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Species Names in the *PhyloCode*: The Approach Adopted by the International Society for Phylogenetic Nomenclature

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On May 24, 2007, the Committee on Phylogenetic Nomenclature (CPN), which consists of 12 elected members from the International Society for Phylogenetic Nomenclature (ISPN), adopted a new article in the *International Code of Phylogenetic Nomenclature* (*ICPN* or *PhyloCode*; Cantino and de Queiroz, 2007) addressing the naming of species in the context of phylogenetic nomenclature. This vote, which took place after more than 10 years of discussion on how to handle species names in phylogenetic nomenclature, represents a major step in the development of the *PhyloCode*. Until now, the successive drafts of the *PhyloCode* have only dealt with clade names, although the application of phylogenetic nomenclature to species has been heavily debated at workshops and symposia on phylogenetic nomenclature (e.g., Cantino et al., 1999a), in the literature (e.g., de Queiroz and Gauthier, 1992; Graybeal, 1995; Schander and Thollesson, 1995; Cantino, 1998; Cantino et al., 1999a, 1999b; Ereshefsky, 1999; Pleijel, 1999; Pleijel and Rouse, 2000a, 2000b, 2003; Artois, 2001; Hillis et al., 2001; Lee, 2002; Spangler, 2003; Dayrat et al., 2004; Dayrat, 2005; Dayrat and Gosliner, 2005; Fisher, 2006; Wolsan, 2007a, 2007b), and at the two meetings of the ISPN (Laurin and Cantino, 2004, 2006; see the Preface to the *PhyloCode* for additional information). The article on species names (Article 21) that the CPN recently adopted was prepared by the four of us. Here, we wish to explain its rationale and advantages.

POINTS OF INCOMPATIBILITY OF LINNAEAN BINOMINAL SPECIES NAMES WITH PHYLOGENETIC NOMENCLATURE

The Linnaean binominal nomenclature used for species names in the rank-based codes (*Bacterial Code* [*BC*], *International Code of Botanical Nomenclature* [*ICBN*], *International Code of Zoological Nomenclature* [*ICZN*]) is not fully compatible with phylogenetic nomenclature because their requirements regarding ranks differ. Under the rank-based codes, the name of a species is a combination of two words, i.e., a binomen (or binomial), the first part of which is a generic name and the second

part of which is a specific name (*ICZN*) or epithet (*BC*, *ICBN*). The first part of the binomen requires reference to the genus rank, and the second part requires reference to the species rank. The rank-based codes currently allow no exceptions. Contrary to a common misconception, ranks are not prohibited in the *PhyloCode*, but a taxon name is not based on its rank (if any), and use of a particular rank cannot be mandatory. Thus, it is not the use of the genus rank *per se* that is incompatible with the *PhyloCode*, nor is it the use of binomina, but the mandatory use of the genus rank in order to name species and the fact that the species binomen is influenced by ranking (i.e., the first part of the species binomen depends on which taxon is ranked as a genus). Although this incompatibility prevents the combining of Linnaean binomina and phylogenetic nomenclature seamlessly into a single integrated system, Linnaean binomina can be reinterpreted and used in the context of phylogenetic nomenclature in the manner described below.

Beyond phylogenetic nomenclature, the mandatory use of genus names sometimes conflicts with the Hennigian principle that all taxa (or at least supraspecific taxa) must be monophyletic. Systematists currently have to assign every species to a particular genus, even in cases where species cannot be referred with confidence to any clade that has been ranked as a genus (Cantino et al., 1999b; Dayrat 2005; Dayrat and Gosliner, 2005). When naming new species in such situations of phylogenetic uncertainty, there are only two solutions under the rank-based codes, neither of which is desirable from a phylogenetic standpoint: (1) to erect new monotypic genera or (2) to assign species to existing nonmonophyletic or questionably monophyletic genera. Under the former approach, a new nomenclatural entity is created that provides no information about the relationships of the species. Under the latter approach, use of generic names that are known to apply to nonmonophyletic or questionably monophyletic taxa does not accurately communicate phylogenetic information and may perpetuate the misconception that these taxa are monophyletic.

