Biological Nomenclature from Linnaeus to the PhyloCode

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Abstract. 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 those early naturalists, ranks functioned merely as devices for indicating hierarchical position that did not affect the application or spelling 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 class. During the 19th Century, an alternative approach to nomenclature emerged that made rank assignment fundamental to the application and spelling of taxon names. Under this rank-based approach, which forms the basis of the current Zoological Code, names are implicitly defined in terms of ranks. As a consequence, names are more strongly associated with ranks than with taxa and thus taxa change their names simply because of changes in rank. For example, if the rank of the taxon *Iguanidae* is changed from family to superfamily, its name must change to *Iguanoidea*. A new approach to nomenclature, termed phylogenetic nomenclature, ties taxon names to explicitly evolutionary concepts of taxa through definitions that describe taxa in terms of ancestry and descent. This tree-based approach to nomenclature once again associates taxon names more strongly with taxa than with ranks and thus represents a return to an approach similar to that practiced by Linnaeus and other early naturalists, updated with evolutionary principles.

Keywords: Linnaeus, names, nomenclature, phylogeny, ranks, taxa, taxonomy.

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INTRODUCTION

In this paper, I will present a brief overview of general approaches to biological nomenclature, from Linnaeus to the present, including a controversial new approach called phylogenetic nomenclature and an alternative code based on it, commonly known as the PhyloCode. Both in the popular press and in the scientific literature, the PhyloCode is often characterized as a challenge to the "Linnaean System." For this reason, describing and indeed endorsing this approach in a symposium celebrating the legacy of Linnaeus may seem out of place. However, I will argue that contrary to common characterizations, phylogenetic nomenclature and the PhyloCode represent, in at least one very important respect, a return to the nomenclatural practices of Linnaeus and other early taxonomists.

To make this case, I will first describe nomenclature as practiced by Linnaeus and other early taxonomists. I will then describe the rank-based approach to nomenclature that emerged in the century after Linnaeus and came to form the basis of the current Zoological Code. And finally, I will describe the recently proposed phylogenetic approach to nomenclature that underlies the PhyloCode. In each case, I will discuss (using herpetological examples) the relationships between taxon names, on the one hand, and taxa versus categorical ranks, on the other, for the purpose of comparing

the three approaches. I should also note that I have published the main ideas presented in this paper previously (de Queiroz, 2005) and have agreed to revisit them here at the request of the symposium organizers.

LINNAEAN NOMENCLATURE

I will use the term "Linnaean nomenclature" to refer to the general approach to nomenclature practiced by Linnaeus. This general approach should not to be confused with the taxon names used by Linnaeus, which is Linnaean nomenclature in a different sense. More importantly, it should not be equated with nomenclature as currently practiced, as I will explain below. I should also clarify that when I refer to Linnaean nomenclature, I am really referring to nomenclature not only as it was practiced by Linnaeus but also as it was practiced by late 18th and early 19th Century naturalists generally—specifically, to nomenclature as it was practiced after the use of categorical ranks became widespread (following Linnaeus) but before the alternative rank-based approach emerged in the mid 19th Century.

Most readers will be familiar with the so-called Linnaean hierarchy, the series of taxonomic categories or categorical ranks instituted by Linnaeus and elaborated upon by subsequent taxonomists. Linnaeus himself used only five ranks consistently: kingdom, class, order, genus, and species (variety was used only in some cases). Subsequent taxonomists added both primary ranks, such as phylum and family, as well as secondary ranks formed by adding rank-modifying prefixes to the primary ranks, resulting in ranks such as subclass, infraorder, and superfamily. Most readers will also know that these categorical ranks were, and still are, used to help indicate position in the taxonomic hierarchy—that is, which groups are nested and which are mutually exclusive.

Relationships between Taxon Names, Taxa, and Categorical Ranks under Linnaean Nomenclature

Although Linnaeus and other early naturalists used ranks to convey taxonomic (hierarchical) relationships, they did not use ranks for nomenclatural purposes. As a consequence, taxon names were more closely associated with taxa than they were with ranks. The evidence supporting this proposition concerns how changes in the assignments of taxa to different ranks affected the names of those taxa, and the relevant cases are those in which different authors recognized the same taxon but assigned that taxon to different categorical ranks. Ideally, these would be examples of how Linnaeus applied names to taxa that had been recognized by previous authors but assigned those taxa to different categorical ranks. However, most authors prior to Linnaeus did not make extensive use of categorical ranks; that was one of Linnaeus's innovations. Therefore, the relevant comparisons are those involving taxa that were recognized both by Linnaeus and by subsequent authors who assigned those taxa to different categorical ranks. In keeping with the theme of the symposium and the taxonomic emphasis of this journal, I will use herpetological examples.

