrams, and several authors have explicitly avoided using Linnaean categories in taxonomies taking the standard form of indented lists (e.g. 3, 32, 42–44, 62, 63, 79, 82, 106, 110, 119; see Appendix).

Wiley (133) criticized the use of indentation without Linnaean categories to convey hierarchical relationships on the grounds that it is difficult to line up the names in taxonomies spanning more than one page. Hennig (60, 62, 63) solved this problem using a code of numeric or alphanumeric characters, which can be used with or without indentation, to indicate position in the hierarchy (see also 55, 56, 82). Criticisms of this proposal (e.g. 3, 30, 132, 133) are based on treating the numeric prefixes as formal substitutes for Linnaean categories rather than simply as a means of keeping track of hierarchical position within a given taxonomy.

Eliminating the Linnaean categories does not require changes in the names of taxa, that is, in the spelling of taxon names. This maintains continuity with previous work, thereby ensuring access to the literature. In contrast, traditional practice may obstruct access to the literature because changes in the categorical assignments of taxa cause changes in their names (56, 115; see Synonymy and Priority). In order to preserve the spellings of taxon names, the suffixes formerly associated with certain Linnaean categories (e.g. -iformes, -idae, -inae, etc.) would be retained, but these suffixes would no longer imply anything about Linnaean categories (56). But regardless of whether the Linnaean categories are retained or abandoned, *the development of a phylogenetic system of taxonomy amounts largely to replacing the Linnaean categories with the principle of common descent as the basis for taxonomic conventions*. This becomes evident upon our consideration of conventions related to the principles of synonymy and priority (see below).

BINOMIALS

Although the taxonomy of species is not our concern in this paper, the problem posed by mandatory categories has implications for the formation of species names. In the Linnaean system, the genus is effectively a mandatory category,

because every species must be assigned to a genus in order to form its binomial name. Consequently, even if the Linnaean categories are otherwise abandoned, under the binomial convention used in the Linnaean system, the genus category would still be mandatory. A mandatory genus category faces the same problem as any other mandatory category, namely, that the ancestors of monophyletic taxa including more than one genus are not themselves parts of monophyletic genera.

For this reason, *a phylogenetic system of taxonomy cannot retain the Linnaean method of forming binomials; specifically, the names of genera cannot be parts of species names* (56). This does not mean that binomials themselves must be abandoned. If they are retained, however, the first name of a binomial species name would not be the name of a genus or a clade of any rank (56). Instead, the first name would simply be one part of a two part species name; Griffiths (56) suggested calling it a *forename* or *praenomen*. Consequently, a given species would not necessarily be more closely related to other species having the same praenomen than to those with a different praenomen, and this would be a potential source of confusion as long as such names continued to carry connotations about genera. Another alternative is uninomial species names (e.g. 17, 92, 93).

A taxonomic system in which the names of species are independent of the names of higher taxa, whether uninomials or non-Linnaean binomials, would also contribute to stabilizing the names of species. As pointed out by Cain (17) and Michener (92, 93), such a system would eliminate the alterations in species names caused by changes in generic assignment (both those involving the binomial combination and changes to the specific epithet necessitated by secondary homonymy). This kind of instability is exacerbated by attempts to achieve a phylogenetic taxonomy within the constraints of the Linnaean system, because eliminating paraphyletic taxa provides another reason for changing generic assignments. Species names that are independent of the names of higher taxa (genera) also permit use of Wiley's (132, 133) convention for including ancestral species in a taxonomy (see Mandatory Categories). Once species names are freed from any associations with the names of genera, the contradictions noted above vanish. (This convention assumes that the species category is a category of biological entities rather than one level or rank in the hierarchy of Linnaean categories—e.g. 113). Modification of the Linnaean approach to forming species names is not only necessary for phylogenetic taxonomy, it would also promote nomenclatural stability, one of the primary functions of the current codes.

TYPES

In the current taxonomic system, name-bearing or nomenclatural types provide objective standards of reference by which the application of names is

determined. According to the principle of typification, every nominal taxon at or below a particular categorical level has such a type (69–71). Traditionally, types are of two basic kinds: organisms (type specimens) and taxa (type species, type genera). In the following discussion, we address only types of the second kind. The use of type specimens for species taxa does not appear to be problematical; in any case, it is outside of the scope of the present paper.

Under the current system, the names of type taxa of the genus category contain the word stems that serve as the bases for the names of taxa assigned to higher categories. Thus, the name of a zoological taxon assigned to the family category is formed by adding the suffix “-idae” to the stem of the name of its type genus (71). Many rules concerning types are tied to Linnaean categories, and the use of nomenclatural types in forming taxon names is itself a taxonomic convention rather than a logical or biological necessity (23). Therefore, basing a new taxonomic system on the principle of descent rather than on the Linnaean categories necessitates a reevaluation of the principle of typification.

Typification is not incompatible with the naming of clades. Although tied to Linnaean categories in the current taxonomic system, the use of nomenclatural types need not be so tied. In the absence of Linnaean categories, one might refer to type populations, or type (sub)clades, or simply type (nominotypical) taxa. Moreover, the name of a clade can be based on the name of one of its subclades or component populations regardless of whether any of the taxa involved are assigned to Linnaean categories. If such a convention is adopted, however, it would be useful to state the definition of each taxon name in terms of a specified relationship to the type (see Definitions of Taxon Names). For example, the name “Lepidosauromorpha” is defined as Lepidosauria and all saurians sharing a more recent common ancestor with Lepidosauria than with Archosauria (43). Such a convention would ensure that the nested relationship between a taxon and its nomenclatural type is preserved in the face of changing ideas about phylogenetic relationships.

DEFINITIONS OF TAXON NAMES

Reformulation of the manner in which taxon names are defined is central to developing a phylogenetic system of taxonomy because it provides a basis for the derivation of secondary principles and rules concerning the use of taxon names. Under the current system, the definitions of taxon names are stated in terms of characters, that is, organismal traits. For example, according to the zoological code, a definition “purports to give characters differentiating a taxon” (71, p. 253). Definitions of taxon names based on organismal traits are fundamentally non-evolutionary. Such definitions were in use long before the widespread acceptance of an evolutionary world view, and furthermore,

they make no reference to common descent or any other evolutionary phenomenon (112, 115).

In the context of a phylogenetic approach to taxonomy, several authors have proposed that the definitions of taxon names are to be based on phylogenetic relationships (e.g. 43, 49, 111, 116, 118, 132, 134). Nevertheless, it was only recently that concrete methods for doing this were devised. De Queiroz & Gauthier (115; see also 112) identified three classes of phylogenetic definitions, that is, three ways of defining the names of taxa in terms of phylogenetic relationships (Figure 2). A *node-based definition* specifies the meaning of a taxon name by associating the name with a clade stemming from the immediate common ancestor of two designated descendants (Figure 2, left). A *stem-based definition* specifies the meaning of a name by associating the name with a clade of all organisms sharing a more recent common ancestor with one designated descendant than with another (Figure 2, middle). And an *apomorphy-based definition* specifies the meaning of a name by associating the name with a clade stemming from the ancestor in which a designated character arose (Figure 2, right). Examples of these three classes of phylogenetic definitions are given by de Queiroz & Gauthier (115) and references cited in that paper.