In consideration of these problems, two divergent approaches to species names have been advocated by proponents of phylogenetic nomenclature who also want to use species names: either develop a mechanism to extend phylogenetic nomenclature to species (e.g., Cantino et al., 1999a; Clarke, 2004; Dayrat, et al., 2004) or restrict the *PhyloCode* to clade names, leaving the governance of species names to the rank-based codes (Lee, 2002). Some proponents of phylogenetic nomenclature reject species altogether and would therefore restrict biological nomenclature to clades (Mishler, 1999; Pleijel, 1999; Pleijel and Rouse, 2000a, 2000b; Fisher, 2006), a viewpoint that we do not share. The approach that we ultimately adopted is closest to Lee's (2002) but with some important differences that evolved in the process of drafting an entire code for species names—a document that we, its authors, eventually rejected.

Historical Development

A set of rules governing species names was included in the first draft of the *PhyloCode*, prepared by Philip Cantino and Kevin de Queiroz for the first Workshop on Phylogenetic Nomenclature (Harvard University, August 1998). However, the 27 participants attending the workshop could not reach a consensus on the form that species names should take. Considerable discussion and a vote during the workshop revealed a deep division among the participants on whether species names under the *PhyloCode* should be binomen based or epithet based. In binomen-based methods, species names take the form of a unique binomen, though the first part of the name has no necessary association with the rank of genus; the methods vary in whether the first part of the name can change with changing ideas about relationship (as opposed to being permanently fixed) and in whether the two parts are separated by a symbol (e.g., a hyphen). In epithet-based methods, species names take the form of a uninomen, which, in the case of conversion from existing Linnaean binomina, consists of the specific name (*ICZN*) or epithet (*BC*, *ICBN*) without the genus name. Because uninominal names are not necessarily unique, the uninomen in most epithet-based methods is combined with a number (as part of the name) and/or associated (not as part of the name) with either a registration number or the names of one or more including clades. The distinctions among these various options have been discussed in detail by Cantino et al. (1999a). The deep disagreement on the form of species names at the Harvard workshop led to a decision to restrict the *PhyloCode* temporarily to clade names, and the first publicly available version of the *PhyloCode* (April 2000; available at http://www.phylocode.org) dealt only with clade names.

The governance of species names was again a major topic of discussion at the Second Workshop on Phylogenetic Nomenclature (Yale University, July 2002), where opinions ranged widely: some participants arguing that species names should never be governed by the *PhyloCode*, and others maintaining that their inclusion is so critical that the code should not be implemented until expanded to cover species. The majority held the intermediate position that species names should eventually be included in the *PhyloCode*, but that the controversy surrounding species names should not delay implementation of the rules for clade names. Thus, it was decided at the 2002 workshop that rules for clade names and for species names would be published in separate documents and that the timing of implementation of the two documents would be independent, with implementation of the rules for clade names likely preceding those for species names.

Apart from these practical questions, the period from 1998 to 2003 saw intense theoretical and philosophical discussions on the status of species in phylogenetic nomenclature. Mishler (1999) argued that species are not fundamentally distinct from clades, that the species is simply a rank, and that species should not therefore be

treated any differently than other clades nomenclaturally. Along the same lines, Pleijel (1999) and Pleijel and Rouse (2000a, 2000b, 2003) argued against the comparability among, and utility of, species taxa and introduced the Least Inclusive Taxonomic Unit (LITU) concept for the least inclusive clades to which individual organisms can be referred. In contrast, de Queiroz (1998, 1999) argued that species and clades are fundamentally different kinds of entities, the former being a segment of a single population lineage, while a clade includes all of the lines of descent from a given ancestor. If species and clades are different kinds of entities, they also should be nomenclaturally distinct.