The first concerns the taxon that Linnaeus, in some of the early editions of his *Systema Naturae* (e.g., Linnaeus, 1735, 1740, 1748) recognized for a group composed of turtles, frogs, lizards, crocodylians, salamanders, and snakes. Linnaeus ranked this taxon as a class, and he named it *Amphibia*. Later, Merrem (1820) recognized the same taxon but assigned it to a higher categorical rank. Although Merrem did not state the exact rank of *Amphibia*, that rank can be inferred to have been above the rank of class, given that the two primary subgroups of *Amphibia* (*Pholidota* and *Batrachia*) were ranked as classes. The relevant point is that Merrem used the same name used by Linnaeus,

Amphibia, despite assigning the group to a different categorical rank.

In later editions of the *Systema Naturae* (1758, 1766–8), Linnaeus recognized a taxon of a somewhat different composition as *Amphibia*, adding various (mostly cartilaginous) "fishes" to the original set of organisms and again ranking it as a class. Later, Scopoli (1777) recognized the same taxon but assigned it to the rank of tribe. Despite the difference in rank, Scopoli used the same name, *Amphibia*, for this taxon.

To cite a final example, Linnaeus (1748, 1758, 1766–8) recognized a group composed of lizards, crocodylians, salamanders, frogs, and turtles (but not snakes or any fishes) as a subgroup of *Amphibia*. He ranked this taxon as an order and called it by the names *Reptilia* and *Reptiles*. Scopoli (1777) once again recognized the same taxon, but ranked it as a division rather than an order. Despite this difference in rank, he used the same name, *Reptilia*. Most other late 18th and early 19th Century authors who used the name *Reptilia* or *Reptiles* (e.g., Laurenti, 1768; Daudin, 1802–1803; 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*, ranking it as a class. The fact that these other authors ranked *Reptilia* as a class, while Linnaeus ranked it as an order, did not prevent them from using the same name.

These examples illustrate that among Linnaeus and his immediate followers, different authors often recognized the same taxa (groups) but assigned them to different categorical ranks, and that when they did this, they often used the same names. This situation constitutes evidence that taxon names were more closely associated with taxa than they were with categorical ranks—a point that should become clearer when we consider an alternative approach to nomenclature that emerged during the century after Linnaeus.

RANK-BASED NOMENCLATURE

I will use the term "rank-based nomenclature" for an approach to nomenclature based on categorical ranks. Under this approach, taxon names are linked to particular ranks, and rank assignment is therefore necessary for the application of those names. The rank-based approach emerged during the middle of the 19th Century, becoming well established roughly 100 years after the publication of the tenth edition of Linnaeus' *Systema Naturae* (1758). It is important to recognize that although this approach is based on the taxonomic ranks introduced by Linnaeus, it differs significantly from the nomenclatural approach adopted by Linnaeus and his immediate followers. The rank-based approach underlies the current nomenclatural codes, including the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature [ICZN], 1999), which are therefore more appropriately designated "rank-based" rather than "Linnaean."

The rank-based approach is used for all names whose application is most closely governed by the rank-based codes. In zoology, this means all names associated with the ranks from subspecies to superfamily (i.e., names in the species, genus, and family groups). It is most obvious, however, for the subset of those names from subtribe to superfamily, which are formed using standardized rank-specific or rank-signifying suffixes. Table 1 is a list of the standardized, rank-signifying endings used in zoology. It is important to note that standardized, rank-signifying endings were not used by Linnaeus and other 18th and early 19th Century naturalists. For example, some of the names of taxa that Linnaeus ranked as classes ended in *-ia*, others in *-es*, and still others in *-a*. In addition, these same endings were also used for the names of taxa ranked as orders. In short, particular endings were not used exclusively and universally in association with particular categorical ranks, the way they are today. The

TABLE (1). The Standardized Rank-signifying Endings used by the Rank-based Zoological Code (ICZN, 1999, Art. 29.2). Note that the rank-based approach applies to names associated with all ranks from subspecies to superfamily in zoology, not only to those with standard rank-signifying endings.

Categorical Rank	Ending	Example
Superfamily	*–oidea*	*Iguanoidea*
Family	*–idae*	*Iguanidae*
Subfamily	*–inae*	*Iguaninae*
Tribe	*–ini*	*Iguanini*
Subtribe	*–ina*	*Iguanina*

standardized, rank-signifying endings were introduced sometime during the early middle of the 19th Century. I have not researched their history thoroughly, but consistent use of the *-idae* ending for zoological taxa ranked as families can be found as early as 1825 in a paper by the herpetologist J. E. Gray, and this practice was endorsed as a general rule as early as 1835 by W. Swainson. It was also adopted by some of the important precursors of the modern rank-based codes, such as the Stricklandian code in zoology (Strickland et al., 1843). Most importantly, it was adopted by the original international codes of both botanical and zoological nomenclature and all of their subsequent revisions.

