

Constraints in naming parts of the Tree of Life

David M. Hillis*

Section of Integrative Biology and Center for Computational Biology and Bioinformatics, University of Texas,
One University Station C0930, Austin, TX 78703, USA

Received 11 July 2006; accepted 3 August 2006

Available online 11 August 2006

Abstract

There are now overlapping codes of nomenclature that govern some of the same names of biological taxa. The *International Code of Zoological Nomenclature (ICZN)* uses the non-evolutionary concept of a “type species” to fix the names of animal taxa to particular ranks in the nomenclatural hierarchy. The *PhyloCode*, in contrast, uses phylogenetic definitions for supraspecific taxa at any hierarchical level within the Tree of Life (without associating the names to particular ranks), but does not deal with the names of species. Thus, biologists who develop classifications of animals need to use both systems of nomenclature, or else operate without formal rules for the names of some taxa (either species or many monophyletic groups). In addition, the *ICZN* does not permit the unique naming of many taxa that are considered to be between the ranks of genus and species. Hillis and Wilcox [Hillis, D.M., Wilcox, T.P., 2005. Phylogeny of the New World true frogs (*Rana*). *Mol. Phylogenet. Evol.* 34, 299–314] provided recommendations for the classification of New World true frogs that utilized the *ICZN* to provide names for species, and the *PhyloCode* to provide names for supraspecific taxa. Nonetheless, they created new taxon names that followed both sets of rules, to avoid conflicting classifications. They also recommended that established names for both species and clades be used whenever possible, to stabilize the names of both species and clades under either set of rules, and to avoid conflicting nomenclatures. Dubois [Dubois, A., 2006. Naming taxa from cladograms: a cautionary tale. *Mol. Phylogenet. Evol.*, 42, 317–330] objected to these principles, and argued that the names provided by Hillis and Wilcox [Hillis, D.M., Wilcox, T.P., 2005. Phylogeny of the New World true frogs (*Rana*). *Mol. Phylogenet. Evol.* 34, 299–314] are unavailable under the *ICZN*, and that the two nomenclatural systems are incompatible. Here, I argue that he is incorrect in these assertions, and present arguments for retaining the established names of New World true frogs, which are largely compatible under both sets of nomenclatural rules.

© 2006 Elsevier Inc. All rights reserved.

Keywords: Phylogeny; Taxonomy; Classification; Clades; Taxa; Species; Frogs; *Rana*

“*Characterem non constituero Genus, sed Genus Characterem*”

Carolus Linnaeus (1751, in *Philosophica Botanica*)

“Such expressions as that famous one of Linnaeus... that the characters do not make the genus, but that the genus gives the characters, seem to imply that something more is included in our classifications, than mere resemblance. I believe that something more is included; and that propinquity of descent—the only known cause of the similarity of organic beings—is the

bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications.”

Charles Darwin (1859, in *The Origin of Species*)

1. Introduction

Although phylogeny is widely considered to be the modern basis for biological classification, rules that govern biological classifications have origins that pre-date the evolutionary and phylogenetic revolutions in biology. Thus, there is a tension between biologists who expect classifications to reflect modern evolutionary and phylogenetic findings, and those who give pre-eminence to the pre-evolutionary systems of biological nomenclature. There are now separate

* Fax: +1 512 471 3878.

E-mail address: dhillis@mail.utexas.edu

rules and organizations that regulate either phylogenetic-based nomenclature (the International Society for Phylogenetic Nomenclature, which publishes rules known as the *PhyloCode*; see <http://www.ohiou.edu/phylocode/>) or type- and rank-based nomenclature (such as the International Commission on Zoological Nomenclature, which publishes the *International Code of Zoological Nomenclature*, henceforth *ICZN*; see http://www.nhm.ac.uk/hosted_sites/iczn/). Recently, a colleague and I attempted to strike a balance between these two viewpoints and taxonomic systems. We based our phylogenetic classification of New World true frogs (Hillis and Wilcox, 2005) on a comprehensive phylogeny of the relevant species, following the principles of phylogenetic nomenclature and the rules of the *PhyloCode*. However, we kept the names of clades that had been proposed under *ICZN* rules, and followed the rules of the *ICZN* in proposing new names so that the same names could potentially be used for taxa under either system. Moreover, we followed the *ICZN* for the correct names of all the species, as species names are not governed under the existing *PhyloCode* rules.

Dubois (2006) has objected to our effort on several counts. He argued that the names proposed by Hillis and Wilcox (2005) were *nomina nuda* (unavailable names) under the *ICZN* rules, that our paper did not contain “character diagnoses,” that the *ICZN* rules do not permit the formal naming of more than one clade between the ranks of genus and species, and that our names were incorrectly formed. I argue here that he is incorrect in each of these assertions. Dubois (2006) also presented a classification for New World frogs that unnecessarily resulted in wholesale changes of species names; these changes are neither necessary under *ICZN* rules nor are they desirable for communication among biologists. I also discuss some areas of agreement with Dubois (2006), in particular the superiority of the *PhyloCode* over the *ICZN* for naming parts of the Tree of Life (especially clades that are considered to be between the ranks of genus and species in the rank-based system).

Below, I consider each of these points in turn.