Phylogenetic definitions clarify other taxonomic issues in the context of a phylogenetic approach to taxonomy. For one, they clarify the distinction between definitions and diagnoses (115; see also 45, 46, 118). *Definitions* are statements specifying the meanings of taxon names (words); they are stated in terms of ancestry. *Diagnoses* are statements specifying how to determine whether a given species or organism is a representative of the taxon (clade) to which a particular name refers; they are most commonly stated in terms

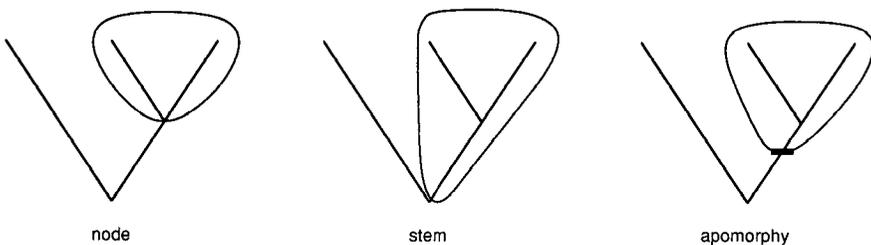


Figure 2 Three possible ways of defining taxon names phylogenetically. *Left*: The name is defined as referring to the most recent common ancestor of two designated taxa and its descendants (node-based definition). *Middle*: The name is defined as referring to all organisms sharing a more recent common ancestor with one designated taxon than with another such taxon (stem-based definition). *Right*: The name is defined as referring to the first ancestor to evolve a designated character (bar) and its descendants (apomorphy-based definition). After de Queiroz & Gauthier (115); see that reference for examples.

of characters. Phylogenetic definitions also permit one to define any given name as referring to a monophyletic taxon and not to a paraphyletic or polyphyletic group or a metataxon (115). Although it is always possible to make mistakes about the contents (included species and organisms) and diagnostic characters of a taxon, a definition such as “the most recent common ancestor of archosaurs and lepidosaurs *and all of its descendants*” necessarily refers to a monophyletic taxon.

Phylogenetic definitions illustrate what it means for a taxonomic principle to be stated in terms of the central tenet of evolution. In contrast with character-based definitions, which make no reference to any evolutionary phenomenon, *phylogenetic definitions of taxon names are stated in terms of common ancestry relationships and the historical entities (clades) resulting from those relationships*. Phylogenetic definitions are thus thoroughly evolutionary in that the concept of common ancestry is fundamental to the meanings of the names they are used to define. Taxon names thus have explicit evolutionary meanings, and this bears on several other taxonomic issues.

SYNONYMY AND PRIORITY

Two taxonomic issues upon which phylogenetic definitions have direct bearing are synonymy and priority (115). Reevaluating these issues from an evolutionary perspective illustrates the difference between a taxonomic system based on the Linnaean categories and one based on the principle of descent. It also reveals fundamental incompatibilities between the current system and a phylogenetic approach to taxonomy.

In the current system, the concept of synonymy is tied directly to the Linnaean categories. Taxon names are considered synonymous if they are based either on the same nomenclatural type (homotypic, objective, or nomenclatural synonyms) or on different nomenclatural types (heterotypic, subjective, or taxonomic synonyms) considered to belong to a single taxon assigned to a particular Linnaean category (70, 71). Not only is this concept of synonymy based on a non-evolutionary criterion, it is also difficult to reconcile with phylogenetic interpretations of the meanings of taxon names.

As a result of being tied to the Linnaean categories, the criterion of synonymy adopted in the current system is responsible for considerable instability in the phylogenetic meanings of taxon names, which vary as the result of changes in, or differences in opinion about, the assignment of taxa to Linnaean categories. For example, if sister taxa originally considered to form two families are later judged to represent a single family, then their names are treated as synonyms. Each name thus shifts its association from a less inclusive to a more inclusive clade. In this particular example, the change in meaning results from an arbitrary decision that the taxa in question do not

deserve to be ranked as separate families. Although such a change in categorical assignment may be judged unnecessary, a similar problem results from attempts to achieve a phylogenetic taxonomy while retaining a criterion of synonymy based on the Linnaean categories. That is, elimination of paraphyletic taxa provides a reason for the so-called lumping or splitting of taxa, which leads to changes in the associations of their names with particular clades (Figure 3).

In pre-Hennigian taxonomies, it is often the case that a particular taxon is paraphyletic with respect to another taxon assigned to the same Linnaean category. One means of eliminating the paraphyletic taxon is to “unite” that taxon with its derivative taxon into a single inclusive taxon at a given categorical rank, the action commonly known as “lumping.” In such cases, the two names are treated as synonyms. Paraphyly of the family Agamidae (Figure 3, left), for example, can be rectified by recognizing a single family for the species formerly included in Agamidae and its derivative family Chamaeleonidae (Figure 3, right) (38). The names of the two previously recognized families are then judged to be synonymous. Associating the name of the paraphyletic taxon with the inclusive clade changes its meaning in terms of content (included species). That association might, however, be justified by the prior implicit association of the name with the ancestor of the inclusive clade (115). In any case, treating the name of the derivative taxon

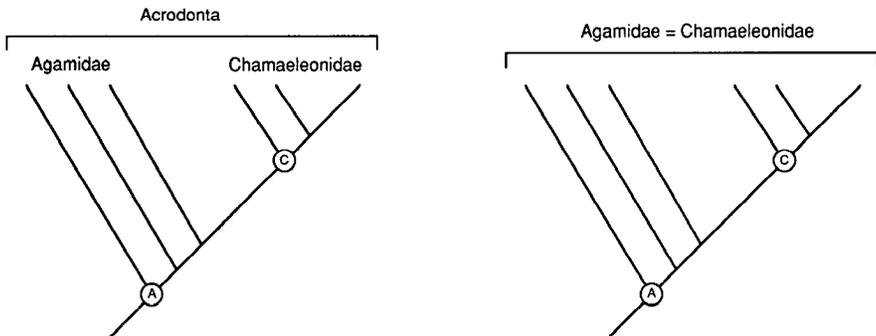


Figure 3 Change in the meaning of a taxon name resulting from an attempt to achieve a phylogenetic taxonomy within the constraints of a criterion of synonymy based on Linnaean categorical assignment. *Left:* Agamidae is paraphyletic if Chamaeleonidae is assigned to the same Linnaean category (family). *Right:* If all species in question are considered to belong to a single taxon assigned to the family category, “Agamidae” and “Chamaeleonidae” are treated as synonyms, and the latter name shifts its association from the clade stemming from ancestor C to that stemming from ancestor A. According to the principle of priority, “Chamaeleonidae” is the valid name of the clade stemming from ancestor A, even though “Agamidae” was originally associated with that ancestor and “Chamaeleonidae” was not. Furthermore, “Acrodonta,” which was originally associated with the clade stemming from ancestor A, is rejected as the name of that clade because it is not a family name.

as a synonym changes the association of that name from a less inclusive to a more inclusive clade (Figure 3). Thus, the criterion of synonymy used in the current system causes instability in the phylogenetic meaning of "Chamaeleonidae" (115).

The instability noted above is highlighted by the manner in which the *valid* name of a taxon is most commonly determined in the current taxonomic system. According to the principle of priority, the valid name of a taxon is the oldest name applied to it (e.g. 70, 71). Because the various names applied to a taxon are synonyms, and because synonymy is currently tied to the Linnaean categories, the issue of priority is also ultimately tied to the Linnaean categories. For example, in zoological nomenclature, the valid name of a taxon assigned to the family category is the oldest family-group name based on the name of one of the genera included within that taxon.