The use of standardized, rank-signifying endings implies a method of definition (i.e., of specifying the reference of a taxon name so that it can be applied in the context of alternative taxonomic proposals) that is strongly tied to the taxonomic ranks. Although this definitional method is not stated explicitly in the rank-based codes, it can nevertheless be inferred from the manner in which names are applied in rank-based nomenclature. The method takes the following form: [taxon name] = the taxon assigned to the rank of [rank name] that includes [name of type]. For example, the taxon name *Iguanidae* is implicitly defined as the taxon assigned to the rank of family that includes the genus *Iguana*. Although this definitional method is most apparent in the case of names with standardized, rank-signifying suffixes, it also applies to names associated with ranks below those having standardized, rank-signifying suffixes—that is, to names associated with ranks from supergenus to subspecies.

Relationships between Taxon Names, Taxa, and Categorical Ranks under Rank-based Nomenclature

The adoption of rank-based nomenclature led to a significant change in the relationships between taxon names, on the one hand, and taxa versus ranks, on the other. As demonstrated above, earlier nomenclatural practices granted more importance to the associations of taxon names with taxa, rather than ranks. In contrast, the rank-based approach reversed the relative importance of those associations. Greater importance was effectively placed on the associations of names with ranks, rather than with taxa. This situation is evident from the way that rank-based nomenclature works, as illustrated in the example in Figure 1.

Suppose we have three taxa, an inclusive group named *Acrodonta*, ranked as a suborder, and two subgroups named *Agamidae* and *Chamaeleonidae*, ranked as families (Fig. 1a). Now suppose that later the same taxa are assigned to different ranks: the inclusive group is demoted in rank from suborder to family and its subgroups are lowered in rank from family to subfamily (Fig. 1b). Under rank-based nomenclature, such a change in ranks would require changing the names of the three taxa to reflect the new ranks. For example, the taxon originally

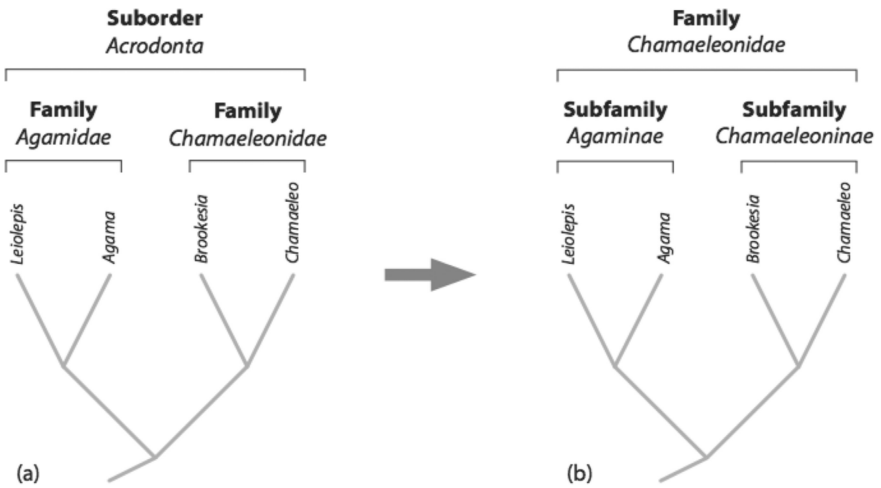

FIGURE 1. The Effects of Changes in Ranks under Rank-based Nomenclature. When the ranks of the three taxa are changed from suborder and family (a) to family and subfamily (b), the names of all three taxa must change to reflect the new ranks. Note that these changes occur even when the hypothesized composition of the taxa remains unchanged (as in this example).

named *Chamaeleonidae* (with a *d*) would have to change its name to *Chamaeleoninae* (with an *n*), to reflect its new rank of subfamily. The change would be more severe in the case of the inclusive taxon, which would have to change from *Acrodonta* to *Chamaeleonidae*. In addition to the taxa changing their names, the names would also change their references. For example, the name *Chamaeleonidae*, which originally applied to one of the two less inclusive taxa, would have to be applied to the more inclusive taxon under the new ranks.

This example illustrates that under rank-based nomenclature, taxon names are more closely associated with categorical ranks than they are with taxa. When the ranks of taxa are changed, taxon names retain their associations with the original ranks, rather than retaining their associations with the original taxa. This situation implies that the rank-based system effectively treats the rank of a taxon as though it is more important to the concept of that taxon than are ideas about properties such as composition, diagnostic characters, or phylogenetic relationships. It is therefore inconsistent with the widespread opinion among biologists that the rank of a taxon is less significant than are those other properties.

