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THE LINNAEAN HIERARCHY AND THE EVOLUTIONIZATION OF TAXONOMY, WITH EMPHASIS ON THE PROBLEM OF NOMENCLATURE

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ABSTRACT

During the post-Darwinian history of taxonomy, the Linnaean hierarchy has maintained its role as a means for representing hierarchical taxonomic relationships. During the same period, the principle of descent has taken on an increasingly important role as the basis for reformulated versions of fundamental taxonomic concepts and principles. Early in this history, the principle of descent provided an explanation for the existence of taxa and implied a nested, hierarchical structure for taxonomic relationships. Although an evolutionary explanation for taxa contradicted the Aristotelian context within which the Linnaean hierarchy was developed, the nested, hierarchical structure of taxonomic relationships implied by evolution was compatible with the practical use of the Linnaean hierarchy for conveying hierarchical relationships and seems to have reinforced this practice. Later changes associated with the development of taxon concepts based on the principle of descent led to changes in the interpretation of the Linnaean categories as well as certain modifications related to use of the Linnaean hierarchy in representing phylogenetic relationships. Although some authors questioned use of the Linnaean hierarchy in phylogenetic taxonomies, most continued to use it in one form or another. More recently, taxonomists have considered the relevance of the principle of descent to nomenclature. They have found fundamental inconsistencies between concepts of taxa based on that principle and methods currently used to define taxon names, which are based on the Linnaean hierarchy. Although these inconsistencies can be corrected without totally eliminating the Linnaean hierarchy, the necessary changes would greatly reduce the importance of that hierarchy, particularly in the area of nomenclature. Moreover, the earlier development of taxon concepts based on the principle of descent effectively proposed taxonomic categories of greater theoretical significance than those of the Linnaean hierarchy. The historical trend of granting increasing importance to the principle of descent has reduced the significance of the Linnaean hierarchy to the point where it may no longer be worth retaining.

Key words: evolution, Linnaean hierarchy, nomenclature, phylogeny, principle of descent, taxon names, taxonomic categories, taxonomic definitions, taxonomy.

INTRODUCTION

For almost 250 years, the Linnaean hierarchy has served as an important part of taxonomy's methodological foundation. During the last 140 of those years, the theory of evolution—or more accurately, the principle of common descent—has steadily increased its contribution to taxonomy's theoretical foundation. These two cornerstones of contemporary taxonomy, the Linnaean hierarchy and the principle of descent, have coexisted harmoniously through most of their common previous history, but recently there have been signs that this situation cannot endure. After surviving the revolution brought about by initial acceptance of an evolutionary world view, as well as the more localized taxonomic reforms of the New Systematics and Phylogenetic Systematics, the Linnaean hierarchy is being challenged by a movement to extend an evolutionary world view into the realm of nomenclature. This challenge affects most directly various nomenclatural principles and rules based on the Linnaean hier-

archy, but it also raises questions about the appropriateness and usefulness of the Linnaean hierarchy itself as the basis for present and future taxonomy.

In this paper I will examine the relationship between the Linnaean hierarchy and the principle of descent in taxonomy, emphasizing their conflict in the area of nomenclature. First, I will present some definitions, both to clarify my use of certain terms and to provide background information on both the Linnaean hierarchy and the principle of descent that are relevant to understanding their roles in modern taxonomy. I will then describe a series of changes in the principles and methods of taxonomy that I interpret as manifestations of the progressively more thorough acceptance of an evolutionary world view. In each case, I will examine the consequences of the change for the Linnaean hierarchy. I will discuss in greatest detail the most recent of these changes, which centers on the issue of nomenclature, describing how this change, unlike the previous ones, involves a more direct conflict between the Linnaean hierarchy and the principle of descent. I

will then address some misunderstandings, both actual and anticipated, concerning the replacement of the Linnaean hierarchy with the principle of descent as the foundation of the nomenclatural system. And finally, I will reassess the more general role of the Linnaean hierarchy in modern taxonomy.

BACKGROUND AND DEFINITIONS OF TERMS

In order to describe changes in the history of taxonomy related to the increasing importance granted to the principle of descent and their implications for the Linnaean hierarchy, I first need to define some terms. These definitions are intended to emphasize the relationship between the Linnaean hierarchy and the principle of descent with regard to their roles as cornerstones of taxonomy in general and nomenclature in particular. In addition, they are meant to make clear how I am using the defined terms rather than to describe how those terms have been used by other authors.

The Linnaean Hierarchy and the Principle of Descent

The *Linnaean hierarchy* is the series of ranked taxonomic categories based on those adopted by Linnaeus (1758) to which *taxa* (named groups of organisms) are assigned. Linnaeus was not the first person to use taxonomic categories (Mayr 1982), but his categories formed the basis of most subsequent taxonomic systems. Linnaeus himself used six taxonomic categories—Regnum (Kingdom), Classis (Class), Ordo (Order), Genus (Genus), Species (Species), and Varietas (Variety). Later taxonomists added the categories Family and Division (botany) or Phylum (zoology), and they reduced the significance of Variety (botany) or eliminated it entirely (zoology), to form a set of seven principal categories. These seven principal categories—Kingdom, Division/Phylum, Class, Order, Family, Genus, and Species—are often treated as obligatory or mandatory (e.g., Simpson 1961; Mayr 1969a), so that a given organism must be assigned to a taxon in every one of them to be considered “satisfactorily classified” (Simpson 1961:18). Contemporary taxonomists also use several nonmandatory primary categories (e.g., Cohort, Tribe, Section, Series) as well as various nonmandatory secondary categories derived from the primary ones by attaching a rank-modifying prefix (e.g., Subclass, Infraorder, Superfamily) (see Jeffrey 1989 for a summary). Nevertheless, the contemporary hierarchy of taxonomic categories is basically Linnaean in that first, it is derived historically from the hierarchy of categories used by Linnaeus himself and second, its core is made up in a large part by the original Linnaean categories. The Linnaean hierarchy is a hierarchy of taxonomic categories and

should not be confused with taxonomic hierarchy in general, that is, with hierarchies of taxa. A series of nested taxa is intrinsically hierarchical (i.e., ranked or graded) regardless of whether its component taxa are assigned to taxonomic categories. Moreover, hierarchies of taxa can be represented by other means than taxonomic categories, for example, using diagrams, alphabetic or numeric position markers, or indentation.

The *principle of descent* is the doctrine that living things are related through common descent (as opposed to a theory about the specific mechanism of evolutionary change). It is what many people call the “fact” of evolution—the idea that the diversity of life is the result of descent with modification. The principle of descent is thus the most general evolutionary principle. In the context of taxonomy, it is more fundamental than the idea of evolutionary change or the similarities and differences resulting from such change. Evolutionary change occurs only in the context of descent, but descent can occur without evolutionary change. Moreover, the fact that similarities and differences in the characters of organisms are produced by evolution does not automatically make a taxonomy based on those properties evolutionary, as is evidenced by countless artificial and preevolutionary taxonomies based on the same characters (see de Queiroz 1988, for further discussion).

Taxonomic and Nomenclatural Systems

The rest of the terms I will define are used to designate different kinds of *methodological systems*, that is, integrated or organized sets of conventions (including principles, rules, and recommendations) designed to achieve some particular end. In the present context, it is important to distinguish between taxonomic and nomenclatural systems. A *taxonomic system* is an integrated set of conventions specifying how taxonomies are to be constructed; a *nomenclatural system* is an integrated set of conventions specifying how names are to be applied—that is, for naming taxa and regulating the use of those names. These two kinds of methodological systems should not be confused with one another, though a given nomenclatural system might be considered part of a more comprehensive taxonomic system. I consider rules concerning what kinds of entities deserve to be recognized as taxa part of the taxonomic system, while the nomenclatural system is concerned with how those entities are named. It should be noted that the term “system” is used in at least two other senses in taxonomy, first, for taxonomies or classifications themselves (e.g., when they are described as natural versus artificial systems, or when we refer to Linnaeus’s or Thorne’s system; see Nicolson 1997), and second, for the biological entities that are recognized as taxa (e.g., when we talk about interbreeding

systems or systems of common ancestry; see Griffiths 1974; de Queiroz 1988).

Linnaean and Phylogenetic Systems

For the purposes of the present paper, two kinds of taxonomic and nomenclatural systems are of primary interest. A *Linnaean system*, whether of taxonomy or nomenclature, is a system based on the Linnaean hierarchy; a *phylogenetic system* is a system based on the principle of descent. The relationships among Linnaean and phylogenetic systems of taxonomy and nomenclature are complex in that taxonomic systems can be both Linnaean and phylogenetic, while nomenclatural systems must be either one or the other. I will therefore briefly discuss some of those relationships and their bearing on the classification of individual taxonomic and nomenclatural systems.

Linnaean systems.—In the case of taxonomic systems, the system used by Linnaeus himself was the original Linnaean system. Although modern taxonomic systems differ from the original Linnaean system in certain respects, they also retain a number of components of that system, one of the most important of which is the assignment of taxa to categories in the Linnaean hierarchy. If this characteristic—which serves to indicate rank or relative position in the taxonomic hierarchy—is considered the defining property of Linnaean taxonomic systems, then most contemporary taxonomic systems are Linnaean systems. This is the sense in which I will refer to Linnaean taxonomic systems in the remainder of the present paper. Among contemporary approaches to taxonomy (e.g., synthetic, phenetic, phylogenetic), there is considerable heterogeneity of opinion concerning the general concept of taxonomic relationship as well as how actual relationships are to be analyzed. Nevertheless, when it comes to the representation of taxonomic relationships—rather than their definition or determination—then (for the most part) the various contemporary taxonomic approaches all use Linnaean systems (e.g., Simpson 1961; Davis and Heywood 1963; Mayr 1969a; Sneath and Sokal 1973; Eldredge and Cracraft 1980; Stace 1980; Wiley 1981). Modern Linnaean systems of taxonomy are heterogeneous, and though their components have been described by various authors, they have not been formally codified in the manner of certain nomenclatural rules (see below).

