Linnaean, rank-based, and phylogenetic nomenclature: Restoring primacy to the link between names and taxa

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Linnaeus and other 18th Century naturalists practiced nomenclature in a way that associated taxon names more strongly with taxa (groups) than with the categorical ranks of the taxonomic ("Linnaean") hierarchy. For 18th century naturalists, ranks functioned merely as devices for indicating hierarchical position that did not affect the application of taxon names. Consequently, taxa did not change their names simply because of changes in rank. For example, the name *Reptilia* did not change when the rank of the taxon designated by that name was changed from order to division or class. During the 19th Century, a different approach to nomenclature emerged that made rank assignment central to the application of taxon names. Under this rank-based approach, which forms the basis of the current botanical and zoological codes, names are implicitly defined in terms of ranks and types and are therefore more strongly associated with ranks than with the taxa to which they refer. Consequently, taxa change their names simply because of changes in rank. For example, if the rank of the taxon *Aceraceae* is changed from family to subfamily, its name must change to *Aceroideae*. Phylogenetic nomenclature is a new approach that ties taxon names to explicitly evolutionary concepts of taxa through definitions that describe taxa in terms of ancestry and descent. This approach once again associates taxon names more strongly with taxa than with ranks and thus represents a return, updated with evolutionary principles, to an approach similar to that practiced by Linnaeus and other 18th Century naturalists.

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In addressing the future of biological nomenclature, it seems appropriate to consider phylogenetic nomenclature (e.g. de Queiroz and Gauthier 1990, 1992, 1994, de Queiroz and Cantino 2001b) – a new approach to biological nomenclature in which the application of taxon names is based on explicitly evolutionary methods. This approach contrasts with the traditional rank-based approach – adopted by the current Bacteriological (IUMS 1992), Zoological (ICZN 1999), and Botanical (IBC 2000) codes – in which evolutionary considerations are entirely taxonomic (i.e. they determine only what kinds of groups are to be recognized as taxa), and nomenclature (i.e. the use of taxon names) is based on categorical or taxonomic ranks. Because of this fundamental difference, phylogenetic nomenclature often differs significantly from traditional rank-based nomenclature concerning which names are to be considered synonyms and homonyms, and thus also the accepted names of particular taxa. Although phylogenetic nomenclature can be considered radical in this respect, in other respects it is not radical at all but instead represents a return to an approach similar to that practiced by Linnaeus and other early naturalists.

In this paper, I will discuss the relationships between 18th Century, rank-based, and phylogenetic nomenclature, emphasizing the relationships between taxon names, on the one hand, and taxa (groups) versus categorical ranks, on the other. I

will first describe how nomenclature was practiced by 18th Century naturalists. In particular, I will provide evidence that the primary associations of taxon names were with taxa (groups) rather than with ranks (taxonomic categories). I will then describe the rank-based approach to nomenclature that emerged during the 19th Century and forms the foundation of the current international codes (e.g. IUMS 1992, ICZN 1999, IBC 2000). In particular, I will describe how the rank-based approach changed the primary associations of taxon names from taxa to taxonomic ranks. Next, I will describe the recently proposed phylogenetic approach that forms the basis of the draft *PhyloCode* (Cantino and de Queiroz 2000, 2003), giving a brief overview of its similarities to, as well as its differences from, traditional rank-based nomenclature. Finally, I will describe how the phylogenetic approach restores the primary association between names and taxa. Although phylogenetic nomenclature de-emphasizes taxonomic ranks, which are commonly considered one of the hallmarks of Linnaean taxonomy, I hope to show that this new approach is, with respect to the function of categorical ranks, more similar to nomenclature as it was practiced by Linnaeus and other early naturalists than is the later rank-based approach that underlies the current codes of botanical and zoological nomenclature.

Linnaean and Late 18th Century Nomenclature

I will use the term *Linnaean nomenclature* for the nomenclatural principles and practices adopted by Carolus Linnaeus (1707–1778). Linnaean nomenclature in this sense should not be confused with the taxon names used by Linnaeus, which is Linnaean nomenclature in a different sense. More importantly, it should not be confused with the nomenclatural approach that forms the basis of the current international codes of nomenclature. Although these codes are based on the taxonomic rank-categories adopted by Linnaeus (i.e. regnum, classis, ordo, genus, species) with the addition of both primary (e.g. division, phylum, family) and secondary (e.g. subclass, infraorder, superfamily) categories, they use those categories in a way that differs significantly from the way in which the categories were used by Linnaeus and other early taxonomists.

I have called attention to Linnaean nomenclature both because of the importance of Linnaeus' contributions to taxonomy and nomenclature and because this paper is part of a tribute to one of his great works, the *Species Plantarum*. Nevertheless, the approach that I really wish to describe is not the approach of Linnaeus in particular but that of 18th Century European naturalists in general – or more specifically, that of European naturalists from the time when they adopted the use of categorical ranks, following Linnaeus, until sometime in the middle of the 19th Century, when the alternative rank-based approach to nomenclature emerged.

In describing how nomenclature was practiced by Linnaeus and other early naturalists, the point I want to make is that for these early taxonomists taxon names were more closely associated with taxa than with categorical ranks. This point can be demonstrated by showing that when particular taxa (groups) were assigned to different ranks, the names of those taxa did not change and thus retained their associations with the taxa to which they originally referred, rather than with the ranks with which they had previously been associated. To demonstrate this, I need to adopt a conceptualization of taxa that approximates that of 18th Century naturalists. Therefore, I will adopt a conceptualization of taxa as sets of organisms, particularly those sharing distinctive characters (see de Queiroz, 1997).