Non-rank-based Contemporary Nomenclature

Oddly, not all of contemporary nomenclature is rank-based. At least some contemporary names are applied in a manner that is more similar to the manner in which Linnaeus and other early naturalists applied them. In both botany and zoology, the application of certain names is not based on ranks, and those names, like those of 18th Century biology, are more closely associated with taxa than with ranks. In zoology, this is true for names above the rank of superfamily, which have neither standardized, rank-signifying suffixes nor implicit rank-based definitions. Consider the case of "*Lacertilia*" (lizards, now known to be a paraphyletic group), *Serpentes* (snakes, which render lizards paraphyletic when treated as a mutually exclusive taxon), and *Squamata*, a more inclusive group containing both "*Lacertilia*" and *Serpentes*. Before the paraphyletic "*Lacertilia*" was abandoned (in truth, this process has not yet been completed), some authors ranked these three taxa as two suborders within an order (e.g., Romer, 1956, 1966; Kuhn, 1966; Carroll, 1988), while others ranked them as two orders within a superorder

(e.g., Gans, 1978; Estes, 1983; Underwood, 1967, 1971). However, because all of these ranks are above the level of superfamily, application of the names was not based on ranks but on composition and diagnostic characters. As a consequence, the taxa retained the same names regardless of which ranking scheme was adopted.

PHYLOGENETIC NOMENCLATURE

The term "phylogenetic nomenclature" has been applied to a nomenclatural approach based on evolutionary principles. This approach ties taxon names to explicitly phylogenetic concepts of taxa using methods that describe taxa in terms of common ancestry and descent. Phylogenetic nomenclature is a relatively new approach that was first proposed in the late 20th Century. Given the theme of the symposium and the taxonomic focus of this journal, it is worth noting that this approach was first proposed by herpetologists (e.g., Gauthier et al., 1988; Estes et al., 1988; de Queiroz and Gauthier, 1990, 1992, 1994). In any case, the methods of phylogenetic nomenclature are inherently tree-based in that they require phylogenetic trees (or some analogous method for describing or representing phylogenetic relationships) for their application. Phylogenetic nomenclature forms the basis of the draft Phylogenetic Code or PhyloCode (Cantino and de Queiroz, 2010), a nomenclatural code currently under development that represents an alternative to the rank-based codes such as the Zoological Code (ICZN, 1999).

Similarities to Rank-based Nomenclature

Before discussing the relationships between names, taxa, and ranks in phylogenetic nomenclature, I want to describe a few general things about this approach, which may be unfamiliar to some readers. Importantly, phylogenetic nomenclature shares several basic goals and methods with rank-based nomenclature. For example, both approaches have the same fundamental goals of promoting nomenclatural clarity and stability, to the extent that doing so does not interfere with the representation of new taxonomic conclusions. Both approaches accomplish this goal by providing unambiguous methods for applying names to taxa and for selecting a single accepted name for each taxon as well as a single accepted referent taxon for each name. Neither approach 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). Furthermore, both approaches use precedence, a clear order of preference, to determine the accepted name of a taxon when synonyms or homonyms exist. Both use priority, the earliest date of publication, as the primary criterion for establishing precedence. And both phylogenetic and rank-based approaches allow a later-established name to be conserved over an earlier-established one—that is, for priority to be set aside—if using the earlier name contradicts the fundamental goal of promoting nomenclatural stability and continuity.

Differences from Rank-based Nomenclature

The main difference between phylogenetic and rank-based nomenclature concerns the methods for applying names to taxa under the alternative systems. As described above, rank-based nomenclature uses implicit definitions that are stated in terms of taxonomic ranks. In contrast, phylogenetic nomenclature uses explicit definitions that are stated in terms of ancestry and descent, or their products, clades. Figure 2 illustrates the three most general kinds of phylogenetic definitions—termed *node-based*, *branch-based*, and *apomorphy-based*—and how they relate to the components of phylogenetic trees. For example, in the case of a node-based definition, a taxon