The non-evolutionary criterion of synonymy adopted in the current taxonomic system can thus lead to drastic changes in the accepted names of clades. Continuing with the previous example (Figure 3), the valid name of the inclusive monophyletic taxon would be "Chamaeleonidae," because that is the oldest name of the family group based on one of the genera included within the taxon. Consequently, not only does "Chamaeleonidae" change its association from a less to a more inclusive clade (Figure 3), but that change in meaning occurs despite two other important facts. First, the taxon with which the name "Chamaeleonidae" was originally associated is still considered monophyletic and now either must be renamed or go unnamed. And second, the more inclusive clade already has a name, "Acrodonta," which is now ignored simply because it is not a family name. In general, the currently accepted criterion of synonymy combined with the practices of lumping and splitting is a major source of taxonomic instability. Lumping several taxa causes names to change their associations from less inclusive taxa to a more inclusive one, and splitting a single taxon results in restricting its name to a less inclusive taxon.

These problems stem from a fundamental incompatibility between the Linnaean and phylogenetic meanings of taxon names. Under the current system, categorical assignment partly determines the meanings of taxon names, because it determines the spellings of the names (i.e. their suffixes) and hence the taxa with which particular names are associated. This situation grants a non-evolutionary tradition primacy over the concept of evolution. That is to say, the association of a taxon name with a particular Linnaean category is, in effect, considered more important to the meaning of that name than its association with a particular clade or ancestor. This is unacceptable from the perspective of phylogenetic taxonomy. Names such as "Agamidae" and "Chamaeleonidae" have very different meanings when judged by their original reference to different sets of species, and thus implicitly to entities

stemming from different common ancestors; in phylogenetic terms, they are not synonymous.

Furthermore, the very acts of lumping and splitting—which are intimately tied to changes in the meanings of taxon names under the current system—are difficult to interpret in phylogenetic terms. Taxonomists can neither lump nor split taxa as named clades, for clades are not things that taxonomists form, erect, unite, or divide, but rather things to which they give names. Outside the context of Linnaean categories, the notions of lumping and splitting make little sense, and they are irreconcilable with the phylogenetic meanings of taxon names.

In short, the criterion of synonymy used in the current taxonomic system is incompatible with the goals of phylogenetic taxonomy, that is, stable meanings of taxon names in terms of what they signify about common ancestry. Under the current system, different authors use the same name for different clades and different names for the same clade, and this can happen as the result of subjective differences concerning assignments to Linnaean categories even when the authors are in full agreement about what organisms and species make up the taxa (56). In the phylogenetic system, the Linnaean categories have nothing to do with the meanings of taxon names; *taxon names are synonymous if and only if they refer to the same clade* (115). Under phylogenetic definitions of taxon names, synonymy can be assessed unambiguously within the context of an accepted phylogeny by determining whether the names refer to clades stemming from the same ancestor (115).

Similarly, *priority in the phylogenetic system is not based on first use of a name in association with a particular Linnaean category but on first use of a name in association with a particular clade* (115). This is not to say that the valid name must always be established by priority. Indeed, recent movements advocating nomenclatural reform within the context of the Linnaean system seek to constrain the use of priority in establishing the validity of taxon names (122, 127). But regardless of whether or to what extent priority is used to establish the valid name of a taxon, in a phylogenetic system of taxonomy, the criterion of priority must be based on ancestry.

REDUNDANCY

Phylogenetic definitions of taxon names also bear on the problem of taxonomic redundancy. Linnaean taxonomies often contain monotypic taxa, which appear to be equivalent in content with the single included taxon at the next lower categorical level. In pre-Hennigian taxonomies, monotypic taxa were recognized in order to reflect distinctiveness (e.g. 14, 85, 121, 125). Phylogeneticists rejected distinctiveness as a justification for assigning a taxon to a Linnaean category of high rank, at least in cases where this practice

resulted in the recognition of paraphyletic taxa (e.g. 59, 133). Nevertheless, monotypic taxa are also common in phylogenetic taxonomies adopting a Linnaean framework because of the constraints imposed by mandatory categories and exhaustive subsidiary taxa (35, 55). The apparent equivalency of, for example, a monotypic order and its single included family seems to contradict the hierarchical relationships between the Linnaean categories as well as the fact that taxonomists consider the two names to refer to different taxa. These seeming contradictions have been discussed by various authors under the name Gregg's Paradox (14, 15, 33–35, 52, 53, 67, 73, 120, 121). Furthermore, if the different names in fact refer to the same taxon, then they are redundant. One name is sufficient for a single clade.

Eliminating the convention of mandatory Linnaean categories (or use of the categories altogether) would solve these problems by removing the reason for recognizing monotypic taxa. But regardless of whether the Linnaean categories are retained, the problems are more apparent than real. On the one hand, apparent equivalency is often an artifact of restricting considerations to extant organisms (55). For example, Simpson (125) and Ruse (121) treat the taxa *Orycteropus*, Orycteropodidae, and Tubulidentata as if they are all monotypic because they are all made up of one and the same living species. There are, however, several known species of fossil aardvarks that have been referred to these taxa in such a way (102, 103) that only Tubulidentata can be considered monotypic in the sense of being made up of the same set of known organisms as Orycteropodidae.

Even taxa composed of the same known organisms are not necessarily identical. Using phylogenetic definitions of taxon names, different names can be defined so that they refer to different clades in a series of increasing inclusiveness, that is, clades stemming from successively more remote ancestors (Figure 4) (see also 59). For example, "Orycteropodidae" might be defined as the clade stemming from the immediate common ancestor of *Orycteropus* and the extinct *Plesiorycteropus*, whereas "Tubulidentata" might be defined as all those mammals sharing a more recent common ancestor with *Orycteropus* than with other extant mammals. Although all known tubulidentates are orycteropodids, the taxa are not necessarily equivalent. As noted above (see Taxa), a taxon as a named clade consists not only of those organisms that we recognize as its members; it consists of an ancestor and all of its descendants, extant and extinct, known and unknown. Therefore, although Orycteropodidae and Tubulidentata may appear equivalent when considerations are restricted to known or extant organisms, the definitions of the names refer to different clades and thus imply a difference in actual content. That difference can potentially be demonstrated by the discovery of currently unknown organisms.

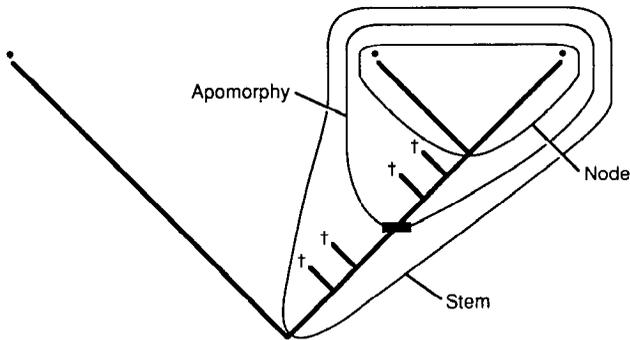


Figure 4 Although taxa may be identical in terms of known content, their names can be defined phylogenetically so that they refer to clades differing in actual content. The nested bubbles illustrate, in order of decreasing inclusiveness, stem-, apomorphy-, and node-based taxa in a nested series. Dots represent extant and/or known species; daggers represent extinct and/or unknown species. See text for example.

STANDARD NAMES

Although not necessary for developing a phylogenetic system of taxonomy, it is worthwhile to consider how the meanings of certain names might be standardized in a way that is most useful for comparative biology. Standardization would make the meanings of names universal, which is important to their function in communication (71, 76, 85, 87). Proposals for standardizing certain higher taxon names not covered by the zoological code have recently been made within the context of the Linnaean categories (e.g. 27, 28, 122); however, it is useful to consider the matter from a phylogenetic perspective.