In the case of nomenclatural systems, modern systems differ from that used by Linnaeus himself (e.g., 1737, 1751) in many respects. Linnaeus and his contemporaries were largely attempting to replace the works of their predecessors (Nicholson 1991), including existing taxon names. But once Linnaeus's general approach became widely accepted, later taxonomists became more concerned with preserving existing

names. In keeping with this difference, the nomenclatural precepts articulated by Linnaeus emphasize the formation of taxon names, whereas many subsequently developed rules (e.g., those related to priority) concern the application of existing names in the context of revised taxonomies (for historical reviews see McNeill and Greuter 1986; Ride 1986, 1988; Nicholson 1991; Melville 1995). In any case, as will be explained in detail below, both Linnaeus and most subsequent taxonomists used a method for defining taxon names based on the Linnaean Hierarchy, and I will treat this characteristic as the defining property of Linnaean nomenclatural systems. According to this definition, and despite differences among the systems used in botany, zoology, and microbiology, all of the widely used contemporary nomenclatural systems are Linnaean systems. Unlike contemporary Linnaean systems of taxonomy, contemporary Linnaean systems of nomenclature have become highly formalized, with official governing congresses, commissions, and committees and published codes (ICZN 1985; IUMS 1992; IBC 1994).

Phylogenetic systems.—Phylogenetic systems of taxonomy attempt to produce taxonomies that reflect phylogenetic relationships accurately and efficiently. As I will describe below, the development of phylogenetic taxonomic systems has been an extended process that has been accomplished largely in conjunction with Linnaean taxonomic systems. Thus, most phylogenetic systems have used the basic conventions of Linnaean systems (e.g., nested, nonoverlapping taxa and the Linnaean hierarchy), though some of the more recent ones have added restrictions concerning what kinds of entities are to be recognized as taxa (monophyly) as well as new conventions for representing relationships (e.g., new categories, sequencing) (see Eldredge and Cracraft 1980; Wiley 1981; Forey 1992). Ideally, however, a phylogenetic system should retain only those elements that do not interfere with the accurate and efficient representation of phylogeny. Therefore, although any particular phylogenetic system is inevitably constrained by its history, if any of its conventions are found to interfere with the accurate and efficient representation of phylogeny, they may have to be modified or eliminated. Consequently, some recent phylogenetic systems have abandoned the Linnaean hierarchy (e.g., Hennig 1969, 1981, 1983; Ax 1987; de Queiroz and Gauthier 1992).

In contrast with phylogenetic systems of taxonomy, which have been developing for more than 100 years, phylogenetic systems of nomenclature are a very recent invention. Indeed, the proposals of de Queiroz and Gauthier (1990, 1992, 1994) seem to be the first attempts to formulate nomenclatural conventions based on the principle of descent. Although the general concepts and principles of this system have been set

out, its specific rules and recommendations are still in the process of active development (e.g., de Queiroz and Gauthier 1990, 1992, 1994; Sundberg and Pleijel 1994; Bryant 1994, 1996; Schander and Thollessen 1995; de Queiroz 1996; Lee 1996; Wyss and Meng 1996; Cantino et al. 1997). In any case, nomenclatural systems based on the principle of descent currently have neither official governing congresses, commissions, or committees nor published codes. Unlike the case with taxonomic systems, phylogenetic systems of nomenclature cannot be developed in conjunction with Linnaean nomenclatural systems, because (as will be explained below) the principle of descent and the Linnaean hierarchy provide alternative theoretical bases for those systems and thus are in direct conflict.

THE EVOLUTIONIZATION OF TAXONOMY

The proposal to replace the Linnaean hierarchy with the principle of descent as the foundation of the nomenclatural system can be interpreted as the beginning of the most recent stage of what I will call the *evolutionization of taxonomy*. I will use this cumbersome term to distinguish the long, drawn out process through which taxonomy has become ever more firmly based on the principle of common descent from the sudden shift in outlook that accompanied the initial widespread acceptance of that principle. Although the extended process can be considered a revolution in the sense that each of its stages involves a fundamental conceptual shift, some people may wish to restrict the term "Darwinian Revolution" to the events in some shorter time interval immediately following the publication of Darwin's (1859) *Origin of Species*. Therefore, I will refer to the extended series of changes through which the principle of descent has taken on a progressively more important role in taxonomy as the evolutionization of that discipline. The account that follows is not intended to be a detailed chronicle of the process of evolutionization; instead, it is intended to describe some important stages in that process, emphasizing the common conceptual shift that underlies each stage and the consequences of specific changes for the Linnaean hierarchy.

Early Stages: The Explanation for Taxa and the Structure of Taxonomic Relationships

Conceptual changes.—The earliest stages in the evolutionization of taxonomy were contemporaneous with the Darwinian Revolution in the restricted sense. Initial acceptance of the idea that living things were related through common descent affected taxonomy in at least two related ways. First, it provided an explanation in the form of an underlying cause for the order that was manifested in existing taxonomies. Prior to 1859, numerous taxa had already been recognized and

named based on similarities and differences in the characters of organisms, but their existence was attributed to the Plan of the Creator or to some unknown natural law (Darwin 1859). The theory of descent with modification provided a scientific explanation for the existence of taxa; in other words, the natural law responsible for the existence of taxa was no longer unknown. Second, the principle of common descent provided justification for a particular structure regarding taxonomic relationships. If the order in nature resulted from a divine plan known only to the Creator, or if the natural law responsible for that order remained undiscovered, then the structure of taxonomic relationships might take several possible forms. For example, taxa might be partially overlapping or mutually exclusive, and they might occur in regular numerical patterns, such as fives, as proposed by the quinarians (see Winsor 1976; O'Hara 1988, 1991). On the other hand, if the order in nature resulted from common descent, then the structure of taxonomic relationships should have one particular form. Specifically, the principle of descent predicted a structure consisting of both nested and mutually exclusive groups. Nested groups were those formed by the descendants of successively more remote common ancestors in a single lineage; mutually exclusive ones by the descendants of ancestors whose lineages had previously diverged. Partially overlapping or intersecting groups were ruled out, or at least relegated to secondary status, nor was there any reason to expect regular patterns of five.

Effects on taxonomic practice.—The first change, accepting evolution as the underlying cause of taxonomic order, contradicted the Aristotelian context within which the Linnaean hierarchy was originally developed (see Cain 1958; Ereshefsky 1994). Although this change was a necessary precursor to all subsequent stages in the evolutionization of taxonomy, it did not otherwise revolutionize taxonomic practice. By its very nature, an evolutionary explanation for the existence of taxa did not call into question either existing (nested, hierarchical) taxonomies or the methods that had been used to produce them. Instead, the taxonomies themselves were effectively assumed as the phenomenon in need of an explanation, and, consequently, the methods that had been used to produce them were also tacitly accepted. The principle of descent was thus granted a rather superficial role as an after-the-fact explanation or interpretation for previously recognized taxa (de Queiroz 1988). Moreover, once the idea of evolution was accepted, it could be used to explain *any* group that had been recognized previously on the basis of shared characters. Just as some groups could be explained as having inherited their shared characters from common ancestors, others could be explained as having evolved them through convergent or parallel

modifications (de Queiroz 1988, 1992a). Accepting evolution as the explanation for previously recognized taxa did not, by itself, cause significant changes in the methods of taxonomy, which seems to account for the common claim that the principle of evolution had no major impact on taxonomy. But this was not the only change brought about by the evolutionary world view, and others had significant effects on taxonomic practice.

Thus, the other major change associated with initial acceptance of the principle of descent—the change concerning the structure of taxonomic relationships—influenced taxonomic practice significantly. The fact that partially overlapping relationships were ruled out, or at least demoted to secondary status, while nested and mutually exclusive ones were granted primacy, affected both the taxonomies and the taxonomic diagrams produced by taxonomists (e.g., O'Hara 1988, 1991). These changes in taxonomic practice resulted from granting to the principle of descent a much more important role. By using the principle of descent to rule out certain kinds of groups and validate others, that principle was not being treated as a mere after-the-fact explanation, as it was in the case of the first change described above. Instead, it was effectively being treated as an axiom or basic principle from which an important taxonomic concept—the general structure of taxonomic relationships—was derived or deduced. This difference in the role played by the principle of descent—that is, no role or mere after-the-fact interpretation versus axiom or first principle—is a useful criterion for assessing the impact of that principle on other taxonomic concepts as well as on other disciplines (de Queiroz 1988). Moreover, all subsequent stages in the evolutionization of taxonomy are interpretable as manifestations of a change in which the principle of descent is granted the same kind of importance in other aspects of that discipline. I will return to this theme shortly, after addressing the effects of these first two changes on the Linnaean hierarchy.

Effects on the Linnaean hierarchy.—Despite the importance of the early changes brought about by acceptance of the principle of descent, those changes did not call the Linnaean hierarchy into question as the basis for the taxonomic system; in fact, they may have promoted its use. The Linnaean hierarchy was easily reconciled with the initial changes stemming from acceptance of an evolutionary world view because its groups-nested-within-groups structure mirrored the taxonomic structure implied by the principle of descent. Therefore, not only could the idea of evolution be accommodated by the Linnaean hierarchy, it almost seemed to provide a justification for that hierarchy's continued use. Darwin (1859:456) himself argued that “the subordination of group to group in all organisms”

followed naturally from “the view of common parentage of [allied] forms . . . together with their modification,” and that “the degrees of modification which the different group have undergone, have to be expressed by ranking them under different so-called genera, sub-families, families, sections, orders, and classes” (p. 422). Most subsequent authors, with a few notable exceptions (e.g., Gilmour 1940, 1961; Sneath and Sokal 1973; Nelson and Platnick 1981), have followed Darwin in adopting the view that biological taxonomy attempts to express evolutionary relationships and uses the Linnaean categories to represent their hierarchical structure (for some relatively recent examples see Simpson 1961; Davis and Heywood 1963; Hennig 1966; Mayr 1969a; Crowson 1970; Eldredge and Craft 1980; Wiley 1981; Mayr and Ashlock 1991).

Intermediate Stages: Concepts of Taxa

Conceptual changes.—Two important stages in the evolutionization of taxonomy, both involving concepts of taxa, occurred almost 100 years after publication of *The Origin*. In the beginning of the 20th century, the principle of descent still played a superficial role with regard to concepts of taxa. Although that principle was now widely accepted, taxa continued to be recognized on the basis of similarity, with common descent invoked after-the-fact to explain why organisms shared the characters in which they were similar. The principle of descent had not yet been granted the role of an axiom or basic principle from which a concept of the biological taxon was derived by deductive reasoning. Changes in this situation were closely associated with two important taxonomic movements, and though the new concepts of taxa associated with those movements were anticipated by earlier authors (for examples see Mayr 1955; Crow 1992; Donoghue and Kadereit 1992), the movements nevertheless seem to correspond with periods of maximum discussion and change.