At the First Meeting of the ISPN (Paris, July 2004), enthusiasm for developing a species code was rekindled as a result of ideas presented by Dayrat and Clarke. The majority of the participants supported a proposal for development of a species code, separate from but compatible with the code for clade names. It was proposed that this code be drafted by the four of us and that it incorporate the following components from the talks of Dayrat and Clarke, respectively: (1) an epithet-based form of species name in which the specific name (*ICZN*) or epithet (*BC*, *ICBN*) is combined with the author's name, the publication date, and the page number of the original publication (Lanham, 1965; Schander and Thollesson, 1995; Dayrat et al., 2004; Dayrat, 2005; Dayrat and Gosliner, 2005); and (2) a general method for defining species names (de Queiroz, 1992) that uses a single internal specifier, is agnostic with respect to alternative species concepts (Clarke, 2004), and permits establishment of new species names that would also be validly published and available under rank-based codes (Clarke, 2004). Soon after the Paris meeting, Cantino and de Queiroz revised the rules governing species names that they had written prior to the 1998 Harvard Workshop and sent the revision to Clarke and Dayrat. A series of written exchanges followed, which raised serious concerns about the feasibility and advisability of implementing this species code. The four of us then met on May 20–21, 2006, at the National Museum of Natural History in Washington, DC, to address these concerns, which led to a realization that species names might be dealt with in a different way. Because the following issues led to the current mechanism for dealing with species names, we review them below.

Problems Encountered with the Development of a Separate Species Code

Coexistence of Two Species Nomenclatures

Perhaps the most serious drawback to developing a new species code would have been the coexistence of two different scientific names for every named species, given that the draft species code adopted Lanham's (1965) epithet-based form of species name. For example, if the code we had been drafting were to be implemented, the brown bear species would then have two accepted scientific names: *Ursus arctos* under the *ICZN*, and *arctos* Linné, 1758:47 under the *PhyloCode*. This situation would cause confusion both within the scientific community and among other users of species names. (In contrast, phylogenetic nomenclature does not propose to change the names of clades [de Queiroz and Cantino, 2001], and the *PhyloCode* explicitly endorses the use of existing clade names [e.g., Art. 10.1]. Consequently, many clades will have the same name under the *PhyloCode* and the appropriate rank-based code.)

The existence of different sets of rules for naming species under the rank-based and phylogenetic systems might lead to even greater differences between species names under the two systems. The problem arises because newly created epithet-based species names (e.g., *californica* Martínez, 2010:3) would not necessarily satisfy the requirements of the rank-based codes. For example, the *ICBN* (Articles 32.1 and 23.1) requires that a specific epithet be combined with a genus name for a species name to be validly published. Similarly, the name would not be available under the *ICZN*, where "A species-group name must be published in unambiguous combination with a generic name (either explicit, or implicit by context)" (Article 11.9.3). Therefore, if the *PhyloCode* were to adopt its own rules for species names, with a form for these names and rules for their establishment that are incompatible with those of the rank-based codes, authors operating under one of the rank-based codes might decide to rename species previously named under the *PhyloCode*, possibly even with a different epithet. This undesirable outcome would further confuse users of species names.

Publication and Registration of Converted Species Names

Under the *PhyloCode*, conversion of existing clade names (i.e., establishing them according to the rules of the *PhyloCode*) requires that the converted name be published and registered in an electronic database that will be implemented with the code. Extending this requirement to the 1.5 to 1.8 million existing species names (Wilson, 2003) would be prohibitively time consuming. Were it to be attempted, there would be a considerable interval of time during which most species names would not be registered and valid under this code. Alternatively, permitting conversion of species names without publication and registration might be considered, but doing so would introduce an inconsistency between the way clade and species names are treated, and the registration database is considered by many to be a highly useful element of the *PhyloCode* project.

The Form of Species Names

Despite many advantages (Dayrat et al., 2004), an epithet-based approach similar to Lanham's method (including author, publication year, and page number as part of the species name), which was used in our draft species code, also has several drawbacks (Wolsan, 2007). For instance, because many people find numbers more difficult to remember than words, the year and page numbers are likely to be omitted in spoken communication, which could lead to confusion when the same epithet is used in different species names.