Inconsistencies in the Current Use of Taxon Names

Of the vast numbers of taxon names that have been coined by taxonomists, some are more widely known and used than others. It is particularly important to standardize the meanings of widely known names to ensure that all biologists who use them are referring to the same entities. Currently, the supposed meanings of those names are inconsistent with the way they are most often used. The nature of that inconsistency is revealed by the following example.

Since its discovery (89, 90), the fossil taxon *Archaeopteryx* has been recognized as an outgroup to the clade stemming from the immediate common ancestor of extant birds (41, 68, 84). *Archaeopteryx* predates members of that clade by some 50 million years, and it retains several ancestral characters relative to extant birds. Nevertheless, that fossil has, with few exceptions, been

referred to the taxon Aves because it has the “key” avian character (84). Indeed, to the extent that taxon names have phylogenetic connotations, they usually appear to be apomorphy-based. Thus, “Aves” is usually thought of as being associated with the clade stemming from first vertebrate possessing feathered wings.

Despite general agreement that Aves includes *Archaeopteryx*, biologists commonly use the name “Aves” (“birds”) when making generalizations that apply to extant birds alone. Thus, supposed meaning and actual use are inconsistent. Furthermore, that inconsistency persists despite the existence of a less well known name coined for the specific purpose of making the relevant distinction. Most biologists continue to use the widely known name “Aves” when referring to the taxon explicitly associated (e.g. 21) with the name “Neornithes.” A comparable situation holds for the fossil taxon *Ichthyostega*, the widely used name “Tetrapoda,” and Gaffney’s (39) less well known name “Neotetrapoda.”

The reason for such inconsistencies seems to be that most well known names have gained wide use through their associations with distinctive groups of extant organisms. Those widely known names associated with clades have therefore most commonly been associated to one degree or another with crown clades—clades stemming from the immediate common ancestor of sister groups with extant representatives (74; see also 60, 62, 63). Distinctiveness is often a consequence of an incomplete fossil record, but even as the gaps are bridged by fossil discoveries, those gaps effectively persist because most biologists study systems that are not preserved in fossils. Nevertheless, discoveries of extinct outgroups to crown clades point to the existence of more inclusive clades, a fact that raises two alternatives concerning the associations of the original names. Either those names can be associated with the crown clades, or they can be associated with one of the larger clades including various extinct relatives. But even when the original names are explicitly defined so as to include at least some of the fossil outgroups, as they most often are, the majority of comparative biologists ignore the fossils. Consequently, the original names tend to be used as if they refer to crown clades, and new names coined specifically for the crown clades seldom gain wide use except among paleontologists.

In addition to the inconsistencies described above, the meanings of widely used taxon names also vary considerably among systematists explicitly addressing the taxonomy of fossils. These latter inconsistencies reflect differing preferences for what are, in effect, node-based, stem-based, and apomorphy-based definitions. For example, some authors use the name “Mammalia” for a crown clade (42–44, 119), whereas others use it for that crown clade and all extinct amniotes more closely related to it than to other extant amniotes (2–4, 81). Still others associate the name with an intermediate

clade diagnosed by possession of a dentary-squamosal jaw joint, thus including the crown clade as well as a few of its extinct outgroups (e.g. 77, 91). And such differences in use often persist in spite of considerable agreement about phylogenetic relationships.

Standard Names for Crown Clades

No scientific enterprise, least of all one that considers the promotion of nomenclatural universality as one of its primary objectives, can accept the inconsistencies and ambiguities current in biological taxonomy. In some sense, progress in any scientific discipline can be measured in terms of further refinement, rather than escalating imprecision, in vocabulary. Therefore, it is imperative that biological taxonomy adopt rules for standardizing the meanings of important names. Because of the way in which those names are most often used, *the phylogenetic meanings of many widely known taxon names are most effectively standardized by tying them to clades within which both branches of the basal dichotomy are represented by extant descendants*. Names can be associated unambiguously with crown clades using node-based definitions (see Definitions of Taxon Names).

Restricting widely used names to crown clades standardizes their meanings in a way that is most useful to the largest number of comparative biologists. Although it will entail changes in the taxonomy of various fossils—*Archaeopteryx*, for example, will no longer be considered part of the taxon named “Aves”—this emphasis on extant organisms is not meant to imply that extant organisms are more important than fossils for establishing relationships. On the contrary, it is clear that phylogenetic relationships are best analyzed by considering both fossil and Recent organisms (26, 44). Nevertheless, most biologists study extant organisms, if for no other reason than that many aspects of the biology of extinct organisms are not only unknown but perhaps unknowable.

Because fossils are so often ignored, this proposal will bring the definitions of widely known names into agreement with the manner in which those names are most often used. It will also ensure that when neontologists and paleontologists use the same name, they will be referring to the same clade. Although paleontologists will have to restrict their use of various names, this is a more effective way to achieve universal meanings than forcing the vast majority of comparative biologists to learn and use more obscure names. Paleontologists will still have to use less well known names, but that is appropriate because the distinctions embodied in those names are of concern mainly to paleontologists. Furthermore, associating widely known names with crown clades is often consistent with a liberal interpretation of a phylogenetic criterion of priority (see Synonymy and Priority). Although most widely known names did not originally have explicit phylogenetic definitions, they

tend to be old names that were used for groups of extant organisms prior to the discovery of their extinct outgroups.

Another advantage of this proposal is that it should discourage biologists from making unsupported generalizations about extinct outgroups while at the same time enabling them to make the greatest number of supportable inferences about the extinct members of taxa associated with widely used names. Biologists commonly make generalizations about the characters of entire taxa based on surveys of their extant representatives; however, it is not justifiable to extend those generalizations to fossil organisms sharing more remote common ancestors with the extant forms. For example, if the name "Tetrapoda" is defined to include *Ichthyostega*, one should not assume that the features common to the limb development of extant tetrapods (e.g. 94) characterize tetrapods as a whole. Therefore, restricting widely known names to crown clades will discourage biologists from making unsupported generalizations about the characters of extinct outgroups such as *Ichthyostega*. At the same time, it will also permit biologists to make the greatest number of inferences about the extinct representatives of taxa associated with widely used names based on properly conducted surveys of extant organisms. For example, if the name "Tetrapoda" is defined as the clade stemming from the most recent common ancestor of amphibians and amniotes, then features common to the limb development of diverse extant amphibians and amniotes can reasonably be inferred to have been present in the ancestral tetrapod.

Standard Names for More Inclusive Clades

Despite the advantages of restricting widely used names to crown clades, it is equally important to name the more inclusive clades, each consisting of a crown clade and all extinct taxa sharing with it common ancestors not shared with any other crown clade. These "total groups" (74, 75) or "panmonophyla" (80) are particularly important because they are stem-based taxa (not to be confused with paraphyletic stem-groups), and only stem-based taxa can be true sister groups, which are equivalent in age (Figure 5). Consequently, *for each standard name defined as the name of a crown clade, there should also be a standard name for the more inclusive clade consisting of the crown clade plus its extinct outgroups*. Such names can be associated unambiguously with the appropriate clade using stem-based definitions (see Definitions of Taxon Names).