The first change in taxon concepts was associated with the New Systematics (e.g., Huxley 1940; Mayr 1942) of the Modern Evolutionary Synthesis (see Mayr and Provine 1980 for general historical review). One of the major contributions of the New Systematics was a reformulated species concept. Concepts of species as groups of similar organisms were replaced with concepts of species as populations (e.g., Mayr 1942) or population lineages (e.g., Simpson 1951). This new species concept was effectively derived from the theory of evolution in that the species category was equated with a class of basic evolutionary units (e.g., Simpson 1961; Hull 1965; Mayr 1969b); not surprisingly, it necessitated the rejection of some taxa that formerly had been considered distinct species as well as the acceptance of other taxa that had not. Thus,

phenotypically distinct forms that made up a single interbreeding population were now considered morphs rather than different species, and phenotypically similar forms that made up separate interbreeding populations were now considered separate cryptic or sibling species rather than single species (de Queiroz 1992b, 1995).

The second change involving concepts of taxa was associated with the movement known as Phylogenetic Systematics or Cladistics (e.g., Hennig 1965, 1966; Crowson 1970; Eldredge and Cracraft 1980; Wiley 1981; Ax 1987). One of the important contributions of Phylogenetic Systematics was a reformulated concept of the higher taxon. Concepts of higher taxa as groups of similar species were replaced with concepts of higher taxa as clades, that is, monophyletic (holophyletic) groups of species. This new concept of the higher taxon was derived directly from the principle of descent in that it equated higher taxa with units of exclusive common ancestry, and once again, it necessitated the rejection of some previously recognized higher taxa as well as the acceptance of others that had not been recognized previously. Thus, new higher taxa were recognized for groups of species that, despite their phenotypic dissimilarity, formed single clades. And previously recognized higher taxa were eliminated, despite the phenotypic similarity of their component species, if they did not correspond with clades. In other words, many new monophyletic taxa were recognized, and many paraphyletic taxa were eliminated (there had already been a trend to eliminate polyphyletic taxa). Botanical examples of new monophyletic taxa that were recognized as a result of reformulated higher taxon concepts include Stomatophyta, Polysporangiophyta, Eutracheophyta, Lignophyta, and Anthophyta (see Crane and Kenrick 1997); examples of paraphyletic taxa that were eliminated include Bryophyta, Pteridophyta, Progymnospermae and Gymnospermae.

Effects on the Linnaean hierarchy.—Both of these changes in taxon concepts amounted to at least minor revolutions within taxonomy, but neither called the Linnaean hierarchy into question as the basis for the taxonomic system. The changes affected the way in which taxa were conceptualized, but they did not challenge the nested hierarchical structure of taxonomic relationships, and consequently, they did not contradict use of the Linnaean hierarchy for representing those relationships. Nevertheless, both had implications for the Linnaean hierarchy that affected it in more subtle ways, and changes related to the evolutionization of higher taxon concepts led some authors to question the use of the Linnaean hierarchy.

Uncoupling of the species category.—The change in species concepts effectively redefined the Linnaean category Species—or more accurately, the term “spe-

cies”—and uncoupled it from the rest of the Linnaean hierarchy. Although Linnaeus himself granted special status to genera (Cain 1958; Mayr 1982), later authors tended to view all taxa as entities of more or less the same kind with the assignment of those taxa to the Linnaean categories indicating only their relative position in the taxonomic hierarchy. The reformulated species concept implied that species (and subspecific taxa) were entities of a fundamentally different kind than supraspecific taxa: species were unitary populations or population lineages, whereas supraspecific taxa were groups of such lineages. Furthermore, the new species concept established an objective (if not entirely operational) criterion for assigning taxa to the species category (“ranking” of some authors), while the criteria for assigning taxa to the various higher categories remained subjective (e.g., Mayr 1969a).

Reformulation of the concept of the higher taxon reinforced the distinction between species and supraspecific taxa. Equating higher taxa with clades established an objective criterion for recognizing such taxa (“grouping” of some authors) but not for assigning them to the various categories of the Linnaean hierarchy. Thus, although higher taxa (as clades) were no longer considered artificial, the higher Linnaean categories remained arbitrary ranks assigned to entities of a single kind (clades), and higher taxa (as clades) remained entities of a fundamentally different kind than species (as population lineages).

Basis of the higher categories.—The evolutionization of higher taxon concepts also prompted systematists to propose various modifications to the Linnaean hierarchy concerning the theoretical basis of the supraspecific categories. One class of proposals attempted to provide a more objective and evolutionarily meaningful basis for those categories. The most basic of these proposals, which I will call Hennig’s rule, was that sister taxa must have the same absolute rank—that is, be assigned to the same Linnaean category (e.g., Hennig 1966). Hennig’s rule gained wide acceptance, at least in certain circles. Moreover, because sister groups are equivalent in terms of age of origin, its application made taxa assigned to the same Linnaean category equivalent in an evolutionarily important respect. This equivalence, however, was local in nature; that is, it did not extend beyond immediate sister taxa.

A related proposal, also put forth by Hennig (1966; see also Crowson 1970; Farris 1976), was to equate the Linnaean categories with age classes. In Hennig’s proposal, taxa originating between the Cambrian and Devonian would be assigned to a category of the Class stage (Superclass, Class, Subclass, etc.) those originating between the Mississippian and Permian to a category of ordinal stage, and so forth. Under this proposal, approximate temporal equivalence would extend

to all taxa assigned to the same Linnaean category, not only to immediate sister groups. Despite the great potential benefits of such equivalence, the proposal to equate the Linnaean categories with age classes was not adopted by most subsequent authors (Ax 1987).

Proliferation of higher categories and ways to avoid it.—Several other modifications to the Linnaean hierarchy resulted from the evolutionization of other aspects of taxonomy, in particular, the development of analytical methods designed specifically to reconstruct phylogenetic relationships. The effects of these new analytical methods on the Linnaean hierarchy were primarily indirect, through the wealth of new monophyletic taxa that were revealed by their empirical application. Although systematists generally did not feel compelled to name and rank (i.e., in one of the Linnaean categories) every new putative clade revealed by their analyses, even the ones that they did choose to name and rank often exceeded the limits imposed by the 20 or so commonly used categories. Even the 34 categories that could be formed with more extensive use of the prefixes Super-, Sub-, and Infra- were insufficient, though earlier authors (e.g., Simpson 1961) had thought that 34 categories was more than would ever be needed. The problem was not that the new taxonomies had more than 20–34 levels. Instead, the new taxonomies often required more than the three secondary categories that could be generated for adjacent primary categories using the standard prefixes if they were to maintain consistency with the ranks of more and less inclusive groups (e.g., to maintain Tracheophyta as a Division and Monocotyledoneae as a Class). Moreover, even if no new clades were named and ranked, systematists often wanted to convey the corresponding information about phylogenetic relationships.

For these reasons, authors who preferred to name newly recognized clades modified the Linnaean hierarchy further (remember that some modifications had already been made) by adding new taxonomic categories. McKenna (1975), for example, in a influential paper on the classification of mammals, used the new primary category Legion and the new prefixes Magn-, Grand-, and Mir- to generate several new levels between the traditional categories Class and Order. Similarly, the new prefixes Capax- and Parv- were used by Gaffney and Meylan (1988). Extending this approach further, Farris (1976) proposed a systematic method for generating new taxonomic categories based on rank-modifying prefixes. In Farris's method, each prefix was assigned a modifier value, which would be added to or subtracted from the value of the primary category with which the prefix was combined (see Table 1). Because no limit was placed on the number of prefixes that could be used, Farris's method could gen-

Table 1. Values of primary categories and rank modifying prefixes used in Farris's (1976) systematic method for generating taxonomic categories.

Primary category ranks		Rank modifying prefixes	
Name	Numeric rank	Prefix	Modifier value
Kingdom	9	Giga	+4
Division/Phylum	8	Mega	+3
Class	7	Hyper	+2
Cohort	6	Super	+1
Order	5	(none)	0
Family	4	Sub	-1
Tribe	3	Infra	-2
Genus	2	Micro	-3
Species	1	Pico	-4

erate an infinite number of categories, including not only new single-prefix categories such as Gigaclass and Picocohort but also novel multiprefix categories such as Supersuperorder and Submicropicofamily (see Kron 1997 for additional examples). Despite the logic of this proposal, it was not followed by most subsequent authors (but see Platnick 1977).

Other authors wished to avoid the proliferation of both taxon names and taxonomic categories. Consequently, they introduced modifications to their taxonomic systems that conveyed information about phylogenetic relationships by other means than the Linnaean taxonomic categories. Nelson (1972, 1973) pointed out that the sequence of taxon names in a list could be used to convey information about relationships, a convention that was adopted by several subsequent authors (see Eldredge and Cracraft 1980; Wiley 1981; and references therein). Taxa branching successively from a single lineage in a tree were assigned to the same category and listed in order of their branching sequence so that each taxon in the list was the sister group of the group composed of all taxa listed below it. This sequencing convention, as it latter became known, greatly reduced the number of both taxa and categories needed to convey information about relationships, but it necessarily left many clades unnamed. It also violated Hennig's rule.

Many of the most severe cases of taxon and category proliferation involved taxonomies that included both extant and extinct taxa. Not only did extinct taxa require their own names and ranks but, without sequencing, so did the more inclusive clades composed of the extinct taxa and their closest relatives. Even with sequencing, the convention that treated the seven principal categories as mandatory often required recognizing redundant (monotypic) taxa. For example, a new species intercalated between several sequenced taxa ranked as classes required the recognition of a new Class, a new Order, a new Family, and a new Genus, all including only that one known species. In the case of ancestral species, these assignments are

misleading (de Queiroz and Gauthier 1992) because the ancestor of a clade assigned to the category Order, for example, does not belong to any of the subordinate clades assigned to lower categorical levels (Hennig 1966). To eliminate redundant taxa (whether extant or extinct) and their associated problems, Farris (1976) proposed abandoning the convention of mandatory categories (see also de Queiroz and Gauthier 1992). Patterson and Rosen (1977) also abandoned the convention of mandatory categories, at least for extinct taxa, as part of their plesion convention. The plesion was a rankless category for extinct taxa that could be used at any taxonomic level (i.e., plesions could be anything from single species to speciose clades). The combination of sequencing and plesions (or otherwise eliminating the convention of mandatory categories) was very effective for reducing the numbers of taxa and categories used to represent phylogenies. Although formulated within the context of Linnaean taxonomic systems, the sequencing and plesion conventions were not themselves based on the Linnaean hierarchy and effectively limited its role.