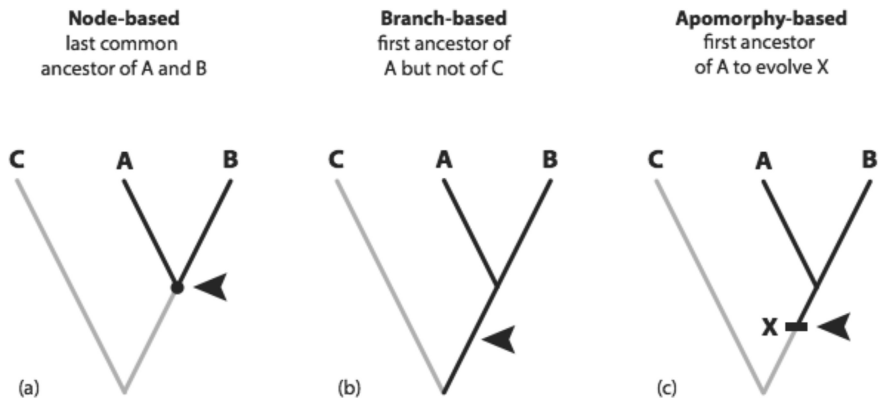

FIGURE 2. Three General Types of Phylogenetic Definitions. A node-based definition (a) associates a name with the clade originating with the last common ancestor of two or more specified species or organisms (A and B in this example). A branch-based definition (b) associates a name with the clade originating with the first ancestor of one (or more) specified species or organisms (A) that is not an ancestor of one or more other specified species or organisms (C). An apomorphy-based definition (c) associates a name with the clade originating with the first ancestor of a specified species or organism (A) to evolve a specified derived character state (X). Arrows point to the node (a), branch (b), and apomorphy (c) specified by the three definitions.

name is defined as referring to the clade originating with the most recent common ancestor of two or more specified species or organisms (labeled A and B in Fig. 2, where the definition is stated in an alternative, more economical, form). As should be evident from this description, the methods of phylogenetic nomenclature are based on trees. In this respect, phylogenetic nomenclature is part of a general trend in biology towards more explicitly tree-based methods (e.g., O'Hara, 1988; Donoghue, 1989; Harvey et al., 1995).

Relationships between Taxon Names, Taxa, and Categorical Ranks under Phylogenetic Nomenclature

As a consequence of its explicitly tree-based methods, taxon names under phylogenetic nomenclature are more closely associated with taxa (conceptualized as clades or monophyletic groups) than with categorical ranks. This situation is demonstrated by the fact that when taxa are assigned to different categorical ranks (all else being equal), taxon names remain associated with the same taxa—that is, they do not change their associations from one taxon to another in order to remain associated with the same ranks, as in rank-based nomenclature.

An example is given in Figure 3, which uses the same taxa, names, and ranks as the example illustrating the effect of changes in rank under rank-based nomenclature (Fig. 1). In this example, the original names (Fig. 3a) have been defined hypothetically using phylogenetic definitions employing species included within the named taxa as reference points (which are called *specifiers* in the terminology of phylogenetic nomenclature and function roughly analogously to the name-bearing types of rank-based nomenclature). The two diagrams (Fig. 3a and 3b) indicate changes in ranks without any changes in ideas about phylogenetic relationships. In one case, the two taxa (clades) are ranked as a suborder and two families (Fig. 3a); in the other, as a family and two subfamilies (Fig. 3b). If the stated definitions are applied in the context of these two ranking schemes, the same names are applied to the same clades. This is to be expected given that the application of names under phylogenetic nomenclature depends on