Because of their equivalence in age, it is critical to use stem-based sister taxa in comparisons where such equivalence is important, as it is in investigations of taxonomic diversity. For example, it may be inappropriate to invoke an apomorphy of Aves to explain why that taxon is more speciose than is Crocodylia. On the one hand, the crown clades Aves and Crocodylia

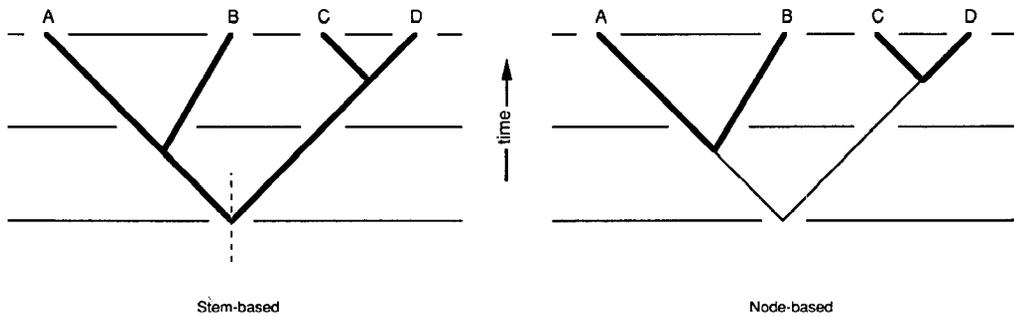


Figure 5 Comparison of stem-based and node-based taxa. *Left:* Stem-based taxa originating from a single cladogenetic event are true sister groups and are equivalent in terms of their age. *Right:* Node-based taxa, even those that are one another's closest relatives in terms of known or extant organisms (terminal taxa A-D), are not true sister groups and generally are not the same age. Thick lines are used to indicate the clades under consideration.

may not be of equal age. If Aves is older than Crocodylia, then the difference in species diversity may simply reflect that difference in age. On the other hand, the sister taxa of which Aves and Crocodylia are respective parts, that is, Ornithosuchia and Pseudosuchia, may have differed in species diversity from shortly after their initial divergence. If Ornithosuchia has always been more speciose than Pseudosuchia, then this difference cannot be explained by an apomorphy that arose in the most recent common ancestor of extant birds. If explicable by an apomorphy at all, then it must be one that arose early in the history of Ornithosuchia.

Since Hennig (58, 59), systematists have been aware of the distinction between the divergence of a lineage from its sister group and its subsequent diversification into lineages represented by extant species. Nevertheless, they have generally used the same name to refer to both entities, distinguishing between them using some notation, for instance, marking the name of the crown clade with an asterisk (e.g. 62, 63, 74, 75, 80). But use of the same name for different clades is likely to generate confusion, and such conventions have not gained wide use. For these reasons, different names should be applied to different clades (115). Thus, we (e.g. 42) use well-known names such as "Mammalia" and "Reptilia" for crown clades, while using less widely known names, in this instance "Synapsida" and "Sauropsida," for the larger clades including the extinct outgroups of Mammalia and Reptilia, respectively (Figure 6). The reasons detailed above underlie recent redefinitions of various taxon names by us and our colleagues (e.g. 6, 7, 32, 41–44, 51, 110, 119; see Appendix).

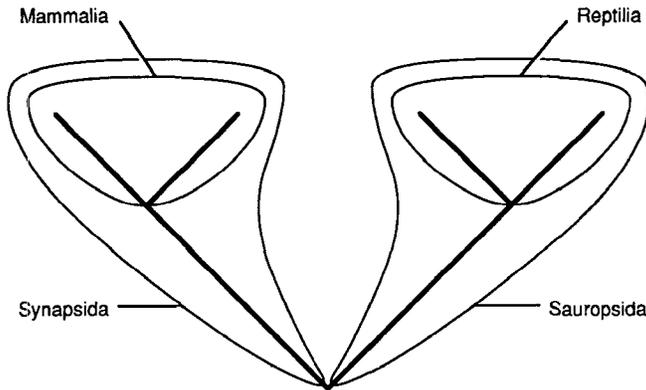


Figure 6 Node-based and stem-based standard taxon names for major clades of amniotes. The widely known names “Mammalia” and “Reptilia” are used for the crown clades in order to promote consistent use by paleontologists and neontologists. The less widely known names “Synapsida” and “Sauropsida” are used for more inclusive clades stemming from the initial divergence of the lineages leading to the crown clades; these taxa are important for making comparisons because of their equivalence in age (see *Figure 5*).

CONCLUSION

A taxonomic system is fundamental to comparative biology. Taxonomies are practical reference systems that permit communication and facilitate access to the literature. They also provide a theoretical context within which to make meaningful comparisons. In order to carry out these functions most effectively, biological taxonomy must be governed by a body of principles and rules designed to accomplish the practical goals within an appropriate theoretical context.

The taxonomic system developed by Linnaeus, and formalized in the various codes of biological nomenclature, has governed taxonomic practices admirably for over 200 years. Indeed, it is a tribute to a taxonomic system based on non-evolutionary principles that it has persisted for well over 100 years into the era dominated by an evolutionary world view—an era in which taxonomy is purported to be evolutionary. But biological taxonomy must eventually outgrow the Linnaean system, for that system derives from an inappropriate theoretical context. Modern comparative biology requires a taxonomic system based on evolutionary principles.

The late Willi Hennig and his followers initiated the development of such a system by granting the principle of descent a central role in establishing the nature of taxa. However fundamental, that advancement represents only the first step in the development of a phylogenetic system of taxonomy, because the system remains constrained by non-evolutionary Linnaean traditions. We

have attempted to further the development of a phylogenetic system of taxonomy by reformulating specific taxonomic principles and rules in terms of its most general principle, the tenet of common descent. Some of our specific principles and rules may not be favorably received, but we hope that their shortcomings will not detract from the general perspective within which they were formulated. That general perspective is one in which the concept of evolution is granted a central role in taxonomy. As such, it embodies a change in the basis of the taxonomic system in which the Linnaean categories are replaced by the tenet of evolutionary descent.

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APPENDIX: A PHYLOGENETIC TAXONOMY OF CRANIATA

In order to illustrate the simplicity of a phylogenetic system of taxonomy, we present (Figure 7) a phylogenetic taxonomy of craniates based on the conventions proposed in this paper and the relationships proposed by Maisey (83) and Gauthier et al (42). This taxonomy is not intended to be complete, but it includes the taxa traditionally considered in introductory texts on vertebrate comparative anatomy. Consequently, it suffers from the problem of differential resolution (101), which is to say that the subordinate taxa within sister taxa do not always receive equal attention (e.g. Sauria vs. Chelonia). This reflects a longstanding bias in craniate taxonomy, in which the lineages leading to birds and mammals have received disproportionate emphasis.

The taxonomy is constructed according to the following conventions:

1. All names refer to clades.
2. The names of subordinate taxa within each clade are indented to indicate hierarchical relationships.
3. Linnaean and other categories (i.e. plesion) are not used.
4. Names formerly associated with the genus category are treated the same as those of all other clades; that is, they are capitalized but not italicized (e.g. "Sphenodon").

5. No redundant names are used.
6. For each pair of sister taxa, the first listed has fewer extant species than the second.
7. Two names are given on each line. The first is the stem-based name of a clade consisting of the crown clade named on the same line plus all extinct taxa more closely related to it than to any other crown clade. For example, the name "Temnospondyli" refers to the clade including Amphibia plus all known and unknown tetrapods sharing a more recent common ancestor with Amphibia than with Amniota. The second name is the node-based name of a crown clade defined as the clade stemming from the immediate common ancestor of its two immediately subordinate crown clades. For example, the name "Amphibia" refers to the clade stemming from the last common ancestor of Gymnophiona and Batrachia.
8. Widely known names are restricted to crown clades, while less well known names are used for stem clades.