Proposals to abandon the Linnaean hierarchy.—Given the problems that Phylogenetic Systematics raised concerning the Linnaean hierarchy, it is not surprising that this movement also produced the first serious proposals to abandon the Linnaean hierarchy. Several authors constructed taxonomies without using the Linnaean categories, employing other devices to represent hierarchical relationships. Once again, Hennig (1969, 1981, 1983) was a pioneer in using numerical prefixes rather than Linnaean categories in his taxonomies of insects and chordates (see also Griffiths 1974, 1976; Løvtrup 1977; Ereshefsky 1994). Other authors simply used indentation (e.g., Ax 1987; de Queiroz 1987; Estes et al. 1988; Gauthier et al. 1988a, b, 1989; Patterson 1988; Rowe 1988; Laurin 1991; de Queiroz and Gauthier 1992; Ford and Cannatella 1993; Sundberg and Pleijel 1994). Although numerical prefixes have been criticized for being cumbersome and difficult to use in verbal communication (Wiley 1979, 1981; Eldredge and Cracraft 1980; Ax 1987), these criticisms assume that numerical prefixes are formal substitutes for the Linnaean categories. On the contrary, they are more appropriately interpreted as simple devices for representing hierarchical relationships (de Queiroz and Gauthier 1992). As such, the set of prefixes used in a particular taxonomy is specific to that publication, and consequently they need not ever be spoken, memorized, or made consistent with the prefixes used in other taxonomies. Angiospermae, for example, might have the prefix “2” in a taxonomy of anthophytes, but it might have the prefix “2.2.2.2.2.1” in a taxonomy of spermatophytes. Such prefixes do not carry any meaning beyond indi-

cating which taxa are sister groups (e.g., 2.2.2.1 and 2.2.2.2) in taxonomies or taxonomically organized treatises spanning several to many pages, that is, in cases where simple indentation is inadequate for conveying the same information.

In addition to avoiding use of the Linnaean hierarchy, several authors presented arguments for abandoning it. Hennig (1969, 1981) argued that use of the Linnaean hierarchy often led to fruitless discussions concerning the categorical assignments of taxa, which he considered a side-issue that diverted attention from the fundamental questions of phylogenetic research. Griffiths (1974, 1976) suggested that use of the Linnaean hierarchy perpetuated confusion between the logical classes of the Linnaean hierarchy (taxonomic categories), with their historical ties to essentialism, and the phylogenetic entities of the taxonomic hierarchy (taxa). Other authors called attention to the nonequivalence of categorical assignments for taxa in different groups and the practical problem of generating enough new categories to cover the all hierarchical levels within large clades (e.g., Gauthier et al. 1988a). Several of these objections were summarized by Ax (1987).

Although the Linnaean hierarchy is not necessary for constructing hierarchical taxonomies, the problems noted above are not caused so much by that hierarchy as by its misinterpretation or misapplication. The Linnaean hierarchy may provide taxonomists with something over which they can engage in fruitless debates, but those debates stem as much from the misplaced emphases of taxonomists as from the Linnaean hierarchy itself. Similarly, most taxonomists are aware that taxa assigned to the Family category, for example, are not equivalent across more inclusive taxa; the Linnaean hierarchy is therefore not directly responsible for the fact that some biologists treat such taxa as if they are equivalent. Likewise, though some systematists continue to confuse taxa and categories, most are aware of the distinction. Finally, historical associations with essentialism are not intrinsic to the Linnaean hierarchy, which can be used as a simple representational device without invoking the metaphysics of essentialism. In short, the criticisms described above can be addressed, at least in theory, without abandoning the Linnaean hierarchy, and thus many systematists who adopt the general phylogenetic perspective underlying those criticisms continue to use and endorse that hierarchy (e.g., Eldredge and Cracraft 1980; Wiley 1979, 1981; Forey 1992).

Summary.—The Linnaean hierarchy has survived (for the most part) the evolutionization of taxon concepts, but not without concessions. Although most authors continue to use taxonomic systems based on the Linnaean hierarchy, many of those systems use a modified hierarchy (i.e., by adding new ranked categories)

and some incorporate distinctly non-Linnaean elements (e.g., sequencing, rankless categories). Some authors have constructed taxonomies without using the Linnaean hierarchy and have questioned its continued use, but the problems they have raised have not been viewed by other authors as necessary reasons for abandoning the hierarchy. On the other hand, the Linnaean hierarchy seems to constitute, as J. Gauthier (pers. comm.) calls it, an "attractive nuisance"—tempting biologists to treat taxa that are equivalent only in terms of their Linnaean categorical assignments as if they are also equivalent in terms of evolutionarily more meaningful properties, and fostering biologically meaningless debates about the categorical assignments of taxa. This is roughly the present situation, though the next stage in the process of evolutionization is already beginning.

Most Recent Stages: Systems of Nomenclature

This next stage in the process of evolutionization will extend a central role for the principle of descent into the realm of biological nomenclature. In this realm, the Linnaean hierarchy and the principle of descent serve as alternative first principles from which other concepts and principles of their respective nomenclatural systems are to be derived, and, consequently, they are in direct conflict. To understand this conflict, it is first necessary to understand the most fundamental principle of nomenclature. Therefore, I will first describe this fundamental principle. I will then review the Linnaean systems of nomenclature in current use and a newly proposed phylogenetic system of nomenclature. I will focus on differences between these two systems with respect to the fundamental principle and the consequences of those differences for nomenclatural practices. Of particular interest will be the relationship between the names of taxa and the assignment of those taxa to categories in the Linnaean hierarchy as well as the advantages of adopting a phylogenetic system of nomenclature. I will also discuss some potential misunderstandings concerning phylogenetic systems of nomenclature and the consequences of adopting such a system for the future of the Linnaean hierarchy.

The most fundamental principle of nomenclature.—Biological nomenclature is a vast set of names. The purpose of a nomenclatural system is to govern the application of those names, that is, their use in designating particular taxa. A definition is a statement specifying the meaning of a word. In the context of biological nomenclature, the words of interest are taxon names, and the meanings of those names are their designations of particular taxa. Furthermore, most of the other basic principles of biological nomenclature, such as those determining which names are to be con-

sidered synonyms and those determining which of several synonyms is to be considered correct or valid, all rest directly or indirectly on definitions. Therefore, the most fundamental principle of any system of biological nomenclature concerns the method by which taxon names are defined.

Systems of nomenclature in current use.—In current systems of nomenclature, the definitions of taxon names are based on the Linnaean hierarchy. Despite the elaborate nature and codification of these systems, their method of definition is implicit rather than explicit. Perhaps this attests to the fundamental nature of definitions, which are so basic that they can be taken for granted. In any case, the codes say virtually nothing about how taxon names are defined (the Zoological Code uses the term "definition" for what the Botanical Code more appropriately calls a description, which concerns taxa rather than taxon names). Consequently, the method of definition must be inferred from nomenclatural practices, the most revealing of which are the practices of taxonomic division and unification (splitting and lumping). When a single taxon is divided, or when two are united, the application of names is determined according to categorical assignments and nomenclatural types, which implies that these two factors are the basis of taxonomic definitions. Thus, the implicit definition of the name "Asteraceae" is something along the lines of "the taxon including the Genus *Aster* that is assigned to the category Family," and the definition of the name "Liliales" is something along the lines of "the taxon including the Genus *Lilium* that is assigned to the category Order." Because such definitions specify the meanings of taxon names in terms of the Linnaean taxonomic categories, I will hereafter refer to them as *Linnaean definitions*.

The Linnaean method of definition is implicit in the nomenclatural rules articulated by Linnaeus (1737, 1751), particularly those regarding the division and unification of genera (see Larson 1971). It was used in the precursors of the international codes (e.g., Strickland et al. 1843; de Candolle 1867) as well as in early versions of those codes (e.g., IBC 1906; ICZN 1905), and it has been retained in the modern codes (ICZN 1985; IUMS 1992; IBC 1994). The Linnaean method of definition was reinforced by the later nomenclatural convention of using standard endings for names associated with particular taxonomic categories (e.g., "-aceae" for plant families, "-ales" for plant orders, etc.; see Jeffrey 1989). A consequence of this convention was that implicit Linnaean categorical assignments became built-in to many taxon names.

Because the method of definition is the most fundamental principle of nomenclature, the use of definitions based on the Linnaean hierarchy implies that the nomenclatural systems embodied in the modern

Table 2. Phylogenetic definitions. See de Queiroz and Gauthier (1990, 1992, 1994) for diagrammatic representations of the same classes of definitions. In the Appendix, the distinction between node-based and stem-based definitions is illustrated in a proposal that uses this distinction to eliminate an inconsistency in the botanical code.

Definition type	General structure
Node-based	The clade stemming from the most recent common ancestor of a and b. ^a
Stem-based	The clade composed of c and all members of x that share a more recent common ancestor with c than with d. ^b
Apomorphy-based	The clade stemming from the first ancestor of y to evolve character e. ^c

^a Where a and b are organisms, species, or clades.

^b Where c and d are organisms, species, or clades, and x is a clade that includes both c and d.

^c Where y is an organism, a species, or a clade, and e is a derived character.

codes are Linnaean systems. The conclusion is inescapable that nomenclatural systems of this kind have survived previous stages in the evolutionization of taxonomy—from the publication of *The Origin* to the reformulation of taxon concepts. Darwin himself was involved in the development of an early zoological code (Strickland et al. 1843) based on the Linnaean method of definition, and this method has been accepted by almost all subsequent authors (but see below). Nevertheless, the evolutionization of taxon concepts—particularly that involving the higher taxa—created an inconsistency between how taxa were conceptualized and how their names were defined. This inconsistency was noted by Griffiths (1976:172), who pointed out that “. . . the categories in which taxa are classified force authors who disagree about the categorical rank of any taxon to apply different names to it even if they are in full agreement about what organisms the taxon includes”, or more generally, that the dependency of nomenclature on Linnaean categorical assignments results in different authors applying “. . . the same name to different taxa, or different names to the same taxon.” But few authors concerned themselves with this inconsistency until a new method of definition, and thus the foundation for an entirely different kind of nomenclatural system, was proposed.