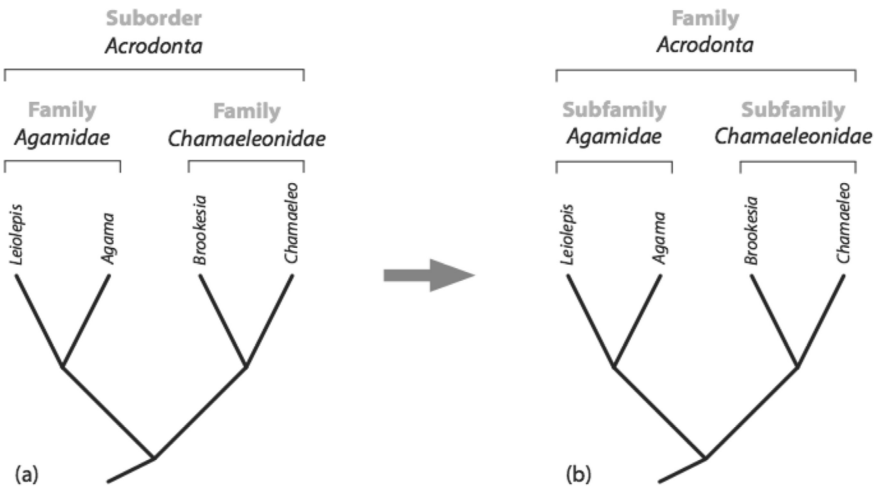

FIGURE 3. The (Absence of) Effects of Changes in Ranks under Phylogenetic Nomenclature. This example uses the same taxa and ranking schemes used to illustrate the effects of changes in ranks under rank-based nomenclature (Fig. 1). However, rather than applying the names using implicit rank-based definitions, the names are applied using the following phylogenetic definitions (based on species originally included in the taxa): *Agamidae* = the least inclusive clade containing both *Leiolepis guttata* and *Agama agama*; *Chamaeleonidae* = the least inclusive clade containing both *Brookesia superciliosa* and *Chamaeleo chamaeleon*; *Acrodonta* = the least inclusive clade containing both *Agama agama* and *Chamaeleo chamaeleon*. When the ranks of the three taxa are changed from suborder and family (a) to family and subfamily (b), the names of all three taxa remain unchanged because the application of names is based on phylogenetic relationships (which have not changed) and is independent of ranks. Compare this example with the same example under rank-based nomenclature (Fig. 1), in which the names of all three taxa change.

phylogenetic relationships, not on ranks, and the tree topologies are identical. The important point is that the names retain their associations with the same taxa, not with the same ranks.

Thus, when only ranks change, and ideas about more significant biological properties (e.g., phylogenetic relationships, hypothesized composition) do not, names in phylogenetic nomenclature remain associated with the same taxa. In this important respect, phylogenetic nomenclature is like Linnaean nomenclature, but unlike rank-based nomenclature. In other words, both phylogenetic nomenclature and nomenclature as it was practiced in the time of Linnaeus grant more importance to the associations of taxon names with taxa, rather than with ranks, which is exactly opposite to the situation in rank-based nomenclature.

Changing Ideas about Phylogenetic Relationships

In the example presented in the previous section, ideas about phylogenetic relationships were held constant. If ideas about phylogenetic relationships change, then the composition of the taxon to which a particular name is applied can also change. This is the case regardless of whether names are governed by rank-based or phylogenetic nomenclature. Under phylogenetic nomenclature, however, such changes occur in ways that make more sense with respect to the associations between names and taxa (Figure 4).

For example, suppose that the taxon *Agamidae* was found to be paraphyletic relative to *Chamaeleonidae*—that *Agama* was found to share a more recent common ancestor with *Brookesia* and *Chamaeleo* than with *Leiolepis*

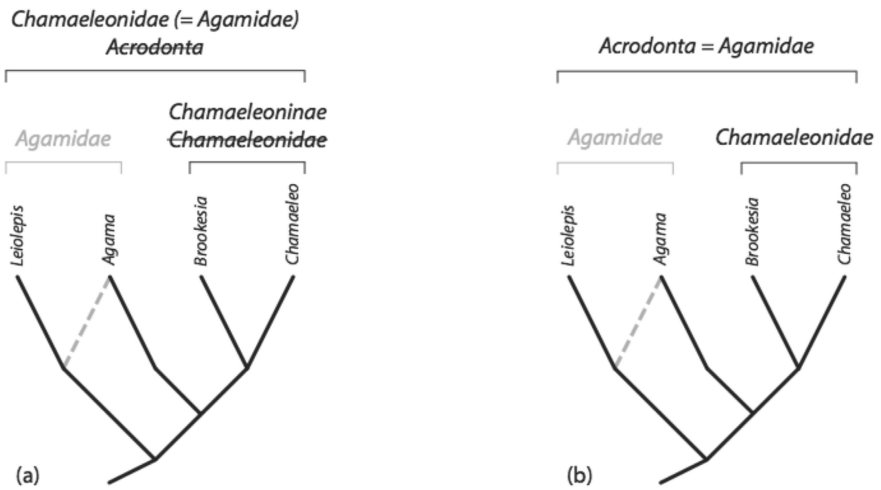

FIGURE 4. The Effect of Changes in Hypotheses about Phylogenetic Relationships under Rank-based (a) and Phylogenetic (b) Nomenclature. In both diagrams, grey dashed lines indicate that *Agama* was inferred to share a more recent common ancestor with *Leiolepis* than with *Brookesia* and *Chamaeleo* under an earlier phylogenetic hypothesis, while black solid lines indicate that *Agama* is inferred to be more closely related to *Brookesia* and *Chamaeleo* than to *Leiolepis* under a later hypothesis. Under rank-based nomenclature (a), one way to eliminate the paraphyletic taxon *Agamidae* (grey) would be to unite the two families into a single family, which would be called *Chamaeleonidae* according to the principle of priority. This action causes both taxa that are still considered monophyletic to change their names. Under phylogenetic nomenclature (b), using the same definitions as in Figure 3, the name *Agamidae* would become a synonym of *Acrodonta*. Although precedence has not been established for these two names, if *Acrodonta* had precedence, then neither of the taxa with the same hypothesized composition would change their names. Even if *Agamidae* had precedence, that name would make more sense as the name of the inclusive clade than would *Chamaeleonidae* given that the new phylogenetic hypothesis implies that *Chamaelonidae* is derived from within *Agamidae* rather than the reverse.