Although some names in each group were formerly associated with paraphyletic taxa (e.g. "Reptilia"), we have nevertheless retained them because of their implicit associations with particular ancestors and, in the case of those associated with the ancestors of crown clades, because of their familiarity. In some cases, the hierarchical relationships between the names of crown and stem clades are reversed from traditional use. That reversal results from our applying names according to widespread uses, even when it contradicts supposed meanings that accord with less common uses. The name "Vertebrata," for example, is most commonly used for a crown clade and less commonly for a more inclusive clade encompassing several extinct forms which, in accordance with the supposed meaning of that name, also have vertebrae. Paleontologists (e.g. 72) thus use "Vertebrata" for the latter clade and apply the obscure name "Myopterygii" to what is otherwise known as "Vertebrata." In such instances, we elected to reverse the names in order to associate the well-known name with the crown clade.

Because of the nested relationship between corresponding crown and stem clades, there are advantages to basing the names of both clades on the same word stem. In keeping with the spirit of phylogenetic taxonomy, which emphasizes common ancestry over characters, the stem of the name of the crown clade could be combined with *gens* or *genea*, the respective Latin and Greek suffixes meaning clan, to form the name of the stem clade. Even if another suffix were used, that practice would simplify the taxonomy, and thus facilitate its memorization, because the names of corresponding crown and stem clades would differ only in their suffixes. Because of space limitations, we have not provided an alternative taxonomy using stem-based names of this kind.

Literature Cited

1. Anderson, S. 1975. On the number of categories in biological classifications. *Am. Mus. Novit.* 2584:1-9
2. Ax, P. 1985. Stem species and the stem lineage concept. *Cladistics* 1:279-87
3. Ax, P. 1987. *The Phylogenetic System: The Systematization of Organisms on the Basis of their Phylogenesis*. Chichester: Wiley. 340 pp.
4. Ax, P. 1989. The integration of fossils in the phylogenetic system of organisms. *Abh. naturwiss. Ver. Hamburg* 28:27-43
5. Ball, I. R. 1975. Nature and formulation of biogeographical hypotheses. *Syst. Zool.* 24:407-30
6. Benton, M. J., Clark, J. M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. In *The Phylogeny and Classification of the Tetrapods*, Vol. 1. *Amphibians, Reptiles, and Birds*, ed. M. J. Benton, 8:295-338. Oxford: Clarendon. 377 pp.
7. Berta, A., Ray, C. E., Wyss, A. R. 1989. Skeleton of the oldest known pinniped, *Enaliarctos mealsi*. *Science* 244:60-62
8. Bock, W. J. 1977. Foundations and methods of evolutionary classification. In *Major Patterns in Vertebrate Evolution*, ed. M. K. Hecht, P. C. Goody, B. M. Hecht, pp. 851-95. New York: Plenum. 908 pp.
9. Bonde, N. 1975. Origin of "higher groups": Viewpoints of phylogenetic systematics. In *Problèmes Actuels de Paléontologie-EGRvolution des Vertébrés, Colloq. Int. CNRS (Paris)* 218: 293-324
10. Bonde, N. 1977. Cladistic classification as applied to vertebrates. See Ref. 8, pp. 741-804
11. Boudreaux, H. B. 1979. *Arthropod Phylogeny with Special Reference to Insects*. New York: Wiley. 320 pp.
12. Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges, with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyliaae. *Kungl. Svenska Vetenskapsakademiens Handlingar* 11:1-471
13. Brundin, L. 1968. Application of phylogenetic principles in systematics and evolutionary theory. In *Current Problems of Lower Vertebrate Phylogeny*, ed. T. Ørvig, pp. 473-95. New York: Interscience. 539 pp.
14. Buck, R., Hull, D. L. 1966. The logical structure of the Linnaean hierarchy. *Syst. Zool.* 15:97-111
15. Buck, R., Hull, D. L. 1969. Reply to Gregg. *Syst. Zool.* 18:354-57
16. Cain, A. J. 1959. Deductive and inductive methods in post-Linnaean taxonomy. *Proc. Linn. Soc. London* 170:185-217
17. Cain, A. J. 1959. The post-Linnaean development of taxonomy. *Proc. Linn. Soc. London* 170:234-44
18. Cannatella, D. C., de Queiroz, K. 1989. Phylogenetic systematics of the anoles: Is a new taxonomy warranted? *Syst. Zool.* 38:57-69
19. Colless, D. H. 1977. A cornucopia of names. *Syst. Zool.* 26:349-52
20. Cracraft, J. 1974. Phylogenetic models and classification. *Syst. Zool.* 23:71-90
21. Cracraft, J. 1986. The origin and early diversification of birds. *Paleobiology* 12:383-99
22. Craske, A. J., Jefferies, R. P. S. 1989. A new mitrate from the Upper Ordovician of Norway, and a new approach to subdividing a plesion. *Palaeontology* 32:69-99
23. Crowson, R. A. 1970. *Classification and Biology*. New York: Atherton. 350 pp.
24. Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection*. London: John Murray. 513 pp. Reprinted 1974. Cambridge, Mass: Harvard Univ. Press
25. Donoghue, M. J., Cantino, P. D. 1988. Paraphyly, ancestors, and the goals of taxonomy: A botanical defense of cladism. *Bot. Rev.* 54:107-28
26. Donoghue, M. J., Doyle, J. A., Gauthier, J., Kluge, A. G., Rowe, T. 1989. The importance of fossils in phylogeny reconstruction. *Annu. Rev. Ecol. Syst.* 20:431-60
27. Dubois, A. 1984. La nomenclature supragénérique des amphibiens anoures. *Mém. Mus. Natl. d'Hist. Nat. Paris, série A, zoologie* 131:1-64
28. Dundee, H. A. 1989. Higher category name usage for amphibians and reptiles. *Syst. Zool.* 38:398-406
29. Dupuis, C. 1984. Willi Hennig's impact on taxonomic thought. *Annu. Rev. Ecol. Syst.* 15:1-24
30. Eldredge, N., Cracraft, J. 1980. *Phy-*