A phylogenetic system of nomenclature.—This new method of definition is based on the principle of descent. In contrast with Linnaean definitions, which specify the meanings of taxon names in terms of the Linnaean taxonomic categories, *phylogenetic definitions* (de Queiroz and Gauthier 1990, 1992, 1994; see also de Queiroz 1992a, 1995, 1996; Bryant 1994, 1996; Sundberg and Pleijel 1994; Schander and Thollesson 1995) specify the meanings of taxon names in terms of ancestry and descent (Table 2). For example, the name “Asteraceae” might be defined as “the clade

stemming from the most recent common ancestor of *Barnadesia* and *Aster*” (node-based definition) and the name “Angiophyta” might be defined as “the clade composed of Angiospermae and all seed plants that share a more recent common ancestor with angiosperms than with Gnetales” (stem-based definition) (see Doyle and Donoghue 1993). Such definitions are phylogenetic in that the concept of common ancestry is fundamental to the specified meanings of the defined names. As I will describe below, the explicitly evolutionary basis of phylogenetic definitions removes the inconsistency between how taxa are conceptualized (i.e., after the evolutionization of taxon concepts) and how their names are defined. In so doing, phylogenetic definitions provide the foundation for a fundamentally different approach to biological nomenclature than that represented by traditional systems based on the Linnaean hierarchy. A system of nomenclature adopting this new approach is a phylogenetic system in that its most fundamental principle, the method of definition, is based on the principle of descent.

Consequences of a phylogenetic system.—Not surprisingly, a change in the basis of the nomenclatural system has consequences for taxonomic practice. Most importantly, a phylogenetic system would fundamentally alter the application of taxon names. This can be seen most clearly in an example (Fig. 1) comparing the application of names under Linnaean (Fig. 2) and phylogenetic (Fig. 3, 4) systems.

In Linnaean systems, definitions are dependent on the Linnaean hierarchy and thus categorical assignments play a critical role in the application of taxon names. Consider the example (Fig. 1) of a taxon and its two immediately subordinate taxa under two different Linnaean ranking (categorical assignment) schemes (Fig. 2) with the following names and Linnaean definitions (these definitions are implicit in the names but are spelled out here for the sake of completeness): Alphineae = the taxon containing Alpha that is assigned to the Linnaean category Suborder; Alphaceae = the taxon containing Alpha that is assigned to the Linnaean category Family; and Alphoidae = the taxon containing Alpha that is assigned to the Linnaean category Subfamily. Under these Linnaean definitions, a given name can designate different taxa under different Linnaean ranking schemes; for example, the name “Alphaceae” designates taxon 2 under the first scheme and taxon 1 under the second. Conversely, a given taxon can be designated by different names under different Linnaean ranking schemes; for example, taxon 1 bears the name “Alphineae” under the first scheme and “Alphaceae” under the second. Under Linnaean systems of nomenclature, differences in Linnaean categorical assignments among authors, or changes in such assignments over

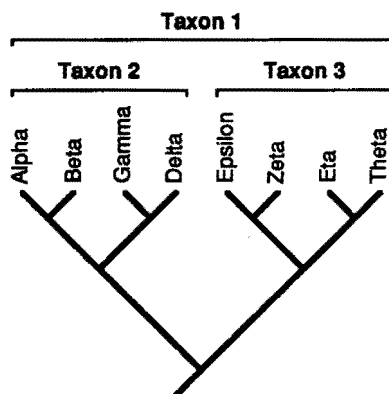


Fig. 1. Phylogeny of hypothetical taxa used to compare the application of taxon names under Linnaean (Fig. 2) and phylogenetic (Fig. 3, 4) systems of nomenclature. For the example of Linnaean systems (Fig. 2), the names of the terminal taxa are treated as if they are the names of genera; for the example of phylogenetic systems (Fig. 3, 4), the categorical assignments of the terminal taxa are irrelevant.

time, can have profound consequences regarding the associations between taxa and taxon names.

In a phylogenetic system, definitions are independent of the Linnaean hierarchy and thus categorical assignments play no role in the application of taxon names. Consider the same example (Fig. 1) of a taxon and its two immediately subordinate taxa under two different Linnaean ranking schemes (Fig. 3) but with the following names and node-based phylogenetic definitions: Alphathetonia = the clade stemming from the most recent common ancestor of Alpha and Theta; Alphadeltina = the clade stemming from the most recent common ancestor of Alpha and Delta; and Thetazetina = the clade stemming from the most recent common ancestor of Zeta and Theta. Under these phylogenetic definitions a given name designates the same taxon regardless of Linnaean categorical assignments; for example, the name "Alphathetonia" refers to taxon 1 whether that taxon is ranked as a Suborder (Fig. 3,

left) or a Family (Fig. 3, right). Conversely, a given taxon is designated by the same name regardless of Linnaean categorical assignments; for example, taxon 3 bears the name "Thetazetina" regardless of whether that taxon is ranked as a Family (Fig. 3, left) or a Subfamily (Fig. 3, right). In this example, I have used neutral endings to avoid Linnaean connotations (e.g., that a name ending in "-aceae" is associated with a taxon assigned to the Family category); however, the same conclusions would apply even if endings traditionally associated with the Linnaean categories had been used, provided that the names had been defined phylogenetically (Fig. 4). Thus, if the name "Alphaceae" (rather than "Alphadeltina") had been defined as designating the clade stemming from the most recent common ancestor of Alpha and Delta, that name would be the name of taxon 2 regardless of whether taxon 2 was ranked as a Family or a Subfamily. Under a phylogenetic system of nomenclature, differences in

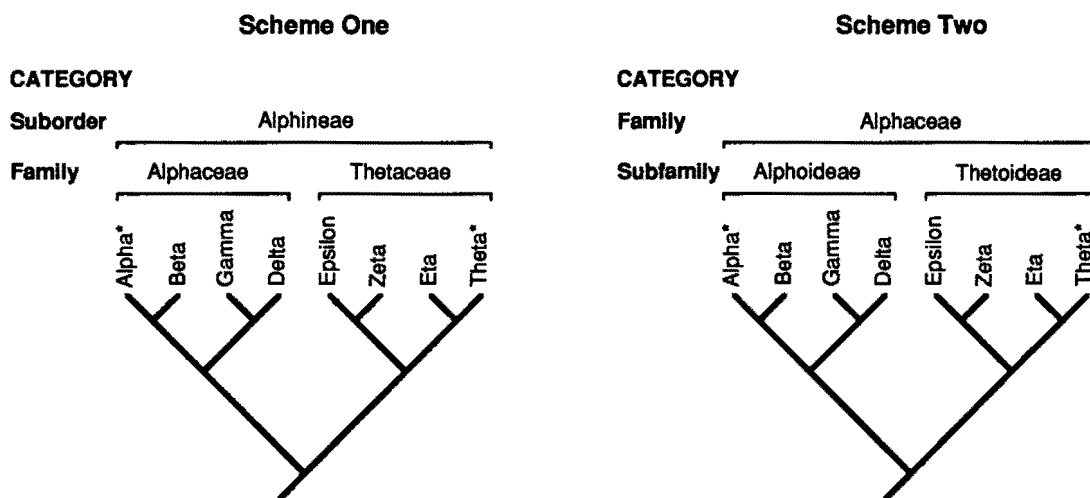


Fig. 2. The meanings of names defined under Linnaean systems vary depending on Linnaean categorical assignments. The names of all three taxa (1–3 of Fig. 1) are different under one ranking scheme (left) versus the other (right), and the only name used under both schemes (Alphaceae) designates a different taxon (2 versus 1) under the different schemes. Types are signified by asterisks (*). See text for definitions.

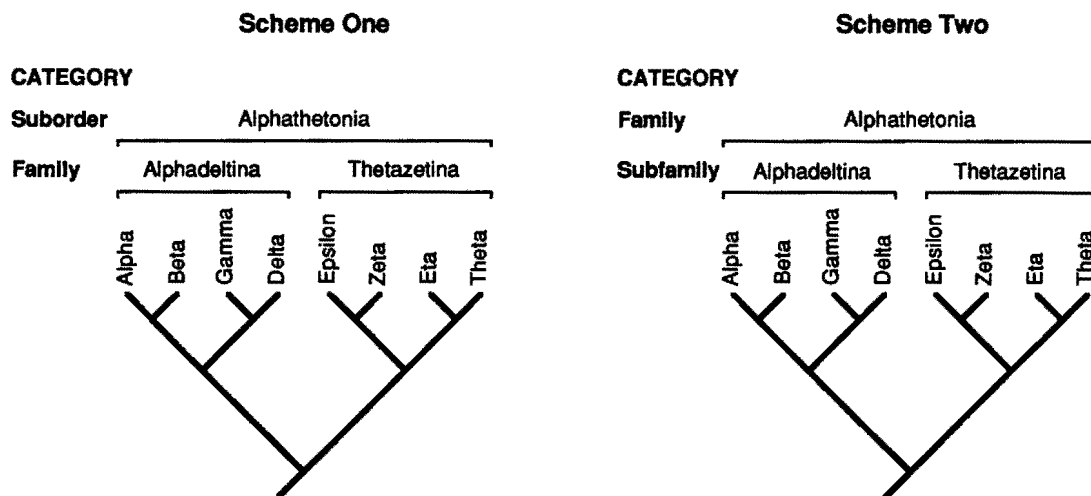


Fig. 3. The meanings of phylogenetically defined names are unaffected by Linnaean categorical assignments I. The names of all three taxa (1–3 of Fig. 1) are identical under the two different Linnaean ranking schemes (left versus right), and all three names designate the same taxa under the different schemes. Neutral endings have been used to avoid the connotations of endings associated with one of the Linnaean categories under Linnaean systems of nomenclature. See text for definitions.

Linnaean categorical assignments among authors, or changes in such assignments over time, have no effect on the associations between taxa and taxon names. A given name designates the same taxon and a given taxon is designated by the same name regardless of categorical assignments.