(Fig. 4). Given the principle that scientific names are to be given only to monophyletic (as opposed to paraphyletic) taxa, a possible solution under rank-based nomenclature is to unite (lump) the two original families, *Agamidae* and *Chamaeleonidae*, into a single family (Fig. 4a). If this were to be done, then the names *Agamidae* and *Chamaeleonidae* would become synonyms, because both names would then refer to the same taxon. The official name of that taxon would be *Chamaeleonidae*, because that name has priority (i.e., a family-group name based on the genus *Chamaeleo* was published before a family-group name based on the genus *Agama*). This outcome makes little sense given that 1) the inclusive group already has a name, *Acrodonta*, 2) the smaller group to which the name *Chamaeleonidae* was previously applied is still thought to be monophyletic but now must be given a new name, and 3) the new phylogenetic hypothesis implies (under the original ranking scheme) that *Chamaeleonidae* is derived from within *Agamidae*, but the name change implies the opposite (in that all former agamids would now be considered subgroups of *Chamaeleonidae*).

Phylogenetic nomenclature handles the same situation in a way that makes more sense with respect to the references of names (Fig. 4b). Using the same definitions adopted in Figure 3 in the context of the new phylogenetic hypothesis, the names *Agamidae* and *Acrodonta* (rather than *Agamidae* and *Chamaeleonidae*) both apply to the inclusive clade and therefore become synonyms. Although precedence of *Acrodonta* versus *Agamidae* has not been established (because the PhyloCode is not yet in operation), either name makes more

sense as the name of the inclusive clade than does *Chamaeleonidae—Acrodonta* because it was previously applied to that clade, and *Agamidae* because the new phylogenetic hypothesis implies that the composition formerly associated with that name referred to a paraphyletic group originating with the same ancestor (i.e., that chamaeleonids are derived from within *Agamidae*). In addition, the name *Chamaeleonidae* is applied to the same clade to which it had been applied previously. Phylogenetic nomenclature thus preserves the associations between names and taxa better than does rank-based nomenclature not only in cases in which only ranks change but also in cases in which both hypothesized relationships and ranks change.

CONCLUSIONS

Phylogenetic nomenclature is a new approach that connects taxon names to evolutionary concepts of taxa by specifying the references of names in terms of common ancestry relationships. As a consequence, taxon names are more strongly tied to taxon concepts than to categorical ranks. In this respect, phylogenetic nomenclature resembles nomenclature as practiced by Linnaeus and other early naturalists but differs from the rank-based approach to nomenclature that underlies the current codes. Of course, phylogenetic nomenclature also differs in one very important respect from nomenclature as practiced by Linnaeus and other 18th Century naturalists. Those early naturalists practiced nomenclature in the context of a non-evolutionary world-view, and consequently, their taxon concepts were also 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 wisdom of Linnaeus and his immediate successors, who treated ranks merely as devices for representing hierarchical relationships that had no bearing on the application or spelling 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 (common descent)—which it uses to specify the referents of taxon names in accord with modern concepts of taxa. Thus, rather than representing a challenge to the Linnaean approach to biological nomenclature, phylogenetic nomenclature represents Linnaean wisdom updated with evolutionary principles. It therefore extends the legacy of Linnaeus and provides a fitting tribute on the tercentenary of his birth.

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REFERENCES

Cantino, P. D., and K. de Queiroz. 2010. International Code of Phylogenetic Nomenclature. Version 4c. http://www.ohiou.edu/phylocode/.

Carroll, R. L. 1988. Vertebrate Paleontology and Evolution. W. H. Freeman and Co., New York.

Daudin, F. M. 1802–1803. Histoire naturelle, générale et particulière, des reptiles. Imprimerie de F. Dufart, Paris.

de Queiroz, K. 2005. Linnaean, rank-based, and phylogenetic nomenclature: Restoring primacy to the link between names and taxa. Symbolae Botanicae Upsaliensis 33:127–140.

de Queiroz, K., and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. Systematic Zoology 39:307–322.

de Queiroz, K., and J. Gauthier. 1992. Phylogenetic taxonomy. Annual Review of Ecology and Systematics 23:449–480.

de Queiroz, K., and J. Gauthier. 1994. Toward a phylogenetic system of biological nomenclature. Trends in Ecology and Evolution 9:27–31.

Donoghue, M. J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. Evolution 43:1137–1156.