- logenetic Patterns and the Evolutionary Process*. New York: Columbia Univ. Press. 349 pp.
31. Engelman, G. F., Wiley, E. O. 1977. The place of ancestor-descendant relationships in phylogeny reconstruction. *Syst. Zool.* 26:1-11
 32. Estes, R., de Queiroz, K., Gauthier, J. 1988. Phylogenetic relationships within Squamata. In *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*, ed. R. Estes, G. K. Pregill, pp. 119-281. Stanford, Calif: Stanford Univ. Press. 631 pp.
 33. Farris, J. S. 1967. Definitions of taxa. *Syst. Zool.* 16:174-75
 34. Farris, J. S. 1968. Categorical ranks and evolutionary taxa in numerical taxonomy. *Syst. Zool.* 17:151-59
 35. Farris, J. S. 1976. Phylogenetic classification of fossils with Recent species. *Syst. Zool.* 25:271-82
 36. Farris, J. S. 1979. The information content of the phylogenetic system. *Syst. Zool.* 28:483-519
 37. Felsenstein, J. 1982. Numerical methods for inferring evolutionary trees. *Q. Rev. Biol.* 57:379-404
 38. Frost, D. R., Etheridge, R. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). *Misc. Publ. Univ. Kans. Mus. Nat. Hist.* 81:1-65
 39. Gaffney, E. S. 1980. Tetrapod monophyly: A phylogenetic analysis. *Bull. Carnegie Mus. Nat. Hist.* 13:92-105
 40. Gaffney, E. S., Meylan, P. A. 1988. A phylogeny of turtles. See Ref. 6, 5:157-219
 41. Gauthier, J. 1986. Saurischian monophyly and the origin of birds. In *The Origin of Birds and the Evolution of Flight*, ed. K. Padian, 8:1-55. Calif. Acad. Sci. Mem.
 42. Gauthier, J., Cannatella, D., de Queiroz, K., Kluge, A. G., Rowe, T. 1989. Tetrapod phylogeny. In *The Hierarchy of Life*, ed. B. Fernholm, K. Bremer, H. Jörnvall, 25:337-53. Amsterdam: Elsevier. 499 pp.
 43. Gauthier, J., Estes, R., de Queiroz, K. 1988. A phylogenetic analysis of Lepidosauromorpha. See Ref. 32, pp. 15-98
 44. Gauthier, J., Kluge, A. G., Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4:105-209
 45. Ghiselin, M. T. 1966. An application of the theory of definitions to systematic principles. *Syst. Zool.* 15:127-30
 46. Ghiselin, M. T. 1969. *The Triumph of the Darwinian Method*. Berkeley: Univ. Calif. Press. Reprinted 1984. Chicago: Univ. Chicago Press. 287 pp.
 47. Ghiselin, M. T. 1980. Natural kinds and literary accomplishments. *Mich. Q. Rev.* 19:73-88
 48. Ghiselin, M. T. 1981. Categories, life, and thinking. *Behav. Brain Sci.* 4:269-313
 49. Ghiselin, M. T. 1984. "Definition," "character," and other equivocal terms. *Syst. Zool.* 33:104-10
 50. Ghiselin, M. T. 1985. Narrow approaches to phylogeny: A review of nine books of cladism. *Oxford Surv. Evol. Biol.* 1:209-22
 51. Good, D. A. 1988. The phylogenetic position of fossils assigned to the Gerhronotinae (Squamata: Anguillidae). *J. Vert. Paleontol.* 8:188-95
 52. Gregg, J. R. 1954. *The Language of Taxonomy: An Application of Symbolic Logic to the Study of Classificatory Systems*. New York: Columbia Univ. Press. 70 pp.
 53. Gregg, J. R. 1968. Buck and Hull: A critical rejoinder. *Syst. Zool.* 17:342-44
 54. Griffiths, G. C. D. 1973. Some fundamental problems in biological classification. *Syst. Zool.* 22:338-43
 55. Griffiths, G. C. D. 1974. On the foundations of biological systematics. *Acta Biotheor.* 23:85-131
 56. Griffiths, G. C. D. 1976. The future of Linnaean nomenclature. *Syst. Zool.* 25:168-73
 57. Hennig, W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Berlin: Deutscher Zentralverlag. 370 pp.
 58. Hennig, W. 1965. Phylogenetic systematics. *Annu. Rev. Entomol.* 10:97-116
 59. Hennig, W. 1966. *Phylogenetic Systematics*. Urbana: Univ. Ill. Press. 263 pp.
 60. Hennig, W. 1969. *Die Stammesgeschichte der Insekten*. Frankfurt: Kramer. 436 pp.
 61. Hennig, W. 1975. "Cladistic analysis or cladistic classification?": A reply to Ernst Mayr. *Syst. Zool.* 24:244-56
 62. Hennig, W. 1981. *Insect Phylogeny*. Chichester: Wiley. 514 pp.
 63. Hennig, W. 1983. Stammesgeschichte der Chordaten. *Fortschr. zool. Syst. Evolutionsforsch.* 2:1-208
 64. Heywood, V. H. 1988. The structure of systematics. In *Prospects in Systematics*, ed. D. L. Hawksworth, 3:44-56. Oxford: Clarendon. 457 pp.

65. Hubbs, C. L. 1956. Ways of stabilizing zoological nomenclature. *Proc. XIV Int. Congr. Zool., Copenhagen 1953*: 548–53
66. Hull, D. L. 1978. A matter of individuality. *Philos. Sci.* 45:335–60
67. Hull, D. L., Buck, R. 1967. Definitions of taxa. *Syst. Zool.* 16:349
68. Huxley, T. H. 1868. On the animals which are most nearly intermediate between the birds and reptiles. *Geol. Mag.* 5:357–65
69. International Association of Microbiological Societies. 1975. *International Code of Nomenclature of Bacteria, and Statutes of the International Committee on Systematic Bacteriology, and Statutes of the Bacteriology Section of the International Association of Microbiological Societies*. Washington: Am. Soc. Microbiol. 180 pp. 1976 revision
70. International Botanical Congress. 1988. *International Code of Botanical Nomenclature*. Königstein: Koeltz Scientific Books. 328 pp. Edition adopted by the 14th Int. Botanical Congress, Berlin, July–August 1987
71. International Commission on Zoological Nomenclature. 1985. *International Code of Zoological Nomenclature*. London: Int. Trust for Zool. Nomenclature. 338 pp. 3rd ed.
72. Janvier, P. 1984. The phylogeny of the Craniata, with particular reference to the significance of fossil “agnathans.” *J. Vert. Paleontol.* 1:121–59
73. Jardine, N. 1969. A logical basis for biological classification. *Syst. Zool.* 18:37–52
74. Jefferies, R. P. S. 1979. The origin of chordates—a methodological essay. In *The Origin of Major Invertebrate Groups*, ed. M. R. House, 17:443–77. London: Academic. 515 pp.
75. Jefferies, R. P. S. 1986. *The Ancestry of the Vertebrates*. London: Br. Mus. (Nat. Hist.). 376 pp.
76. Jeffrey, C. 1973. *Biological Nomenclature*. New York: Crane, Russak. 69 pp. 2nd ed. 1977
77. Kemp, T. S. 1988. Interrelationships of the Synapsida. In *The Phylogeny and Classification of the Tetrapods*, Vol. 2: *Mammals*, ed. M. J. Benton, 1:1–22. Oxford: Clarendon. 329 pp.
78. Kraus, O. 1976. Phylogenetische Systematik und evolutionäre Klassifikation. *Verh. Deutsch. Zool. Ges.* 69:84–99
79. Laurin, M. 1991. The osteology of a Lower Permian eocushman from Texas and a review of diapsid phylogeny. *Zool. J. Linn. Soc.* 101:59–95
80. Lauterbach, K.-E. 1989. Das Pan-Monophylum—Ein Hilfsmittel für die Praxis der phylogenetischen Systematik. *Zool. Anz.* 223:139–56
81. Loconte, H. 1990. Cladistic classification of Amniota: A response to Gauthier et al. *Cladistics* 6:187–90
82. Løvtrup, S. 1977. *The Phylogeny of Vertebrata*. London: Wiley. 330 pp.
83. Maisey, J. G. 1986. Heads and tails: A chordate phylogeny. *Cladistics* 2: 201–56
84. Martin, L. D. 1985. The relationship of *Archaeopteryx* to other birds. In *The Beginnings of Birds: Proceedings of the International Archaeopteryx conference Eichstätt 1984*, ed. M. K. Hecht, J. H. Ostrom, G. Viohl, P. Wellnhöfer, pp. 177–83. Eichstätt: Freunde des Jura-Museums Eichstätt. 382 pp.
85. Mayr, E. 1969. *Principles of Systematic Zoology*. New York: McGraw-Hill. 428 pp.
86. Mayr, E. 1982. *The Growth of Biological Thought. Diversity, Evolution, and Inheritance*. Cambridge, Mass: Harvard Univ. Press. 974 pp.
87. Mayr, E., Ashlock, P. D. 1991. *Principles of Systematic Zoology*. New York: McGraw-Hill. 475 pp. 2nd ed.
88. McKenna, M. C. 1975. Toward a phylogenetic classification of the Mammalia. In *Phylogeny of the Primates: A Multidisciplinary Approach*, ed. W. P. Luckett, F. S. Szalay, 2:21–46. New York: Plenum. 483 pp.
89. von Meyer, H. 1861. Vogel-Federn und *Palpites priscus* von Solnhofen. *Neues Jahrb. Mineral. Geol. Palaeontol.* 1861:561
90. von Meyer, H. 1861. *Archaeopteryx lithographica* (Vogel-Feder) und *Pterodactylus* von Solnhofen. *Neues Jahrb. Mineral. Geol. Palaeontol.* 1861:678–79
91. Miao, D. 1991. On the origins of mammals. In *Origins of the Higher Groups of Tetrapods*, ed. H.-P. Schultze, L. Trueb, 16:579–97. Ithaca: Cornell Univ. Press. 724 pp.
92. Michener, C. D. 1963. Some future developments in taxonomy. *Syst. Zool.* 12:151–72
93. Michener, C. D. 1964. The possible use of uninominal nomenclature to increase the stability of names in biology. *Syst. Zool.* 13:182–90
94. Müller, G. B., Alberch, P. 1990. Ontogeny of the limb skeleton in *Alligator mississippiensis*: Developmental invariance and change in the evolution of archosaur limbs. *J. Morphol.* 203:151–64
95. Nelson, G. 1971. “Cladism” as a phi-