Because this symposium commemorates the publication of Linnaeus' *Species Plantarum*, I would have liked to use names from that work to illustrate my point. However, I am a zoologist, which is to say that I am sufficiently unfamiliar with the historical use of plant taxon names that using those names as examples would have greatly delayed the completion of my paper. For this reason, I will emphasize zoological taxon names, particularly those of vertebrates, the group with which I am most familiar.

In addition, it is not particularly informative to

compare Linnaeus' use of taxon names with use of the same names by earlier authors, at least not as they relate to differences in rank assignments. The reason is that taxonomic ranks were used infrequently by earlier authors; their consistent and systematic use derives largely from the work of Linnaeus. Therefore, I will illustrate my point with zoological names used by Linnaeus and later 18th and early 19th Century authors. Of particular interest are cases in which a taxon recognized by Linnaeus (or some other author) was also recognized by a subsequent author but assigned to a different taxonomic rank.

In these cases, the change in rank did not require a change in the name of the taxon. I do not mean to say that the names of taxa never changed. Authors who recognized taxa of similar or identical composition but based their taxonomic systems on different characters often gave different names to those taxa, since it was common to use taxon names that described the characters upon which the systems were based. For example, several authors recognized a taxon composed of what would later be considered amphibians and reptiles (excluding mammals and birds); however, some of those authors emphasized the use of both aquatic and terrestrial habitats by at least some of those organisms and used the name *Amphibia* (< Greek *amphibios* = double life) for that taxon (e.g. Linnaeus 1735, 1748, Linnaeus and Gmelin 1788, Shaw 1802), while others emphasized the mode of locomotion and used the name *Reptilia* or *Reptiles* (< Latin *reptare* = to creep or crawl) (e.g. Laurenti 1768, Brongniart 1800, 1805, Oppel 1811).

In addition, sometimes the composition of a taxon would change significantly (i.e. not merely through the inclusion of newly discovered species), yet the same name would be used. For example, in the first edition of *Systema Naturae*, Linnaeus (1735) included only taxa that would later be considered amphibians and reptiles in his class *Amphibia* (see also Linnaeus 1748). Later, however, Linnaeus (e.g. 1758, 1766) included in a taxon of the same name and rank various organisms that he had previously included in his class *Pices*, such as lampreys (*Petromyzon*), sharks (*Squalus*), skates (*Raja*), and sturgeons (*Acipenser*).

Figure 1. Application of taxon names by late 18th and early 19th Century naturalists. For these early naturalists, categorical ranks served to indicate the nested or mutually exclusive relationships of taxa but had no effect on the application of taxon names. Therefore, a taxon could be designated by the same name regardless of the rank to which it was assigned. In this example, the same names, *Amphibia* and *Reptilia*, were used by Linnaeus (e.g., 1758, 1766) for nested taxa that he ranked as a class and an order (left), and by Scopoli (1777), who ranked the same taxa as a tribe and a division (right).

These taxa were once again excluded from *Amphibia* in the 13th Edition of the *Systema Naturae* (Linnaeus and Gmelin 1788). (I have not attempted a thorough survey of the various editions of Linnaeus' *Systema Naturae* but instead have chosen the first (1735), sixth (1748), tenth (1758), and twelfth (1766) editions as the sources of my examples.)

With the preceding clarifications in mind, the point I want to make is that the categorical ranks to which particular taxa were assigned sometimes changed without any significant changes concerning the composition or diagnostic characters of those taxa, but such changes did not necessitate changes in taxon names (Fig. 1). For example, Linnaeus (1735, 1748, see also Linnaeus and Gmelin 1788) assigned the taxon *Amphibia* (not including any "fishes") to the rank of class. Later, Merrem (1820) assigned the same taxon to a higher categorical rank. (Merrem did not explicitly state the rank of this taxon; that rank is inferred to have been above the rank of class because the taxon's two primary subgroups were ranked as classes.) Despite this difference in ranks, Merrem (1820) used the same name, *Amphibia*, for this taxon. In later editions of the *Systema Naturae*, Linnaeus (e.g., 1758, 1766) recognized a taxon of a somewhat different composition (i.e., including certain "fishes") as the class *Amphibia*. Scopoli (1777) recognized the same taxon but ranked it as a tribe; nevertheless, he used the same name, *Amphibia*.

Another example concerns the name *Reptilia*, which Linnaeus (1748, 1758, 1766, see also Lin-

naeus and Gmelin 1788) used for a subgroup of *Amphibia* that he assigned to the rank of order (he also used the name *Reptiles* for this taxon). Scopoli (1777) used the same name for a taxon of similar composition despite assigning it to the rank of division. Most other late 18th and early 19th Century authors who used the name *Reptilia* or *Reptiles* (e.g. Laurenti 1768, Daudin 1802–3, Lamarck 1809) applied that name to a more inclusive taxon corresponding in composition to the one that Linnaeus (e.g. 1735, 1748, see also Linnaeus and Gmelin 1788) called *Amphibia* (i.e. including not only Linnaeus' order *Reptilia* but also his order *Serpentes*). They used the same name that Linnaeus had used for an order despite ranking the taxon as a class.