Infraspecific Taxa

We were also uncertain how to address names of infraspecific taxa. Some such taxa may be clades within species, in which case they can be named like any other clade using the *PhyloCode* (the specifiers would have to be specimens rather than species, but this is permitted). Other infraspecific taxa may be partially distinct species, and the naming of these entities is problematical. Requiring that they be treated as ranked taxa within species would be inconsistent with the lack of mandatory ranks in the *PhyloCode*. Alternatively, these entities could be named as species, thus permitting species to be nested within species (de Queiroz, 2005), a radical departure from the traditional view that every organism belongs to only one species. Departure from tradition is not in itself a reason to reject this approach, but the practical ramifications, particularly for nonscientists who use species names, are a concern.

Typification Inconsistencies among Rank-Based Codes

As in the rank-based codes, each species in our draft species code was linked to a single specimen that would serve as a reference point for application of the name. Unfortunately, the rules concerning typification under the *ICBN* and the *ICZN* differ in some regards. For example, isotypes and epitypes exist under the *ICBN* but not under the *ICZN*, and the concepts of lectotype and neotype differ somewhat. A paratype may be selected as a lectotype under the *ICBN* but not under the *ICZN* (in which only a syntype may be chosen as a lectotype); and the *ICBN* does not allow designation of a neotype if paratypes are extant, whereas the existence of paratypes does not prevent designation of a neotype under the *ICZN*. As a result, a single set of rules for specifiers might generate confusion due to disagreement about the status of specimens used as types for the same species name under the *PhyloCode* versus the appropriate rank-based code. We do not consider this, in and of itself, to prohibit the development of a species code, but it is a complicating factor. There is disagreement among the four of us about how serious an impediment this issue would have been.

Insufficient Benefits

Although none of these issues individually would prevent the development of a species code, their cumulative effect led us to question its feasibility and advisability. Even if the obstacles could be overcome, we came to doubt that implementing such a code would be beneficial for the scientific community. Changing the names of all previously named species is a large drawback, which would only be justifiable if there were a counterbalancing major benefit. On the contrary (and unlike phylogenetic nomenclature of clades), the manner in which species names were defined in our draft species code was not fundamentally different from rank-based nomenclature; i.e., species names were defined as the species containing a designated type specimen. Consequently, in spite of having devoted a lot of time to drafting a species code, we ultimately rejected the project in favor of an alternative approach that is intermediate between creating an entirely new set of rules to govern species names and simply ignoring them in the *PhyloCode*.

An Alternative Approach

Under the new approach that we devised, governance of establishment and precedence of new species names is left to the rank-based codes, but provisions are added to the *PhyloCode* that allow those names to be interpreted and used in a way that is consistent with the basic principles of phylogenetic nomenclature. We proposed the approach at the second meeting of the ISPN (Yale University, June 2006). This solution was well received by the participants, and the four of us were charged with formalizing these ideas as a new article in the *PhyloCode*. This article (Article 21) was prepared over the subsequent months and submitted to the CPN for discussion. In the course of the discussion, Mieczyslaw Wolsan, a member of the CPN, made an alternative proposal ("Method T" in Wolsan, 2007b). Wolsan's proposal differs from the one presented here in only one way: a species name adopted in the context of phylogenetic nomenclature would take the form of the oldest potentially valid (*ICZN*) or legitimate (*ICBN*, *BC*) species binomen (generally the original combination) and would be permanently fixed. In contrast, under the approach presented here, the species name that is currently accepted under the appropriate rank-based code would be used. Although fixing the original combination would stabilize species names, it would result in a massive and immediate divergence of the species names accepted under phylogenetic versus traditional nomenclature. After discussion of both approaches, the CPN rejected Wolsan's proposal in May 2007 and adopted the one presented here.

A New Article in the PhyloCode

The new article, Article 21, has four main properties. (1) It requires compliance with the corresponding rank-based codes for the establishment and precedence of new species names. (2) The two parts of established Linnaean binomina are then interpreted in a way that is consistent with the basic principles of phylogenetic nomenclature, most notably absence of mandatory ranks. Once binomina are established under the appropriate rank-based codes, the first word of a binomen is interpreted as a species "prenomen" (see below) rather than as a genus (ranked) name. (3) Use of a species prenomen is not mandated once the species name is established; if a prenomen is used, it is not tied to any categorical rank under the *PhyloCode*. (4) Recommendations are provided to guide the choice of genus names under the rank-based codes in a way that is maximally compatible with clade names governed by the *PhyloCode*, and symbols are recommended to convey phylogenetic information about the genus names (prenomina).