Estes, R. 1983. *Sauria terrestria*, *Amphisbaenia*. Handbuch der Paläoherpetologie 10A:1–249.

Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within *Squamata*. Pp. 119–281 *In*: R. Estes and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families, Stanford University Press, Stanford, California.

Gans, C. 1978. The characteristics and affinities of the *Amphisbaenia*. The Transactions of the Zoological Society of London 34:347–416.

Gauthier, J., R. Estes, and K. de Queiroz. 1988. A phylogenetic analysis of *Lepidosauromorpha*. Pp. 15–98 *In*: R. Estes and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families, Stanford University Press, Stanford, California.

Gray, J. E. 1825. A synopsis of the genera of *Reptiles* and *Amphibia*, with a description of some new species. Annals of Philosophy 10:193–217.

Harvey, P. H., A. J. Leigh Brown, and J. Maynard Smith, eds. 1995. New uses for new phylogenies. Philosophical Transactions of the Royal Society of London B, Biological Sciences 349:1–118

International Commission on Zoological Nomenclature (ICZN). 1999. International Code of Zoological Nomenclature. Fourth edition. International Trust for Zoological Nomenclature, London.

Kuhn, O. 1966. Die Reptilien. System und Stammesgeschichte. Verlag Oeben, München (Munich).

Lamarck, J. B. 1809. Philosophie Zoologique. Chez Dentu, Paris. English translation, Zoological Philosophy, published 1984 by The University of Chicago Press, Chicago.

Laurenti, J. N. 1768. Specimen Medicum, Exhibens Synopsin Reptilium Emendatam cum Experimentis circa Venena et Antidota Reptilium Austriacorum. Joan. Thomae Nob. de Trattnern, Viennae (Vienna).

Linnaeus, C. 1735. Systema Naturae, sive Regna Tria Naturae Systematice Proposita per Classes, Ordines, Genera, & Species. First edition. Theodorum Haak, Lugduni Batavorum (Leyden). Facsimile reprinted 1964 by B. de Graff, Nieuwkoop.

Linnaeus, C. 1740. Systema Naturae in quo Naturae Regna Tria, Secundum, Classes, Ordines, Genera, Species, Systematice Proponuntur. Second edition. Gottfr. Kiesewetter, Stockholmiae (Stockholm).

Linnaeus, C. 1748. Systema Naturae Sistens Regna Tria Naturae, in Classes et Ordines Genera et Species Redacta Tabulisque Aeneis Illustrata. Sixth edition. Godofr. Kiesewetteri, Lipsiae (Leipzig).

Linnaeus, C. 1758. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tenth edition. Laurentii Salvii, Holmiae (Stockholm).

Linnaeus, C. 1766–1768. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Twelfth edition. Laurentii Salvii, Holmiae (Stockholm).

Linnaeus, C., and J. F. Gmelin. 1788. Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Regnum Animale. Thirteenth edition. Georg. Emanuel. Beer, Lipsiae (Leipzig).

Merrem, B. 1820. Tentamen Systematis Amphibiorum. Johann Christian Krieger, Marburg.

O'Hara, R. J. 1988. Homage to Clio, or, toward an historical philosophy for evolutionary biology. Systematic Zoology 37:142–155.

Romer, A. S. 1956. Osteology of the Reptiles. The University of Chicago Press, Chicago and London.

Romer, A. S. 1966. Vertebrate Paleontology. Third edition. The University of Chicago Press, Chicago and London.

Scopoli, G. A. 1777. Introductio ad Historiam Naturalem Sistens Genera Lapidum, Plantarum, et Animalium Hactenus Detecta, Caracteribus Essentialibus Donata, in Tribus Divisa, Subinde ad Leges Naturae. Wolfgangum Gerle, Pragae (Prague).

Strickland, H. E., J. Phillips, J. Richardson, R. Owen, L. Jenyns, W. J. Broderip, J. S. Henslow, W. E. Shuckard, G. R. Waterhouse, W. Yarrell, C. Darwin, and J. O. Westwood. 1843. Series of propositions for rendering the nomenclature of zoology uniform and permanent. The Annals and Magazine of Natural History 11:259–275.

Swainson, W. 1835. A Treatise on the Geography and Classification of Animals. Longman, Rees, Orme, Brown, Green, and Longman and John Taylor, London.

Underwood, G. 1967. A Contribution to the Classification of Snakes. Trustees of the British Museum (Natural History), London.

Underwood, G. L. 1971. A modern appreciation of Camp's "Classification of the lizards". Pp. iii–xvii *In*: Camp's Classification of the Lizards. Society for the Study of Amphibians and Reptiles, Facsimile Reprints in Herpetology.