Thus, for 18th Century taxonomists, changes in the assignments of taxa to categorical ranks did not necessitate changes in the names of those taxa. This situation indicates that the categorical ranks did not have a significant nomenclatural function. Instead, the ranks served a more or less exclusively taxonomic function of indicating the relative hierarchical positions (inclusiveness) of taxa. The independence of 18th Century nomenclature from categorical ranks contrasts sharply with situations in what has now become traditional nomenclatural practice, in which the application of taxon names is based on categorical ranks.

Rank-based Nomenclature

I will use the term *rank-based nomenclature* for an approach to nomenclature in which taxon names are tied to particular categorical ranks and rank assignment is necessary for the application of taxon names. A particular name is applied to whichever taxon contains the designated type and is assigned to the categorical rank associated with that name. For example, the name *Aceraceae* is applied to whichever taxon contains the type of the genus *Acer* and is assigned to the rank of family. As in this example, at least some of the names in rank-based nomenclature have intrinsic components – mandatory, standardized, rank-specific endings (*–aceae* in the example) – that tie those names to particular categorical ranks (in this case, family). Table 1 summarizes the standardized rank-signifying endings used in botany and zoology.

Table 1. Mandatory standardized ranking signifying endings used by the rank-based codes of botany and zoology

Categorical Rank	Botany[1,3]	Zoology[2]
Ordo (order)	*–ales*	–
Subordo (suborder)	*–ineae*	–
Superfamilia (superfamily)	–	*–oidea*
Familia (family)	*–aceae*	*–idae*
Subfamilia (subfamily)	*–oideae*	*–inae*
Tribus (tribe)	*–eae*	*–ini*
Subtribus (subtribe)	*–inae*	*–ina*

[1] IBC (2000): Arts. 17.1, 18.1, 19.1, 19.3.
[2] ICZN (1999): Art. 29.2.
[3] In botany, the standardized, rank-signifying endings for orders and suborders are only mandatory for names based on the names of included families based on generic names (automatically typified names), that is, as opposed to names taken from distinctive characters of the taxon (descriptive names) (IBC 2000: Art. 16.1). Standardized, rank-signifying endings are also recommended (but not mandatory) for names of taxa assigned to the higher ranks division, subdivision, class, and subclass (IBC 2000: Rec. 16A).

Although rank-based nomenclature is commonly referred to as *Linnaean*, this characterization is misleading. Despite being based on the hierarchy of taxonomic categories derived from those used by Linnaeus (commonly termed the *Linnaean hierarchy*) and in using binominal species names, the rank-based approach differs significantly from that adopted by Linnaeus and other early naturalists in granting greater importance to the associations of taxon names with categorical ranks than with taxa. On the other hand, this property is manifested in some of Linnaeus' (e.g. 1737, 1751) practices regarding genera (see also Larson 1971: 131, de Queiroz 1997: 133). In any case, I have reserved the adjective *Linnaean* for the approach used by Linnaeus himself. Because the nomenclatural system that underlies the modern codes contains many components developed in the 250 years since the time of Linnaeus, and because its use depends on categorical ranks (including

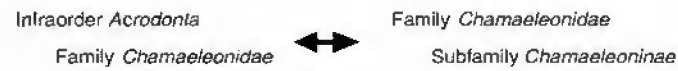

Figure 2. Application of taxon names under rank-based nomenclature. In this approach, the name of a taxon depends on the rank to which that taxon is assigned. Therefore, if the same taxon is assigned to a different categorical rank, it must be designated by a different name. In this example, two nested taxa are designated by the names *Acrodonta* and *Chamaeleonidae* when the taxa are ranked as an infraorder and a family (left), but the same two taxa are designated by the names *Chamaeleonidae* and *Chamaeleoninae* when the taxa are ranked as a family and a subfamily (right). Notice also that the name *Chamaeleonidae* refers to different (less and more inclusive) taxa under the two ranking schemes. Compare with Figure 1.

several that were not used by Linnaeus), that system is more accurately termed *rank-based* rather than *Linnaean* (see also Stuessy 2000).

Rank-based nomenclature became widely accepted sometime during 19th Century, though I have not attempted a thorough investigation of its origin and history. One of its most obvious manifestations is the use of standardized, rank-specific endings (Table 1). In zoology, the earliest explicit endorsement of such endings as a general nomenclatural convention that I have so far been able to find is that of Swainson (1835), who stated that the names of all families are terminated in *–idae* and those of subfamilies in *–inae*, though the former convention had been adopted in practice by earlier authors (e.g. Gray 1825). In an early attempt to develop a code of zoological nomenclature, Strickland (1837:175) proposed the general rule (16), attributed to Swainson, that "the names of tribes, families and subfamilies should have a distinctive termination," though he did not specify what those terminations should be. Later, the so-called Stricklandian Code (Strickland et al. 1843:272–3), an important precursor of the zoological code, adopted the recommendation that "*families* should be uniformly named by adding the termination *–idae* to the name of the earliest known, or most typically characterized genus in them; and ... their subdivisions, termed *subfamilies*, should be similarly constructed, with the termination *–inae*." Most importantly, similar rules were adopted in the original international codes of both zoological and botanical nomenclature (ICZN 1905: Art. 4, IBC 1906: Art. 23) and perpetuated in all subsequent versions of those codes up to the present ones (ICZN 1999: Art. 29.2, IBC 2000: Arts. 17–19).