We explain below how Article 21 addresses the incompatibility between Linnaean binominal species names

and phylogenetic nomenclature. The complete Article 21 is available in the most recent version (4b) of the *PhyloCode* (at http://www.phylocode.org), but some excerpts are cited here for clarity.

Governance versus Interpretation of Species Names

Article 21 provides a mechanism for using species names established under the rank-based codes in the context of phylogenetic nomenclature. (The term "established," which is used in the *PhyloCode*, is used here to encompass "validly published" [*BC*, *ICBN*] and "available" [*ICZN*].) The main challenge was to address the incompatibility between traditional species nomenclature (in which the use of the genus rank is mandatory) and phylogenetic nomenclature (in which ranks are not mandatory). In order to resolve this incompatibility, Article 21 introduces a subtle but important distinction between how names are governed and how they are interpreted. Article 21.1 states that the *PhyloCode* does not govern establishment or precedence of species names. All rules of the appropriate rank-based codes (*BC*, *ICBN*, *ICZN*) must be followed whenever a new species name is published and when determining precedence.

In order that these names be compatible with phylogenetic nomenclature (e.g., that the use of ranks not be mandatory), they must be interpreted. The interpretation of species names provided by Article 21.2 consists of removing any mandatory reference to genus and species ranks. Thus, it states: "Because this code is independent of categorical ranks, the first part of a species binomen is not interpreted as a genus name but instead as simply the first part of the species name (a prenomen), and the second part of a species binomen is associated with the species as a kind of biological entity, not as a rank."

Clades and species are regarded as kinds of biological entities under the *PhyloCode*. They are not ranks because they do not refer to formal levels in a taxonomic hierarchy. Under the *PhyloCode*, a clade is defined as a group composed of an ancestor (an organism, population, or species) and all of its descendants, whereas a species is defined as a segment of a population-level lineage that is evolving separately from other such lineage segments, regardless of how it is recognized (e.g., by criteria of interbreeding, monophyly, diagnosability, etc.). Clades and species may be variously hierarchically organized; for example, the species *Paradoris dubia* is nested within the clade *Paradoris*, which is nested within the clade *Discodorididae*. (We follow *PhyloCode* Recommendation 6.1A in italicizing all scientific names.) However, "clade" and "species" do not refer to formal ranks denoting levels of a taxonomic hierarchy (e.g., genus level for *Paradoris*, family level for *Discodorididae*). In some cases, the names of both a clade and a species may refer to the same set of organisms under current circumscriptions. However, those two names would remain nomenclaturally distinct; e.g., the clade name cannot be a synonym of the species name, and vice versa. Because the clade includes all the descendants but the species does not necessarily, the names would no longer refer to the same set of organisms if the species were to speciate or if the set of organisms were found to consist of more than one species.

Article 21.3 extends the biological entity interpretation to taxa that are traditionally associated with infraspecific ranks (subspecies and varieties): "... the third (and subsequent) part(s) of an infraspecific name is (are) associated with the species category rather than the subspecific (and varietal) rank of traditional nomenclature. Thus, infraspecific names [established under the rank-based codes] may be used to refer to incompletely separated species ..."

The Concept of Prenomen and Establishment of New Species Names

The purposes of Article 21.4 and its three recommendations are to define what the *PhyloCode* refers to as a "prenomen" and to provide guidelines for selecting a prenomen when establishing a new species name, for indicating its nomenclatural status under the *PhyloCode*, and for conveying some phylogenetic information about it. Article 21.4 states: "A prenomen is the first part of a species binomen. A prenomen has no necessary tie to any categorical rank under this code. However, to satisfy the requirements of the rank-based codes, a prenomen must be used (and implicitly or explicitly associated with the rank of genus) when establishing a new species name..." A prenomen used when establishing a new species name need not have been established as a clade name under the *PhyloCode*.