- losophy of classification. *Syst. Zool.* 20:373-76
96. Nelson, G. 1972. Phylogenetic relationship and classification. *Syst. Zool.* 21:227-31
97. Nelson, G. 1972. Comments on Hennig's "Phylogenetic Systematics" and its influence on ichthyology. *Syst. Zool.* 21:364-74
98. Nelson, G. 1973. Classification as an expression of phylogenetic relationships. *Syst. Zool.* 22:344-59
99. Nelson, G. 1974. Darwin-Hennig classification: A reply to Ernst Mayr. *Syst. Zool.* 23:452-58
100. Nelson, G. 1978. The perils of perfection: A reply to D. H. Colless. *Syst. Zool.* 27:124
101. O'Hara, R. J. 1992. Telling the tree: Narrative representation and the study of evolutionary history. *Biol. Philos.* 7:135-60
102. Patterson, B. 1975. The fossil aardvarks (Mammalia: Tubulidentata). *Bull. Mus. Comp. Zool., Harvard Univ.* 147:185-237
103. Patterson, B. 1978. Pholidota and Tubulidentata. In *Evolution of African Mammals*, ed. V. J. Maglio, H. B. S. Cooke, 12:268-78. Cambridge, Mass: Harvard Univ. Press. 641 pp.
104. Patterson, C. 1978. Verifiability in Systematics. *Syst. Zool.* 27:218-22
105. Patterson, C., Rosen, D. E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bull. Am. Mus. Nat. Hist.* 158:81-172
106. Patterson, D. J. 1988. The evolution of Protozoa. *Mem. Inst. Oswaldo Cruz, Rio de Janeiro* 83:580-600
107. Platnick, N. I. 1977. The hypochiloid spiders: A cladistic analysis, with notes on the Atypoidea (Arachnida, Araneae). *Am. Mus. Novit.* 2627:1-23
108. Platnick, N. I. 1977. Cladograms, phylogenetic trees, and hypothesis testing. *Syst. Zool.* 26:438-42
109. Platnick, N. I. 1978. Gaps and prediction in classification. *Syst. Zool.* 27:472-74
110. de Queiroz, K. 1987. Phylogenetic systematics of iguanine lizards. A comparative osteological study. *Univ. Calif. Publ. Zool.* 118:1-203
111. de Queiroz, K. 1988. Systematics and the Darwinian revolution. *Philos. Sci.* 55:238-59
112. de Queiroz, K. 1992. Phylogenetic definitions and taxonomic philosophy. *Biol. Philos.* 7:295-313
113. de Queiroz, K., Donoghue, M. J. 1988. Phylogenetic systematics and the species problem. *Cladistics* 4:317-38
114. de Queiroz, K., Donoghue, M. J. 1990. Phylogenetic systematics or Nelson's version of cladistics. *Cladistics* 6:61-75
115. de Queiroz, K., Gauthier, J. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. *Syst. Zool.* 39:307-22
116. Ridley, M. 1986. *Evolution and Classification: The Reformation of Cladism*. London: Longman. 201 pp.
117. Rosen, D. E. 1974. Cladism or Gradism?: A reply to Ernst Mayr. *Syst. Zool.* 23:446-51
118. Rowe, T. 1987. Definition and diagnosis in the phylogenetic system. *Syst. Zool.* 36:208-11
119. Rowe, T. 1988. Definition, diagnosis, and origin of Mammalia. *J. Vert. Paleontol.* 8:241-64
120. Ruse, M. E. 1971. Gregg's Paradox: A proposed revision to Buck and Hull's solution. *Syst. Zool.* 20:239-45
121. Ruse, M. E. 1973. *The Philosophy of Biology*. London: Hutchinson Univ. Library. 231 pp.
122. Savage, J. M. 1990. Meetings of the Int. Commission on Zool. Nomenclature. *Syst. Zool.* 39:424-25
123. Scott-Ram, N. R. 1990. *Transformed Cladistics, Taxonomy and Evolution*. Cambridge: Cambridge Univ. Press. 238 pp.
124. Simpson, G. G. 1959. Anatomy and morphology: Classification and evolution: 1859 and 1959. *Proc. Am. Philos. Soc.* 103:286-306
125. Simpson, G. G. 1961. *Principles of Animal Taxonomy*. New York: Columbia Univ. Press. 247 pp.
126. Sneath, P. H. A., Sokal, R. R. 1973. *Numerical Taxonomy*. San Francisco: Freeman. 573 pp.
127. Stace, C. A. 1991. Naming names in botany. *Nature* 350:466
128. Stevens, P. 1984. Metaphors and typology in the development of botanical systematics 1690-1960, or the art of putting new wine in old bottles. *Taxon* 33:169-211
129. Swofford, D. L., Olsen, G. J. 1990. Phylogeny reconstruction. In *Molecular Systematics*, ed. D. M. Hillis, C. Moritz, 11:411-501. Sunderland, Mass: Sinauer. 588 pp.
130. Tubbs, P. K. 1991. The International Commission on Zoological Nomenclature: What it is and how it operates. *Bull. Zool. Nomen.* 48:295-99

131. Turrill, W. B. 1942. Taxonomy and phylogeny (Parts I-III). *Bot. Rev.* 8:247-70, 473-532, 655-707
132. Wiley, E. O. 1979. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Syst. Zool.* 28:308-37
133. Wiley, E. O. 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. New York: Wiley. 439 pp.
134. Wiley, E. O. 1989. Kinds, individuals, and theories. In *What the Philosophy of Biology Is*, ed. M. Ruse, pp. 289-300. Dordrecht: Kluwer. 337 pp.
135. Willmann, R. 1987. Phylogenetic systematics, classification and the plesion concept. *Verh. naturwiss. Ver. Hamburg* 29:221-33
136. Willmann, R. 1989. Palaeontology and the systematization of natural taxa. *Abh. naturwiss. Ver. Hamburg* 28:267-91
137. Woodger, J. H. 1952. From biology to mathematics. *Br. J. Philos. Sci.* 3:1-21



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