The adoption of these and related rules lead to a drastic change in the relationships between taxon names, on the one hand, and taxa versus ranks, on the other. Compared with earlier nomenclatural practices (see previous section), the rank-based approach reversed the relative strengths of the associations of taxon names by placing greater emphasis on their associations with particular ranks than on their associations with particular taxa. Categorical ranks no longer served simply as devises for indicating position in the taxonomic hierarchy; now they became fundamental to the application of taxon names. This situation is evident in cases where the rank of a taxon changes without any other changes regarding the conceptualization of the taxon (e.g. in terms of hypothesized composition, diagnostic characters, or phylogenetic relationships). In such cases, the name shifts its association from one taxon to another to maintain its association with a particular rank.

For example, if three nested taxa were earlier assigned to the ranks of suborder, family, and subfamily, but later assigned to the ranks of family, subfamily, and tribe, the names of those taxa would have to be changed (i.e. through changes in their rank-specific endings) to reflect the changes in ranks (Fig. 2). Thus, if the taxon originally ranked as a family were named *Aceraceae*, its name would have to be changed to *Aceroideae*; if it were originally named *Chamaeleonidae*, its name would have to be changed to *Chamaeleoninae*. Concomitantly, the original names would have to shift their associations to more inclusive taxa. Thus, the name *Aceraceae* (and *Chamaeleonidae*) would have to be applied to the more inclusive taxon that was formerly ranked as a suborder.

These examples illustrate that under rank-based nomenclature, taxon names are more closely asso-

ciated with particular ranks than they are with particular taxa. Consequently, when the ranks of taxa are changed, the relevant taxon names retain their associations with the original ranks of the taxa to which they previously referred rather than their associations with the taxa themselves. In effect, taxon names have become disassociated from taxa (whether conceptualized in terms of composition, diagnostic characters, or phylogenetic relationships) in that they are tied to those taxa only in the context of a particular ranked taxonomy. The only permanent associations of taxon names are with particular ranks and types.

The primary association of names with ranks in rank-based nomenclature is not restricted to names with standardized rank-specific endings. Genera, for example, do not have rank-signifying endings under either the botanical or the zoological code. Nonetheless, the names of genera behave similarly to those of taxa with rank-signifying endings. Thus, if two closely related genera are united (lumped) in the absence of any change in the hypothesized relationships among their included species, both of the original genus names shift their associations to the more inclusive group that formerly contained both genera (though only one, of course, would be used as the accepted name of the taxon). For example, if the lizard genera *Crotaphytus* and *Gambelia*, which are the only members of a more inclusive taxon commonly ranked as either a subfamily (*Crotaphytinae*) or a family (*Crotaphytidae*), are united into a single genus, then both names, *Crotaphytus* and *Gambelia*, will be applied to that genus and thus considered synonyms (*Crotaphytus*, which has priority over *Gambelia*, will be the accepted name). In other words, both names will shift their references from less inclusive taxa to a more inclusive one rather than retaining their associations with the original taxa. This situation demonstrates that the names are more closely associated with the rank of genus than with particular taxa (groups of species).

In the case of names associated with the rank of genus, this situation can be partially ameliorated through the use of subgenera, because the names of genera and subgenera, unlike those associated with higher ranks, can be identical (i.e. spelled exactly the same). For example, if the genera *Crotaphytus* and *Gambelia* were to be united into a single genus *Crotaphytus*, the two formerly recognized taxa could still be referred to using the names *Crotaphytus* and *Gambelia* by treating those names as the names of subgenera. Consequently, the names would (ignoring their status as the names of genera versus subgenera) remain associated with the same taxa. On the other hand, using the same name for a genus and one of its subgenera violates a fundamental principle of at least the zoological code, which states that one of its primary objectives is "to ensure that the name of each taxon is unique and distinct" (ICZN 1999: Preamble).

The behavior of rank-based nomenclature in the face of changes in taxonomic ranks derives from the fact that names have fixed associations with particular ranks. Some names (e.g. family and subfamily names) have standard endings that tie them to particular ranks (e.g. ICZN 1999: Art. 29.2; IBC 2000: Art. 18.1, 19.1). These names are automatically typified in that the names are based on the names of their types (ICZN 1999: Art. 29.1; IBC 2000: Art. 10.6). Other names (e.g. those of genera and subgenera) do not have standard endings that tie them to particular ranks, and therefore they must be explicitly tied to those ranks, for example, by a declaration that a name is the name of a new genus (e.g. IBC 2000: Art. 35.1). These names are not automatically typified; therefore, their types must be independently designated (ICZN 1999: Arts. 67–69; IBC 2000: Arts. 10.2, 37.1).

In rank-based nomenclature, both the association with a particular rank and typification are necessary for the application of taxon names. Typification is necessary to determine which of several taxa assigned to a particular rank is to be designated by a particular name (e.g. the name *Aceraceae* is not to be applied to any family whatsoever but only to the one that contains the type of the genus *Acer*). Conversely, association with a particular rank is necessary to determine which of several nested taxa containing the relevant type is to be designated by a particular name (e.g. the name *Aceraceae* is not to be applied to any taxon whatsoever that contains the type but only to the one

Figure 3. Application of taxon names under current practices when names are untypified. In these cases, the application of taxon names is not determined by ranks despite the fact that other aspects of the names are regulated by the rank-based codes. Therefore, the same taxon can be designated by the same name regardless of the rank to which it is assigned. In this example, the same names, *Squamata*, *"Lacertilia,"* and *Serpentes*, are applied to the same three taxa regardless of whether those taxa are ranked as an order and two suborders (e.g. Romer 1956, 1966, Kuhn 1966, Carroll 1988; left) or as a superorder and two orders (e.g. Gans 1978, Estes 1983, Underwood 1967, 1971; right). Compare with Figures 1 and 2.

that is ranked as a family). In this sense, the combination of rank association and typification constitutes an implicit definition based on rank and type (de Queiroz and Gauthier 1994, de Queiroz 1997, de Queiroz and Cantino 2001b). It provides an unambiguous criterion for applying a taxon name to a taxon. It is also the reason that taxon names are more strongly tied to ranks than to taxa.