Recommendation 21.4A addresses the status of prenomina under the *PhyloCode*: "When establishing a new species name (binomen) under the appropriate rank-based code, some mechanism should be used to indicate whether the generic name (prenomen) is an established clade name under this code." This status may be indicated in a text explanation or by the use of symbols. The recommendation does not mandate a standard set of symbols, but two examples are provided, one of which follows: "*Hypotheticus* (with no symbol) could indicate that this prenomen has been established as a clade name under this code, while [R]*Hypotheticus* could indicate that the prenomen *Hypotheticus* is not an established clade name ('R' meaning governed by a rank-based code)." Alternatively, one might use symbols to indicate both situations (e.g., both "R" and "P," the latter meaning governed by the *PhyloCode*). Using absence of a symbol to designate nomenclatural status is potentially confusing because its absence may simply result from accidental omission of the symbol. Furthermore, some readers may misinterpret absence of a symbol because they are unaware of the author's convention. The meaning of symbols, if they are used, would be given in the body of the establishing publication. It is common practice to indicate nonmonophyly with quotation marks. If this convention were used for a prenomen, the use of a symbol to indicate that the name is not an established clade name would be superfluous (see Note 21.4A.1).

Recommendation 21.4B provides guidelines for selecting a prenomen for use as a generic name when

publishing a new species name:

> When publishing the name of a new species, selection of a generic name (prenomen) will require consideration of the nomenclatural consequences under both the appropriate rank-based code and this code. In general, a generic name (*BC*, *ICBN*) or genus-group name (*ICZN*) that is also an established clade name (or is simultaneously being established as a clade name) under this code should be selected if possible. (If the names of more than one clade in a nested series of clades satisfy these conditions, any one of the names may be selected.) If this is not possible, an existing generic (or genus-group) name may be used, even if the monophyly of the associated taxon under the rank-based code is unknown or doubtful, or a new generic name (prenomen) may be used. If the species to be named cannot be assigned to any taxon with which a generic (or genus-group) name has been associated under the appropriate rank-based code, then the only option is to publish a new name to serve as a generic name under the appropriate rank-based code (a prenomen under this code). This name may be simultaneously established as a clade name under this code.

In cases of phylogenetic uncertainty, the alternatives are the same as under the rank-based codes when establishing a new species name: (1) coin a new name or (2) use an existing name for a taxon that is of uncertain monophyly or nonmonophyletic. The necessity of complying with one of these two alternatives in the face of uncertainty is a recognized disadvantage mandated by the rank-based codes and a drawback of the approach to species names adopted in the *PhyloCode*. In contrast to the rank-based codes, however, the *PhyloCode* offers recommendations for conveying information about the phylogenetic status of the taxon used as the prenomen, which we think constitutes significant improvement.

Recommendation 21.4C addresses the evidentiary basis for naming a new species, analogous to the reference phylogeny or list of synapomorphies that is required when establishing a clade name (Article 9.6). Its motivation is to increase the explicitness of alpha taxonomic practice relative to that required by the rank-based codes. Although both the theory and methods for species delimitation have increased in sophistication and rigor (see *Systematic Biology*, volume 56, issue 6), new species are commonly described without integrating these developments. For example, whether a diagnosis is based on autapomorphies versus a unique combination of characters is not always indicated, expectations based on patterns of geographic variation commonly are not considered, and the criteria according to which a set of organisms is regarded as a new species commonly are not stated.

Recommendation 21.4C suggests that the evidence employed to delimit a new species (and, by extension, to refer other specimens to it) should be made explicit: "When establishing a new species name under the appropriate rank-based code, the protologue should include a description of the evidence indicating that the named species represents a separately evolving lineage from other named species, or an unambiguous bibliographic citation to a previous publication containing this information." The *PhyloCode* is explicitly agnostic with respect to species concept, and subsequent specialists are not required to accept the species concept and evidentiary basis given at establishment (Note 21.4C.2).