The use of phylogenetic definitions has important consequences for the Linnaean hierarchy. Specifically, the assignments of taxa to categories in the Linnaean hierarchy would become superfluous, at least with respect to nomenclature. Categorical assignments would not have any bearing on the names of taxa, and con-

versely, they would not have any bearing on the meanings of taxon names. Once defined phylogenetically (and regardless of endings), the name of a taxon would not change when the rank of the taxon was changed. For example, the name “Alphadeltina” (or “Alphaceae”) would not change simply because the categorical assignment of the taxon designated by that name changed from Family to Subfamily (Fig. 3, 4). Consequently, the endings or suffixes associated with particular Linnaean categories under the nomenclatural systems in current use would no longer have any significance in terms of categorical assignment. The fact

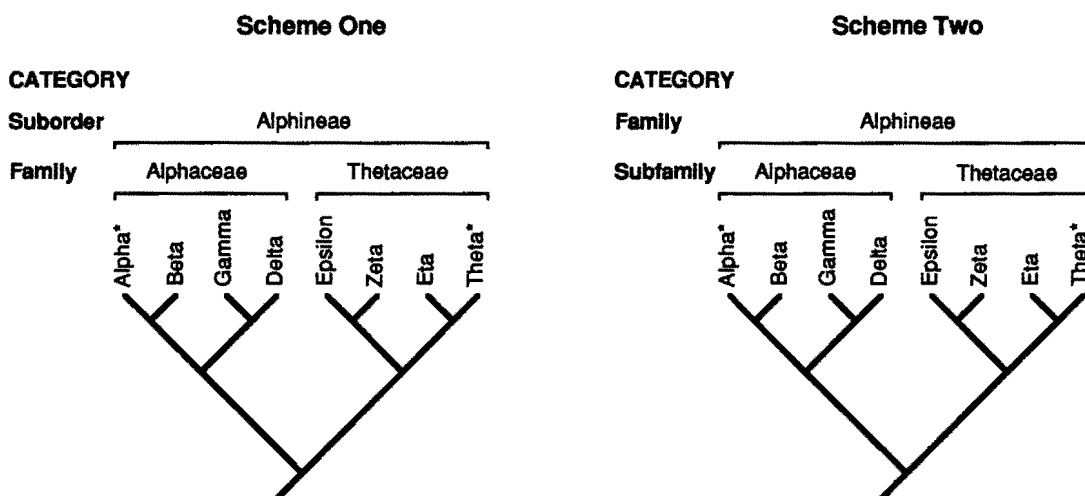


Fig. 4. The meanings of phylogenetically defined names are unaffected by Linnaean categorical assignments II. This example is identical to that illustrated in Fig. 3 except that the names have endings traditionally associated with particular Linnaean categories (in this case, Suborder, Family, and Subfamily). The names are defined as follows: *Alphineae* = the clade stemming from the most recent common ancestor of Alpha and Theta; *Alphaceae* = the clade stemming from the most recent common ancestor of Alpha and Delta; and *Thetaceae* = the clade stemming from the most recent common ancestor of Zeta and Theta. Under these definitions, the names of all three taxa (1–3 of Fig. 1) are identical under the two different Linnaean ranking schemes (left versus right), and all three names designate the same taxa under the different schemes.

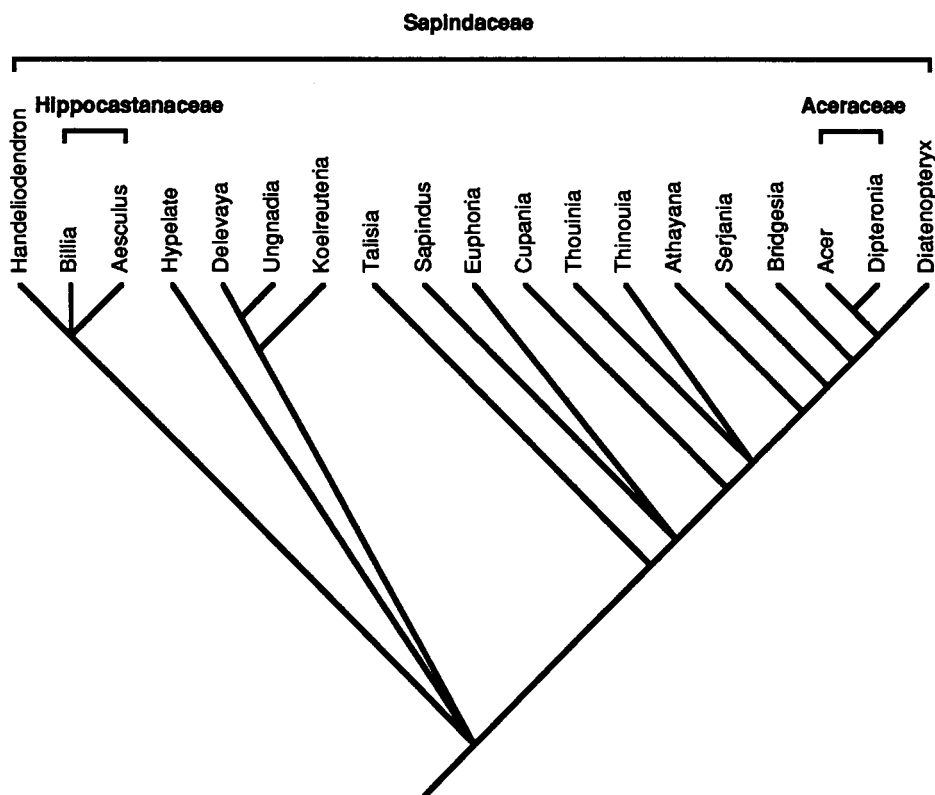


Fig. 5. Under phylogenetic definitions, names with identical endings can refer to nested rather than mutually exclusive clades. For the purpose of this example, "Aceraceae" is defined as the clade stemming from the most recent common ancestor of *Acer* and *Dipteronia*, and Sapindaceae is defined as the clade stemming from the most recent common ancestor of *Handeliiodendron*, *Hypelate*, *Koelreuteria*, *Sapindus*, *Athayana*, and *Diatenopteryx*. Although the names of both taxa end in "-aceae", Aceraceae is a subgroup of Sapindaceae. The situation with Hippocastanaceae is similar to that for Aceraceae. Names and tree (but not definitions) are from Judd et al. (1994).

that a taxon name ended in "-aceae," for example, would not imply that the taxon designated by that name was a Family; it might in fact be an Order, and it need not be assigned to any Linnaean category at all. Nor would this ending imply anything about hierarchical relationships. With revised ideas about phylogeny, names with the same ending might turn out to designate nested (rather than mutually exclusive) taxa. For example, according to the phylogeny of Judd et al. (1994), node-based phylogenetic definitions of the names "Sapindaceae" and "Aceraceae" based on current hypotheses about the composition of the taxa designated by those names implies that Aceraceae is nested within Sapindaceae (Fig. 5). (This situation already exists, to a certain degree, for names with endings that do not have a mandatory association with one of the Linnaean categories, for example, those ending in "-phyta.") In summary, the evolutionization of taxonomic definitions would render the categorical assignments of taxa irrelevant with respect to nomenclature and thus reduce the importance of Linnaean hierarchy considerably.

Advantages of a phylogenetic system.—By granting the principle of descent a central role in the definitions of taxon names, the nomenclatural proposal described

above represents yet another stage in the evolutionization of taxonomy. But apart from continuing the historical process of evolutionization, one might ask why—from the viewpoint of the practicing taxonomist—we would want to make such a fundamental change. The reason is simple and concerns the basic goals and purposes of nomenclatural systems in general and the current codes in particular; that is, to promote nomenclatural clarity, universality, and stability. These concepts can be defined as follows (de Queiroz and Gauthier 1994): *clarity* means that the associations between names and taxa should be unambiguous; *universality* means that all biologists should use the same names for the same taxa; and *stability* means that the associations between names and taxa should remain constant over time. Although the current systems of nomenclature promote nomenclatural clarity, universality, and stability, they do so in an inappropriate theoretical context.

Under the current Linnaean systems of nomenclature, that which is clear, universal, and stable is the association between a taxon name and one of the Linnaean taxonomic categories. For example, both "Alphaceae", the name of a hypothetical taxon, and "Brassicaceae", the name of a real taxon, are unam-

biguously associated with the Family category by all taxonomists operating under a Linnaean system of nomenclature, and they will remain associated with that category even if the taxa assigned to it change. Thus, "Alphaceae" remains associated with the Family category even if the taxon designated by that name changes from taxon 2 to taxon 1 (Fig. 2) and "Brassicaceae" remains associated with the Family category even if the taxon designated by that name changes from a clade that excludes the species referred to Caparaceae to one that includes them (see Judd et al. 1994). But these and other associations with the Linnaean taxonomic categories are not the most relevant aspect of meaning for the modern taxonomist. Because of the earlier stages in the evolutionization of taxonomy, taxon names now have at least implicit phylogenetic meanings, and this is true even for those systematists who continue to operate under Linnaean systems of nomenclature. In other words, taxon names now have associations not only with the Linnaean categories but also with particular parts of the phylogenetic tree of life—that is, with particular clades or the sets of species of which they are composed.

For anyone who accepts the advances of earlier stages in the evolutionization of taxonomy, the second aspect of meaning is more significant. This explains why taxonomists so often balk at proposals that would change the circumscription of a taxon and thus the implicit phylogenetic meaning of its name. Continuing with the previous hypothetical example (Fig. 2), taxon 2 is a different entity than taxon 1; therefore, changing the designation of a name from one taxon to the other goes against clarity, universality, and stability in implicit evolutionary meaning. If some authors accept the proposal and others reject it, the association of the name with a particular taxon (clade) is not universal among authors; consequently, this aspect of the name's meaning is ambiguous. And even if all biologists eventually come to accept the proposal, the association of the name with a particular taxon/clade will have changed over time. If we accept evolutionary concepts of higher taxa, we can hardly deny that Linnaean systems of nomenclature fail to accomplish their primary purpose.

In contrast with the situation under Linnaean systems of nomenclature, under a phylogenetic system, that which is clear, universal, and stable is the association between a taxon name and a clade or monophyletic group of species. Under Linnaean definitions, names have no explicit associations with clades or monophyletic taxa; any such associations are implicit. Phylogenetic definitions make those associations explicit by expressly defining taxon names as designating particular taxa (clades). Consequently, the association of a taxon name with a clade or monophyletic group of species becomes the most fundamental aspect of the

name's meaning. That is to say, association of the name with a part of phylogeny becomes more important than its association with one of the Linnaean categories. This is the reason that the associations between names and taxa are unaffected by changes in categorical assignments, as is illustrated in the examples above (Fig. 3, 4). Thus, provided that all authors adopt the same definitions (as presumably they would under a phylogenetic code), they will apply the same names to the same taxa. By emphasizing phylogenetic relationships instead of categorical assignments, phylogenetic definitions promote nomenclatural clarity, universality, and stability in terms of a theoretically significant aspect of meaning.