In spite of the situation just described, some contemporary names continue to be applied in much the same way that they were by Linnaeus and other early naturalists – that is, even though they are at least partly regulated by the rank-based codes (e.g. ICZN 1999: Art. 1.2.2; IBC 2000: Arts. 16, 17). These names are not typified, meaning that their references are not tied to a subordinate taxon or specimen, the type. More importantly, they are not tied to any particular categorical rank. Such names include zoological names above the rank of superfamily and descriptive botanical names above the rank of family. Because these names are not tied to any particular rank, they continue to be applied in a manner that is unaffected by rank assignment (Fig. 3). For example, the currently recognized taxon *Squamata* ("lizards" and snakes) and its subordinate taxa "*Lacertilia*" ("lizards") and *Serpentes* (snakes) are assigned to the respective ranks of order and suborder by some authors (e.g. Romer 1956, 1966, Kuhn 1966, Carroll 1988) and superorder and order by others (e.g. Gans 1978, Estes 1983, see also Underwood 1967, 1971). However, because the application of these names is not based on categorical ranks, the taxa in question retain the same names regardless of their assignments to different ranks (see also IBC 2000: Art. 16.1). On the other hand, these names are relatively unregulated; in particular, there are no rules for establishing their relative precedence (e.g. IBC 1999: Art. 11.9).

Phylogenetic Nomenclature

In the approach called *phylogenetic nomenclature*, taxon names are tied to explicitly phylogenetic concepts of taxa through definitions of taxon names that describe taxa in terms of ancestry and descent (e.g. de Queiroz and Gauthier 1990, 1992, 1994, de Queiroz and Cantino 2001b). The three most general types of phylogenetic definitions – termed *node-based*, *stem-based*, and *apomorphy-based* – are illustrated in Figure 4, the legend of which also includes definitions of some relevant terms. The statements in question are called *definitions* because they specify the meanings of words, in this case, taxon names (de Queiroz 2000, de Queiroz and Cantino 2001a). They should not be confused with what are commonly called definitions in taxonomy – that is, lists of characters that distinguish the organisms of a particular taxon from those of other taxa and thus serve to diagnose the taxon in question. Although such lists serve to define taxa as conceptualized prior to the adoption of an evolutionary worldview (i.e. as groups of organisms sharing particular characters), they do not specify how taxon names are to be applied (i.e. in different taxonomic contexts) and therefore do not qualify as definitions in the nomenclatural (as opposed to the taxonomic) sense.

Phylogenetic definitions function like the implicit definitions of rank-based nomenclature in

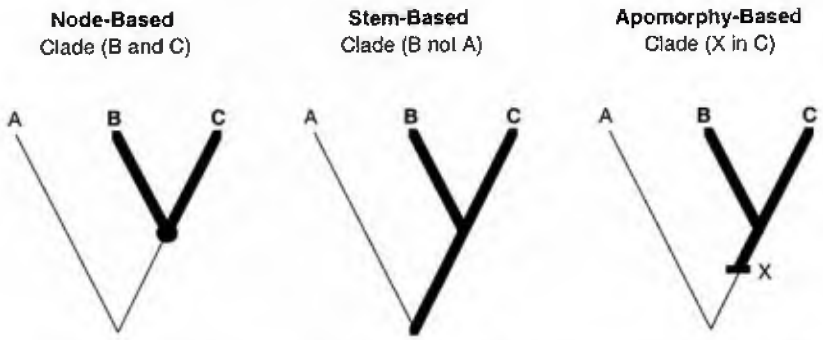

Figure 4. Three general classes of phylogenetic definitions. The designations of three classes of definitions – *node-based*, *stem-based*, and *apomorphy-based* – are given above, shorthand example definitions are given below the designations, and diagrams illustrating application of the example definitions are given below. In the node-based definition, *Clade (B and C)* stands for *the least inclusive clade containing both B and C*. In the stem-based definition, *Clade (B not A)* stands for *the most inclusive clade containing B but not A*. In the apomorphy-based definition, *Clade (X in C)* stands for *the clade stemming from the first ancestor of taxon C to evolve character X homologous with that in taxon C*. The taxa (A, B, C) or characters (X) used in the definitions are termed *specifiers*, because they are used to specify the taxon to which the name refers. *Internal specifiers* are explicitly included in the named taxon (B and C in the node-based definition, B in the stem-based definition, C in the apomorphy-based definition); *external specifiers* are explicitly excluded from the named taxon (A in the stem-based definition). Thick lines and bold letters indicate lineages and terminal taxa that make up the clade specified by the corresponding definition. After de Queiroz and Gauthier (1990), Schander and Thollesson (1995), Cantino and de Queiroz (2000), and de Queiroz and Cantino (2001b).

that they provide unambiguous criteria for applying names to taxa. A given name is applied, in the context of a specified phylogenetic hypothesis, to whichever clade fits the stated definition (i.e. regardless of the clade's precise composition, except for the necessary inclusion of internal specifiers and the necessary exclusion of external specifiers). For example, if the name *Mammalia* is defined phylogenetically as referring to the clade stemming from the most recent common ancestor of platypuses (*Ornithorhynchus anatinus*) and humans (*Homo sapiens*), then certain fossil taxa may or may not be included within *Mammalia* depending on their hypothesized phylogenetic relationships – that is, depending on whether or not they are inferred to be descended from the last common ancestor of platypuses and humans.