The Use of Previously Established Species Names

The requirement that new species names used in the context of the *PhyloCode* be established under the rank-based codes guarantees that they are also regarded as available (*ICZN*) or validly published (*BC*, *ICBN*) under those codes. However, once a name is available or validly published, it may be used in various forms that are more consistent with the principles of phylogenetic nomenclature. To this end, Article 21.5 introduces some conventions that permit the use of uninominal (epithet-based) species names (Cantino et al., 1999a; Dayrat et al., 2004; Dayrat, 2005). Article 21.5 states that: "Subsequent to a species binomen becoming available (*ICZN*) or validly published (*ICBN*, *BC*) under the appropriate rank-based code, the second part of the species binomen may be treated as the name of the species (i.e., a species uninomen) under this code. In this context, the species uninomen may be combined with the names of clades other than the prenomen."

When the second part of a binomen (previously established under a rank-based code) is used as the name of the species, it is recommended (Recommendation 21.5B) that it be accompanied by the prenomen and/or the author(s) and publication year of the specific epithet (*BC*, *ICBN*) or name (*ICZN*). For example, the species that is referred to as *Vultur gryphus* or *Vultur gryphus* Linnaeus under the *ICZN* might be referred to under the *PhyloCode* as *Vultur gryphus* or *Vultur gryphus* Linné or *gryphus* Linné 1758. (Note 21.5B.1 states that if the prenomen is not used in combination with the specific name or epithet, both the author and year should be cited; however, if the prenomen is used, citation of the author and year are optional.) As discussed in the previous section, symbols may be used to indicate whether the prenomen is an established clade name or if the taxon to which it refers is thought to be nonmonophyletic, but such symbols are omitted from the examples in this section for simplicity.

Article 21.5 introduces some flexibility in species nomenclature by allowing systematists to combine specific epithets or names with clade names that are ranked above the genus level under the ranked-based codes after establishment of the species names. These codes require systematists to assign every species to a taxon of genus rank, even in cases in which systematists know very little about phylogenetic relationships. In such cases, assignment to a genus may be poorly supported, leading to subsequent transfers to other genera and multiplication of synonyms. Conveying accurate phylogenetic information, by substituting a clade name for the name of a nonmonophyletic or monotypic genus, is more consistent with the principles of phylogenetic nomenclature than maintaining the tradition that every species belongs to a genus.

It is sometimes useful to associate a uninominal species name with more than one prenomen or with names of more inclusive clades, as a flexible mechanism for providing phylogenetic information. The hierarchical relationships among these taxa can be indicated in a

variety of ways, but for the sake of consistency, the *PhyloCode* recommends listing the names of such taxa in order of decreasing inclusiveness from left to right. For example, the species originally named *Anolis auratus* Daudin 1802 has been placed in at least two different genera, named *Anolis* and *Norops*. If those names were to be established under the *PhyloCode* as the names of nested clades, the name and relationships of the species could be indicated in any of the following ways (the list is not exhaustive): *Norops auratus* Daudin 1802, or *Anolis/Norops/auratus* Daudin 1802, or *Anolis Norops auratus* Daudin 1802 (Recommendation 21A, Example 1). Similarly, if the name of a species under the *ICZN* is *Diaulula sandiegensis* (Cooper 1863), and if *Diaulula* has not been established as a clade name under the *PhyloCode* (for example, because there is presently insufficient data to establish monophyly), and if the name *Discodorididae* has been established as the name of a more inclusive clade under the *PhyloCode*, then the name and relationships of the species could be indicated in any of the following ways (this list is not exhaustive): *Diaulula sandiegensis* Cooper 1863, or *Discodorididae Diaulula sandiegensis* Cooper 1863, or *Discodorididae/sandiegensis* Cooper 1863, or *Discodorididae sandiegensis* Cooper 1863 (Reccommendation 21A, Example 2).

Recommendation 21A addresses the use of parentheses when citing author names, which (under the rank-based codes) indicate that a specific name or epithet was originally combined with a different genus name. For example, in the name *Norops auratus* (Daudin 1802), the parentheses indicate that *auratus* was combined with a genus name other than *Norops* in the original publication. Under the rank-based codes, this use of parentheses is mandatory if the author is cited. In contrast, under the *PhyloCode*, the use of parentheses in such situations is optional, even if the author is cited. Because the *PhyloCode* is independent of ranks, conveying information about the changing associations of specific names or epithets with particular prenomina of generic rank is not as important as it is in the rank-based codes. The *PhyloCode* allows specific names or epithets to be combined with various clade names, including multiple names associated with the genus (e.g., both *Anolis* and *Norops*, see above) in rank-based codes, names associated with ranks other than genus in those codes (e.g., order, family), and names not associated with any formal rank.