Clarifications.—Replacing the foundation of the nomenclatural system would constitute a minor revolution, at least within systematic biology. One might therefore expect that the change will not be made easily. Considering the previous stage in the evolutionization of taxonomy reinforces this concern. During the 1970s and 80s, bitter intellectual battles were fought over concepts of higher taxa, and debates continue to the present (e.g., Stuessy 1997). In addition, the principles and rules of nomenclature are formalized to a much greater degree than concepts of higher taxa ever were. Concepts of higher taxa were never endorsed by official congresses, commissions, or committees, nor were they formalized in published codes. If resistance to change is correlated with degree of formalization, then we can expect future battles over nomenclature to be even more bitter than past ones over concepts of higher taxa. For this reason, I would like to clarify some areas of potential confusion in hopes of avoiding criticisms based solely on misunderstandings.

Implications for the Linnaean hierarchy, hierarchical taxonomies, and names.—Several potential misunderstandings concern the implications of a phylogenetic system of nomenclature for certain taxonomic traditions, in particular, the Linnaean hierarchy, hierarchical taxonomies, and familiar taxon names. Although adopting a phylogenetic system of nomenclature would greatly limit the importance of the Linnaean hierarchy in the realm of nomenclature, it would not require total elimination of the Linnaean hierarchy from taxonomy. That is to say, taxa could still be categorized (ranked) as Orders, Families, Subfamilies, etc., even if those categorical assignments had no influence on taxon names. The categories would then be treated as simple representational devices lacking both theoretical and nomenclatural significance, much like the numerical prefixes discussed above. On the other hand, a phylogenetic system of nomenclature would permit total elimination of the Linnaean hierarchy from taxonomy; otherwise, total elimination of the Linnaean hierarchy is impossible. As long as the ap-

plication of taxon names is governed by a Linnaean system of nomenclature, even taxonomies that avoid explicit use of the Linnaean categories are still using those categories implicitly.

A second potential misunderstanding concerns the hierarchical structure of taxonomies. Even if the Linnaean hierarchy is totally eliminated from taxonomy, this does not mean that taxonomies would no longer be hierarchical. As noted above, the Linnaean hierarchy of taxonomic categories should not be confused with hierarchical taxonomies in general. A system of ranked taxonomic categories is not the only way to represent nested hierarchical relationships, which can be represented using branching diagrams, Venn diagrams, numeric prefixes, indentation, and various other devices. Because nested, hierarchical taxonomic structure is a deduction from the principle of descent, it cannot be contradicted by a method of definition derived from that same principle.

A third potential misunderstanding is the idea that eliminating the Linnaean hierarchy means eliminating or replacing established and familiar taxon names. Linnaean definitions can be replaced with phylogenetic definitions without replacing the names themselves. For example, the name "Adoxaceae" is traditionally defined (implicitly) as "the Family containing the Genus *Adoxa*," but the same name could be redefined phylogenetically as "the most recent common ancestor of *Viburnum*, *Sambucus*, [and] *Adoxa*, and all of its descendants" (Judd et al. 1994:25). The names need not change, only their definitions. Alternatively, new names could be coined (e.g., using different endings) to emphasize their novel definitional basis (e.g., Kron 1997). The advantage of redefining existing names is continuity with the previous literature; the disadvantage is their Linnaean connotations (e.g., "Adoxaceae" might be assumed to be the name of a Family even if the taxon designated by that name was assigned to a different Linnaean category or if it was not assigned to a Linnaean category at all). The advantage of coining new names is that they would have no Linnaean connotations; the disadvantage is loss of continuity with the previous literature.

Clarity, universality, and stability.—By explicitly associating taxon names with particular taxa (clades), phylogenetic definitions promote the unambiguous application of names to taxa, and in this respect they also promote the development of a universal and stable nomenclature. Linnaean definitions also promote the unambiguous application of names to taxa and the development of a universal and stable nomenclature, though they do so in very different theoretical context. In an ontological sense, acceptance of a definition—whether Linnaean or phylogenetic—ensures that a particular name will always be applied to the same taxon.

Sameness in this context refers to an ideal truth—the true taxon assigned to a particular Linnaean category (whatever that may mean) or the true clade as it exists in reality (as opposed to our conjectures about reality). Such truths, however, cannot be known with certainty. Because names can only be applied in the context of taxonomic hypotheses, there can be no guarantee that the taxon to which a particular name is applied will be identical in terms of its hypothesized composition from one taxonomic hypothesis to the next, and this is the case under both Linnaean and phylogenetic systems of nomenclature.

Under Linnaean systems, different authors will only apply the same names to taxa of identical hypothesized composition if those authors both recognize taxa of identical composition and assign those taxa to the same categories in the Linnaean hierarchy (e.g., if they all adopt the ranking scheme on one side, left or right, of Fig. 2). If different authors recognize taxa that differ in composition, or if categorical assignments differ between authors (e.g., if some adopt the scheme on the left side of Fig. 2 and others adopt the scheme on the right), then those authors will not apply the same names to taxa of identical composition. Categorical assignments are irrelevant under phylogenetic systems (Fig. 3), but taxonomic hypotheses are critical to the application of taxon names. Under phylogenetic systems, different authors will only apply the same names to taxa of identical hypothesized composition if the relevant aspects of their phylogenies are the same. If the relevant aspects of the phylogenies differ between authors, then those authors will not apply the same names to taxa of identical composition (Fig. 6; see also de Queiroz and Gauthier, 1990; de Queiroz 1996). Differences or changes in ideas about phylogenetic relationships can also lead to differences in the hypothesized composition of taxa under Linnaean systems (Fig. 7; see also de Queiroz 1996).

These examples illustrate that neither phylogenetic nor Linnaean systems guarantee clarity, universality, and stability in terms of hypotheses about the relationships and composition of taxa. The reason is that both types of nomenclatural systems clearly separate taxonomic hypotheses from nomenclatural rules. Taxonomic hypotheses, ideas about relationships and the composition of taxa, must be free to differ and change if taxonomy is to be a nonauthoritarian and evolving discipline. Therefore, in both Linnaean and phylogenetic systems of nomenclature, rules governing the application of names are deliberately formulated so that they are independent of specific taxonomic hypotheses. That is to say, both systems deliberately separate the purely formal process of applying names from the more creative and intellectual processes of reconstructing phylogeny and, in the case of the Linnaean system, assigning ranks. One consequence of this separation is

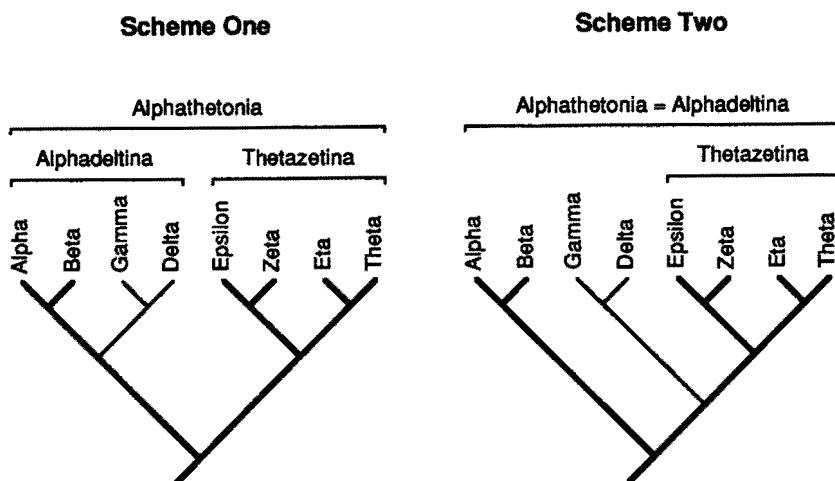


Fig. 6. The hypothesized composition of taxa designated by phylogenetically defined names can vary depending on the accepted phylogeny. The Gamma-Delta clade is most closely related to the Alpha-Beta clade in the scheme (phylogeny) on the left but to the Epsilon-Theta clade in the scheme (phylogeny) on the right. The name "Alphadeltina," defined as the clade stemming from the most recent common ancestor of Alpha and Delta, designates a clade that includes four terminal taxa (Alpha-Delta) in the context of the former phylogeny, but it designates a clade that includes all eight terminal taxa (Alpha-Theta) in the context of the latter.

that names governed by either system can be applied unambiguously under any taxonomic hypotheses framed within the general context of that system—that is, under any hypothesis about relationships (under phylogenetic systems) or about relationships and categorical assignments (under Linnaean systems). This permits the same names to be applied unambiguously as taxonomic knowledge is continually improved and refined. Another consequence is that the hypothesized

composition of taxa is only guaranteed to be unambiguous, universal, and stable when authors agree about the relevant aspects of their taxonomic hypotheses.

The difference between Linnaean and phylogenetic systems of nomenclature thus boils down to a difference in how taxonomic hypotheses are conceptualized, which is related to the difference in the underlying bases of those systems. In Linnaean systems, the Lin-

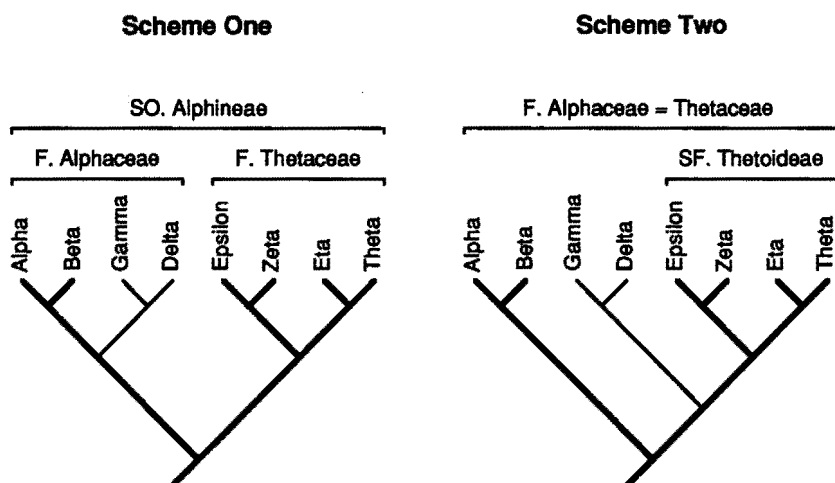


Fig. 7. The hypothesized composition of taxa designated by names defined using Linnaean definitions can vary depending on the accepted phylogeny. The Gamma-Delta clade is most closely related to the Alpha-Beta clade in the scheme (phylogeny and set of categorical assignments) on the left but to the Epsilon-Theta clade in the scheme (phylogeny and set of categorical assignments) on the right. The name "Alphaceae," defined as the clade including Alpha that is assigned to the Family category, designates a clade that includes four terminal taxa (Alpha-Delta) in the context of the former scheme, but it designates a clade that includes all eight terminal taxa (Alpha-Theta) in the context of the latter. Notice that composition of the taxon designated by the name "Thetaceae" also differs between the two schemes. Because the designations of names defined using Linnaean definitions depend on categorical assignments, other designations are possible. For example, in the context of the phylogeny (but not the categorical assignments) on the right, "Alphaceae" might refer to a clade that includes only two terminal taxa (Alpha and Beta), rather than four or eight, in which case the Gamma-Delta clade would either be recognized as its own Family or be included in Thetaceae, thus creating a difference in the composition of that taxon between the two phylogenetic hypotheses. (F=Family, SF=Subfamily, SO=Suborder.)