Phylogenetic nomenclature was proposed in the last part of the 20th Century (e.g. de Queiroz and Gauthier 1990, 1992, 1994, Sundberg and Pleijel 1994, Schander and Thollesson 1995) and forms the theoretical foundation of the draft *PhyloCode* (Cantino and de Queiroz 2000, 2003), a proposed set of rules and recommendations that represents an alternative to the codes of rank-based nomenclature. This approach can be considered an outgrowth of the phylogenetic or cladistic approach to systematics (e.g. Hennig 1966, Eldredge and Cracraft 1980, Wiley 1981) in that 1) the principle of common ancestry or cladistic relationship (Cain and Harrison 1960) is fundamental to the application of names, 2) categorical ranks are de-emphasized, following Hennig (e.g. 1969, 1981, 1983) and some other proponents of phylogenetic systematics (e.g. Løvtrup 1977, Ax 1987), and 3) clades or monophyletic groups are emphasized as the entities to be named, following Hennig (e.g. 1966) and other proponents of phylogenetic systematics (e.g. Eldredge and Cracraft 1980, Wiley 1981, Ax 1987).

Nevertheless, phylogenetic nomenclature is logically independent from Hennig's principle that all formally recognized taxa must be monophyletic. On the one hand, Hennig's principle can be adopted in the context of either rank-based or phylogenetic nomenclature, though in the former

case taxon names do not necessarily retain their associations with particular monophyletic taxa. On the other hand, phylogenetic nomenclature can, in theory, accommodate other evolutionary approaches (see de Queiroz and Gauthier 1990:311), such as the traditional evolutionary approach to taxonomy that allows paraphyletic taxa (e.g. Simpson 1961, Davis and Heywood 1963, Mayr 1969), though proponents of phylogenetic nomenclature do not advocate this practice.

Phylogenetic nomenclature shares several basic goals and methods with rank-based nomenclature. Both systems have the same fundamental goals of providing unambiguous methods for applying names to taxa, for selecting a single accepted name for a taxon from among competing synonyms or homonyms, and for promoting nomenclatural stability and continuity to the extent that doing so does not contradict new systematic conclusions. Neither system infringes upon the judgment of taxonomists with respect to inferring the composition of taxa or to assigning taxonomic ranks (contrary to a widely held misconception, phylogenetic nomenclature does not prohibit the use of ranks). Both systems use precedence, a clear order of preference, to determine the accepted name of a taxon when synonyms or homonyms exist. Both systems use priority with regard to the date of publication as the primary criterion for establishing precedence. And both phylogenetic and rank-based systems allow a later-established name to be conserved over an earlier name for the same taxon (i.e. for priority to be set aside) if using the earlier name contradicts the fundamental goal of promoting nomenclatural stability and continuity.

Phylogenetic nomenclature also differs from rank-based nomenclature in a number of ways (see Cantino and de Queiroz 2000, 2003, de Queiroz and Cantino 2001b); however, the most fundamental difference concerns the methods that the alternative systems use for applying names to taxa (de Queiroz 1997). As noted above, phylogenetic nomenclature uses explicit definitions that describe taxa in terms of ancestry and descent. In contrast, rank-based nomenclature uses implicit definitions that describe taxa in terms of ranks and types. To repeat one of my earlier examples, the implicit rank-based definition of the name *Aceraceae* is the taxon ranked as a family that contains the type of the genus *Acer*. These statements can be considered definitions in that they specify the references of words (in this case, taxon names). They function analogously to phylogenetic definitions in that they provide unambiguous criteria for applying names in the context of different taxonomic hypotheses (phylogenetic trees in the case of phylogenetic definitions, sets of ranked groups in the case of rank-based definitions). And like phylogenetic definitions, they are applied, in the context of a specified taxonomy (in this case, a set of categorically ranked groups), to whichever ranked group fits the stated definition (i.e. regardless of the group's precise composition, except for the necessary inclusion of the type).

The difference between rank-based and phylogenetic nomenclature regarding methods for applying names to taxa is the cause of a fundamental difference concerning the relative strengths with which the two approaches associate names with taxa versus ranks. Under rank-based nomenclature, the method for applying names to taxa is based on ranks and types; consequently, taxon names are more strongly associated with ranks than with taxa. Under phylogenetic nomenclature, the method for applying names is based on specified phylogenetic relationships; consequently, taxon names are more strongly associated with taxa, as conceptualized and described by the specified phylogenetic relationships, than with ranks. For the case of rank-based nomenclature, I described in the previous section how taxon names change their references from less inclusive to more inclusive taxa, or vice versa, when the ranks of those taxa are changed.