Species as Specifiers in Phylogenetic Definitions

One important reason for addressing the use of species names in the context of Phylogenetic Nomenclature is that species may be used as specifiers in phylogenetic definitions (which determine the application of clade names in the *PhyloCode*). Examples of phylogenetic definitions are given in Article 9 of the *PhyloCode*. When used as specifiers, the names of species can be cited in any of the ways described as examples in the previous section of this paper and with (or without) the symbols discussed earlier to provide additional information about the prenomen. For example, suppose that *Discodorididae* were defined as "the clade originating with the first organism or species to possess a notched upper lip of the bilabiate anterior margin of the foot, as inherited by *Diaulula sandiegensis* (Cooper 1863)." Suppose further that *Discodorididae* is an established clade name while *Diaulula* is not and, moreover, the taxon *Diaulula* is thought to be non-monophyletic. Given this situation, the species used as a specifier in this definition could be cited in any of the following additional ways (not an exhaustive list): "*Diaulula*" *sandiegensis* (Cooper 1863), or [P]*Discodorididae* [R]*Diaulula sandiegensis* Cooper 1863, or *Discodorididae/sandiegensis* Cooper 1863, or [P]*Discodorididae sandiegensis* Cooper 1863, or *sandiegensis* Cooper 1863.

As phylogenetic knowledge grows, species names are frequently assigned to new genera under rank-based nomenclature. Such changes will likely affect the names of species that had been used as specifiers in phylogenetic definitions. (Avoiding this kind of nomenclatural instability could be regarded as an argument in favor of using species uninomina [e.g., *sandiegensis* Cooper 1863] in the context of phylogenetic nomenclature.) As a consequence of splitting and lumping of species, as well as new combinations under rank-based nomenclature, the names of some species used as specifiers will become synonyms of other names. The key to handling this is implicit in Note 11.1.1, which states, "[w]hen a species is cited as a specifier, the implicit specifier is the type of that species name." Thus, whichever currently accepted species includes the type specimen of the species name cited in the definition is the specifier. If the species name originally cited as a specifier is no longer accepted, either because the species has been recircumscribed or assigned to a different genus, then the species name with which it has been synonymized automatically becomes the name of the specifier species. However, the type of the name originally used as a specifier, rather than that of the currently accepted species name, remains the implicit specifier. Note that the issue discussed above does not exist when specimens are used as specifiers (as permitted by Article 11). However, using specimens as specifiers may be ill advised when naming clades composed of species (Lee and Skinner, 2008).

Conclusions

The article on species names recently adopted in the *PhyloCode* eliminates a major shortcoming of that code and has several important benefits: (1) Species names used in the context of phylogenetic nomenclature will be established following the appropriate rank-based code and will thus be validly published or available under that code. (2) The *PhyloCode* is now complete in addressing both clade and species names. (3) It eliminates the need to republish and register as many as 1.8 million existing species names (as would be the case if the *PhyloCode* governed species names). (4) It allows phylogeneticists who wish to use both the *PhyloCode* and species names to do so in a way that is consistent with

the principles of phylogenetic nomenclature. (5) It helps systematists convey accurate phylogenetic information by introducing symbols to indicate whether names are established clade names and whether taxa to which various names refer are monophyletic or non-monophyletic and by permitting increased flexibility in the way specific names or epithets are combined with supraspecific names.

More broadly, Article 21 promotes nomenclatural continuity and communication of phylogenetic information by combining the most effective standard practices of our taxonomic community, most notably the use of single specimens (types) as reference points for the application of names, with critical innovations. These innovations include greater flexibility in the way specific names or epithets can be combined with supraspecific names and encouraging increased explicitness in alpha taxonomic practice by recommending that authors indicate the criteria used for recognizing species. In so doing, this approach both represents an advance in species nomenclature and hopefully removes a major obstacle to acceptance of the *PhyloCode*.

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