naean hierarchy is fundamental to the conceptualization of taxonomic hypotheses in that the application of taxon names requires assignment of taxa to categories in the Linnaean hierarchy. Nevertheless, the principle of descent is also important in that hypotheses about phylogenetic relationships affect ideas about the composition of taxa. In phylogenetic systems, the principle of descent is fundamental to the conceptualization of taxonomic hypotheses in that the application of taxon names requires a phylogeny; the Linnaean hierarchy, however, is irrelevant. Consequently, in Linnaean systems, universality and stability in the hypothesized composition of taxa designated by particular names are compromised by differences or changes in ideas about both phylogenetic relationships and categorical assignments, while in phylogenetic systems, they are compromised only by differences or changes in ideas about relationships. In other words, as the basis for a system of nomenclature, the Linnaean hierarchy interferes with effective communication about evolutionary taxa by allowing differences in categorical assignments to generate ambiguity, nonuniversality, and instability even when there is complete agreement about phylogenetic relationships.

Phylogenetic knowledge.—Perhaps the most common misconception about a phylogenetic system of nomenclature is that its use requires more extensive and definitive knowledge about phylogeny than is currently available for many groups. On the contrary, a phylogenetic system requires neither extensive nor definitive knowledge about phylogeny. As noted above, a phylogenetic system allows names to be applied unambiguously and consistently in the context of alternative phylogenies, which implies that use of such a system does not require definitive phylogenetic knowledge but only the willingness to make phylogenetic conjectures. Phylogenetic hypotheses do not have to be certain or correct, but they do have to be put forward.

Indeed, the impossibility of obtaining definitive phylogenetic knowledge—that is, the fallibility and concomitant impermanence of phylogenetic hypotheses—is the reason for having a formal system of nomenclature. If all the details of phylogeny were known with certainty, there would be no need to concern ourselves about how to apply names to taxa; it would be obvious. Our ideas about phylogeny would never change; hence there would be no alternative taxonomic hypothesis nor any need for rules about how to apply existing taxon names in the context of alternative hypotheses. But this is not how taxonomy works. Reconstructed phylogenies are provisional hypotheses that are continually being revised and refined. Unless we want to replace or redefine existing names every time a new phylogeny is proposed, we need rules for

applying those names unambiguously in the context of new phylogenetic hypotheses. In short, the purpose of a phylogenetic system of nomenclature is not to provide rules for applying names after we figure out all the details of phylogeny; instead, its purpose is to provide rules for applying names in a phylogenetically meaningful way as we continue to work out those details.

CONCLUSION

The Linnaean hierarchy has been an integral part of biological taxonomy for nearly two and a half centuries. It has proved highly useful for representing the hierarchical relationships of taxa, and it has experienced remarkable longevity. One of the greatest triumphs of the Linnaean hierarchy and a factor that was probably critical to its longevity, in particular, its persistence into modern taxonomy, was the ease with which it accommodated an evolutionary world view. Indeed, the groups-within-groups structure of the Linnaean hierarchy seemed almost ideally suited for representing the structure of taxonomic relationships implied by the principle of common descent.

If the Linnaean hierarchy had been used only as a device for representing hierarchical relationships, similar to the numerical prefixes or indentation of later authors, it might never have come into direct conflict with the principle of descent. But the Linnaean hierarchy was treated as more than a simple representational device; it was granted considerable theoretical significance. For most taxonomists after Linnaeus, the very concept of a taxon became inseparable from that taxon's categorical assignment, and this was reflected in the systems of nomenclature developed by those taxonomists. This explains why taxonomists commonly confused taxa and categories (Mayr 1969a; Griffiths 1976), why they placed so much emphasis on categorical assignments—as manifested in their frequent debates about the categorical assignments of taxa (Hennig 1969, 1981), and most importantly, why they used a method of definition in which associations with the Linnaean taxonomic categories are fundamental to the meanings of taxon names.

Because the theoretical significance granted to Linnaean categorical assignments is most evident in Linnaean taxonomic definitions, it is not surprising that a conflict between the Linnaean hierarchy and the principle of descent has arisen in the area of nomenclature. This conflict arises because systems of nomenclature based on the Linnaean hierarchy effectively grant more importance to the association of a name with one of the Linnaean categories than with a unit of common descent (de Queiroz and Gauthier 1994). Although resolution of this conflict does not require total elimination of the Linnaean hierarchy from taxonomy, it does

require nearly complete restructuring of the nomenclatural systems in current use, replacing the Linnaean hierarchy with the principle of descent as the basis for those systems. A consequence of this change is that the significance of the Linnaean hierarchy will be greatly reduced. The Linnaean hierarchy will become irrelevant to nomenclature, and in so becoming, it will lose most of its former implicit theoretical significance. Fortunately, this fate seems appropriate.

In Linnaeus's time and for nearly 100 years afterward, the theoretical significance granted to the Linnaean hierarchy was not unreasonable. At that time, it was at least conceivable that life's diversity was organized into a fixed number of discrete hierarchical levels, which might have been designated by the categories of the Linnaean hierarchy. Alternatively, if taxa were merely artificial collections of organisms, then the number of categorical levels could be dictated solely by convenience. After acceptance of the principle of descent, however, the interpretation of taxa as evolutionary units rather than artificial collections of organisms directly contradicted the latter position and made the position untenable. The continuity of descent and the presumed frequent and continual branching of phylogeny contradicted the notion of a fixed number of discrete hierarchical levels; certainly, the possibility that the hierarchical structure of life's diversity could be fully accommodated with seven or even 100 taxonomic categories became inconceivable. Consequently, although taxonomists after Darwin have continued to grant considerable implicit significance to the Linnaean categories through their use of Linnaean definitions, they have explicitly called the significance of those categories into question. Specifically, they have acknowledged that the assignment of Linnaean categorical ranks, particularly above the species level, is subjective, arbitrary, and artificial (e.g., Simpson 1961; Davis and Heywood 1963; Mayr 1969a).

In this context, one of the most important outcomes of the evolutionization of taxonomy was that it effectively proposed alternative taxonomic categories of greater theoretical significance. By equating species with evolving population lineages, the New Systematics replaced an artificial category with a evolutionarily meaningful one. Because that new category was given the same name, "species," the species category became natural—or at least theoretically significant. Similarly, by equating higher taxa with clades, groups of species united by common descent, Phylogenetic Systematics identified another evolutionarily meaningful category. Because that category was given a different name, "clade," the higher Linnaean categories did not thereby become natural or theoretically significant; instead, they remained arbitrary ranks assigned to entities of a single kind, though now the entities themselves became natural—or at least theoretically

significant. This change also emphasized the distinction between the natural higher taxa and the artificial Linnaean categories to which they were assigned.

As biological taxonomy has progressively reformulated its basic concepts and principles to reflect an ever more fully evolutionary world view, it should have become apparent that the significant taxonomic categories are not Kingdom, Division, Class, Order, Family, Genus, and Species (in the Linnaean sense); the significant categories are clade and species (in the evolutionary sense). The taxa that make up these categories exist at a multitude of hierarchical levels, far too many to be accommodated by the standard Linnaean hierarchy, and their names can only be adequately defined through explicit reference to common descent. Now that we have figured out what are the theoretically significant taxonomic categories, as well as how to reformulate our nomenclatural systems to make them consistent with those categories, the importance of the Linnaean hierarchy has been reduced to the point where we must seriously consider whether it is worth retaining. The Linnaean hierarchy has become obsolete.

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APPENDIX.

A PROPOSAL TO ELIMINATE REDUNDANCY IN PLANT TAXON NAMES
BASED ON PHYLOGENETIC DEFINITIONS

The distinction between node-based and stem-based definitions (Table 2) can be used to eliminate an inconsistency in the Botanical Code (IBC 1994) involving redundant taxon names. One of the basic principles of the Botanical Code, Principle IV, states that each taxonomic group can bear only one correct name. However, the Code tolerates several exceptions to this basic principle in the form of alternative names, such as "Asteraceae" and "Compositae", "Poaceae" and "Gramineae", and five other pairs, sanctioned under Article 18. A useful way to eliminate this redundancy, yet preserve all the names, would be to use a node-based definition to define one name of each pair as designating a crown group and a stem-based definition to define the other as designating the more inclusive clade including both the crown and its extinct relatives. Zoologists have adopted a similar convention for comparable cases, such as those of "Anura" (frogs) and "Salientia" (Anura and its extinct relatives), "Caudata" (salamanders) and "Urodela" (Caudata and its extinct relatives), and "Gymnophiona" (caecilians) and "Apoda" (Gymnophiona and its extinct relatives) (e.g., de Queiroz and Gauthier 1992; Cannatella and Hillis 1993; Ford and Cannatella 1993). As for which name should be used for which clade, one alternative would be to tie the names whose suffixes conform with those of other taxa traditionally ranked as families (i.e., those ending in "-aceae"), as well as the names of those other taxa, to crown clades. The names whose suffixes do not conform (i.e., those ending in "-ae") would then be tied to the more inclusive clades consisting of the crowns plus all extinct plants that share a more recent common ancestor with those crowns than with other extant plants. The obvious advantage of this alternative is consistency in the endings of the names in terms of their reference to crown versus stem clades. On the other hand, if the names with nonconforming endings are judged to be more widely known and used, then it might be preferable to use those names for the appropriate crown clades following the reasoning of de Queiroz and Gauthier (1992).