For the case of phylogenetic nomenclature, changes in rank alone have no effect on the application of taxon names (Fig. 5). For example, suppose that the names *Squamata* and *Serpentes* were defined as referring to the clades stemming from the most recent common ancestors of the species currently included in those taxa. (The name *Lacertilia*, traditionally applied to a paraphyletic group, would, if defined similarly, be a synonym of *Squamata*.) Under these definitions, the names *Squa-*

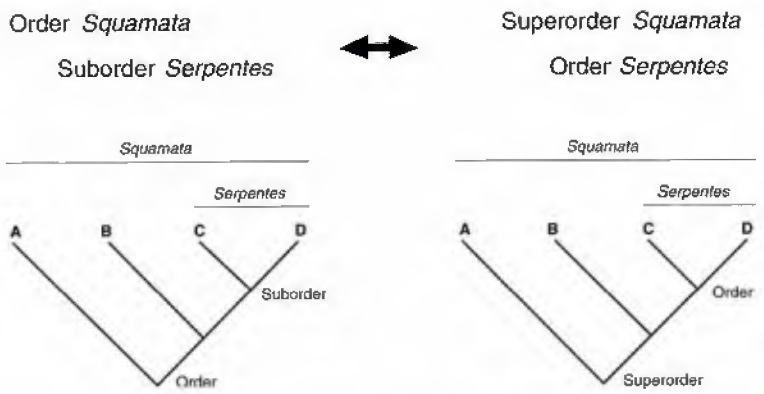

Figure 5. Application of taxon names under phylogenetic nomenclature. In this approach, names are applied according to their phylogenetic definitions, which are independent of categorical ranks. Therefore, the same taxon is designated by the same name regardless of the rank to which it is assigned. In this example, the same two nested taxa are designated by the same names, *Squamata and Serpentes*, regardless of whether they are ranked as an order and a suborder (left) or as a superorder and an order (right). For this example, the names have been defined hypothetically using the following node-based definitions: *Squamata* = the least inclusive clade containing A and C; *Serpentes* = the least inclusive clade containing C and D. The name *Lacertilia*, defined as referring to the least inclusive clade containing A and B, is synonymous with *Squamata* in the context of the phylogenetic hypothesis used in the example. Compare with Figures 1, 2, and 3.

mata and *Serpentes* would remain associated with the same clades (and sets of species) regardless of whether those taxa were ranked as an order and a suborder, a superorder and an order, or anything else. Phylogenetic nomenclature thus applies names similarly to the nomenclatural practices of Linnaeus and other early naturalists, as well as to the current codes for names that are untypified and thus lack implicit rank-based definitions.

The closer association of taxon names with taxa than with ranks under phylogenetic nomenclature also holds for taxon names with terminations connoting particular ranks under rank-based nomenclature (Fig. 6). Consequently, under phylogenetic nomenclature, those endings would no longer have any significance with regard to categorical ranks. For example, taxa with names such as *Chamaeleonidae* and *Aceraceae* might be ranked as families, or they might be ranked as subfamilies, or they might not be ranked at all. Moreover, those names would be applied to the same taxa, all else being equal (i.e. with respect to hypothesized phylogenetic relationships), regardless of their associations with particular categorical ranks (Fig. 6).

Under phylogenetic nomenclature, taxon names will not always remain associated with the same sets of species (de Queiroz and Gauthier 1990, de Queiroz 1997). Changes in the hypothesized composition of taxa can occur under phylogenetic nomenclature just as they can occur under rank-based nomenclature. However, under phylogenetic nomenclature, such changes can occur only when hypotheses about relevant phylogenetic relationships change. In contrast, under rank-based nomenclature, changes in composition can also occur solely as the result of changes in the assignments of taxa to categorical ranks.

The important point is that, relative to the situation under rank-based nomenclature, phylogenetic nomenclature effectively reverses the relative strengths of the associations between taxon names, one the one hand, and ranks versus taxa, on the other. In so doing, phylogenetic nomenclature not only differs from rank-based nomenclature but also resembles nomenclature as practiced by Linnaeus and other late 18th and early 19th Century naturalists. Of course, phylogenetic nomenclature also differs in important ways from the nomenclatural practices of 18th and early 19th Century naturalists. The most obvious and important difference

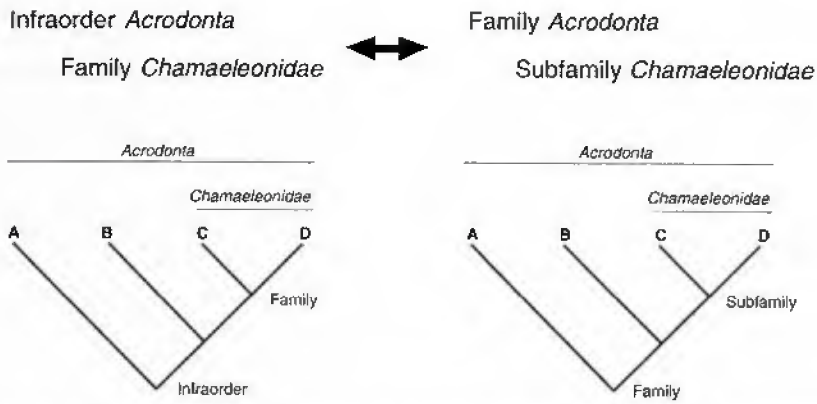

Figure 6. Application of taxon names under phylogenetic nomenclature for cases involving endings that signify rank under rank-based nomenclature. Because taxon names are applied independently of categorical ranks in phylogenetic nomenclature, the standardized, rank-signifying endings of rank-based nomenclature no longer have any significance in terms of ranks. In this example, the names *Acrodonta* and *Chamaeleonidae* remain unchanged regardless of whether the taxa designated by those names are ranked as an infraorder and family (left) or as a family and a subfamily (right). For this example, the names have been defined hypothetically using the following node-based definitions: *Acrodonta* = the least inclusive clade containing A and C; *Chamaeleonidae* = the least inclusive clade containing C and D. Compare with Figures 1, 2, 3, and 5.

is that in 18th and early 19th Century nomenclature, conceptualizations of taxa were non-evolutionary; in phylogenetic nomenclature, they are explicitly evolutionary.

Despite this fundamental difference regarding the conceptualization of taxa, at least some of the taxa recognized by 18th and early 19th Century naturalists correspond closely in terms of their composition with clades. In such cases, names under phylogenetic nomenclature are applied to more or less the same entities, at least in terms of composition. For example, consider the following phylogenetic definitions of the name *Mammalia*: 1) (node-based) the least inclusive clade containing platypuses (*Ornithorhynchus anatinus*), opossums (*Didelphis marsupialis*), and humans (*Homo sapiens*); 2) (stem-based) the most inclusive clade containing humans (*Homo sapiens*) but not birds (e.g. *Aquila chrysaetos*) or turtles (e.g. *Emys orbicularis*) or squamates (e.g. *Lacerta vivipara*); 3) (apomorphy-based) the clade stemming from the first ancestor of humans (*Homo sapiens*) to evolve mammary glands. If any of these three definitions were to be applied in the context of recent estimates of vertebrate phylogeny (e.g. Laurin and Reisz 1995, Novacek 1992) to the species known at the time of Linnaeus (1758), the species of *Mammalia* would be precisely the same as those included in *Mammalia* by Linnaeus.

Conclusion

Phylogenetic nomenclature represents an alternative to traditional rank-based nomenclature. Although rank-based nomenclature is commonly characterized as *Linnaean* (a misleading terminology that I confess to having been partly responsible for perpetuating), phylogenetic nomenclature more closely approximates the nomenclatural practices of Linnaeus and other 18th Century naturalists in granting greater importance to the associations of taxon names with taxa than with categorical ranks. In other words, phylogenetic nomenclature is not so much at odds with true Linnaean nomenclature as it is with the rank-based approach to nomenclature that developed in the 19th Century and came to form the foundation of the original international codes of nomenclature (e.g. ICZN 1905, IBC 1906) and their contemporary descendants (e.g. ICZN 1999, IBC 2000). The critical dif-

ference concerns how the three approaches use categorical ranks.

Given that the primary purpose of a taxon name is to refer to a taxon, then the use of categorical ranks by Linnaeus and other early naturalists was appropriate. For these early naturalists, categorical ranks functioned simply as devices for indicating relative position in the taxonomic hierarchy, serving much the same purpose as a branching diagram, a Venn diagram, or an indented list – that is, to indicate which taxa were considered nested and which mutually exclusive. Taxon names were more strongly tied to taxon concepts than to categorical ranks, and therefore, the assignments of taxa to categorical ranks did not affect the spelling or application of taxon names. Consequently, the categorical rank of a taxon could be changed without requiring a change in the name of the taxon.

In contrast, the use of categorical ranks in rank-based nomenclature is inappropriate; ranks have become too important. Instead of functioning simply as devices for indicating relative position in the taxonomic hierarchy, ranks have become critical to the application and spelling of taxon names. Consequently, changes in the rank of a taxon require changes in the name of that taxon, even when other aspects of the taxon concept remain the same. Thus, regardless of whether taxa are conceptualized in terms of included organisms, diagnostic characters, or phylogenetic relationships, taxon names are more strongly tied to ranks than to taxa. Given that categorical ranks are less biologically significant than are these other properties, this emphasis on ranks is misplaced. It also compromises taxonomic freedom, thus contradicting an explicitly stated goal of the zoological code (ICZN 1999: Preamble). Because one must rank a taxon to name it, the use of ranks has effectively become mandatory.

Phylogenetic nomenclature represents a return to the general nomenclatural approach adopted by Linnaeus and other late 18th and early 19th Century naturalists in which taxon names have their primary associations with taxa, rather than with categorical ranks. On the other hand, phylogenetic nomenclature also differs in at least one important respect from nomenclature as it was practiced by Linnaeus and other 18th Century naturalists. 18th Century nomenclature developed in a non-evolutionary theoretical context, and therefore, its taxon concepts were non-evolutionary. In contrast, taxon concepts in phylogenetic nomenclature are explicitly evolutionary.

Phylogenetic nomenclature thus combines both Linnaean and modern components. On the one hand, it embodies the general approach of Linnaeus and his immediate successors, who treated categorical ranks merely as devices for representing hierarchical relationships that had no bearing on the application of taxon names. On the other hand, it embraces the most important theoretical development in biology since the time of Linnaeus – the principle of evolution, or descent with modification – which it uses to specify the references of taxon names under modern evolutionary concepts of taxa. In short, phylogenetic nomenclature represents Linnaean wisdom updated with evolutionary principles, and it therefore provides a fitting tribute to Linnaeus on the 250th anniversary of his *Species Plantarum*.

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