2. Are the names created by Hillis and Wilcox (2005) *nomina nuda*?

Dubois’ (2006) first argument is that the new names created by Hillis and Wilcox (2005) are *nomina nuda* under the *ICZN* rules. He is simply incorrect in this claim. To be available under *ICZN* rules, scientific names published after 1930 must:

“13.1.1. be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon, or

13.1.2. be accompanied by a bibliographic reference to such a published statement, even if the statement is contained in a work published before 1758, or in one that is not consistently binominal, or in one that has been sup-

pressed by the Commission (unless the Commission has ruled that the work is to be treated as not having been published [Art. 8.7]), or

13.1.3. be proposed expressly as a new replacement name (*nomen novum*) for an available name, whether required by any provision of the Code or not.”

(all quotes of the *ICZN* rules are from <http://www.iczn.org/iczn/index.jsp>)

First, the *ICZN* rules are clear that a description in words of characters that are purported to differentiate the taxon is sufficient to meet this requirement. Although Dubois claims that no such descriptions are provided by Hillis and Wilcox (2005), his assertion is false. For instance, here is the wording that we used to describe the characters that differentiate *Torrentirana* from other species of *Rana*:

“All members of this species group lack vocal sacs and slits, have reduced or absent external tympana, and no calls have been recorded for any of the species.” (Hillis and Wilcox, 2005, p. 308)

Under the *ICZN* rules, this is sufficient to make the name *Torrentirana* available. There is no requirement that this description of differentiating characters be placed next to the name where it is first proposed, or be labeled a “diagnosis,” or any other requirement that prevents our character descriptions from satisfying the requirements of the *ICZN* for availability of the names. Dubois does acknowledge that we provided information “... regarding some of the characters of the supraspecific taxa ... but this information is provided cursorily in the course of the main body of the paper, not in Appendix B, which gives the classification of New World *Rana*...” Nowhere in the *ICZN* rules is there a requirement that states where in the paper the description of characters must be located. Therefore, these descriptions of characters are completely consistent with the *ICZN* requirements.

Even where Dubois acknowledges that we did provide descriptions of characters for our newly named taxa, he argues that our descriptions were not diagnostic for the taxa. For instance, Dubois comments specifically on our character description for *Scurrilirana*, but he inaccurately describes the character descriptions in Hillis and Wilcox (2005). Dubois (2006) wrote:

“Even when provided, these characters are not given as strictly ‘diagnostic’; for example, it is stated that the advertisement calls of ‘most of the species’ of the ‘clade’ called ‘*Scurrilirana*’ ‘sound like chuckling laughter’, but this is not a ‘diagnostic’ character as it is not common to all the species of the taxon.” (Dubois, 2006, p. 322)

However, contrast Dubois’ statement to the wording in Hillis and Wilcox (2005):

“In contrast [to the calls of other taxa], the species of *Scurrilirana* all have some form of ‘chuckle-like’ mating call, that superficially resembles some of the other ele-

ments of the advertisement call of species such as *R. pipiens*. The ‘chuckle-like’ calls of species of *Scurrilirana* consist of a series of pulses of variable number (typically 4–12), each group with a slower pulse rate compared to a snore, and greater spacing between successive groups than between successive pulses (see examples in Fig. 4). As in a snore, these pulses are often modulated in frequency and amplitude, and the calls are sometimes likened to the sound of rapid human laughter.” (Hillis and Wilcox, 2005, pp. 309–310)

Two points seem clear: first, the character descriptions provided by Hillis and Wilcox (2005) are not nearly as superficial as suggested by Dubois (2006); and second, the characters were clearly described as applying to all the species of the taxon and diagnosing it from other taxa. Thus, *Torrentirana* and *Scurrilirana* are not *nomina nuda* as claimed by Dubois (2006), but are available under the ICZN rules.

Even if there were no character descriptions provided for the taxa described by Hillis and Wilcox (2005), the ICZN makes it clear in Article 13.1.2 (quoted above) that names are available if they are “accompanied by a bibliographic reference” to a character description that “states in words characters that are purported to differentiate the taxon.” We did provide bibliographic references to papers that provided clear character descriptions of all our taxa. For instance:

“Hillis et al. (1983) recognized two major divisions of *Pantherana* (then the *R. pipiens* complex), which they informally termed the α and β divisions. Their α division consisted of two species groups, the *R. montezumae* group (here termed *Lacusirana*, Fig. 2 and Appendix B) and the *R. areolata* group (here termed *Nenirana*, Fig. 2 and Appendix B).”

The bibliographic reference to Hillis et al. (1983), which clearly contains descriptions in words of the characters that are purported to differentiate *Lacusirana* and *Nenirana* from other groups of frogs, is all that is required by the ICZN to make these names available. The same conditions (bibliographic references to character descriptions) also hold for the other new names we proposed.

Dubois’ final argument for considering our names *nomina nuda* is that he was not the first person to make this claim. He notes that Frost et al. (2006, p. 255) wrote about the names proposed by Hillis and Wilcox (2005): “inasmuch as these were not associated with organismal characteristics that purport to delimit them, they are *nomina nuda*.” Darrel Frost, the first author of Frost et al. (2006), has since acknowledged to me in writing that his statement was incorrect, and that the taxa in question are not *nomina nuda*. Unfortunately, the mistake has now been repeated by Dubois (2006).

3. What is the modern relevance of a “diagnosis?”

Given the concern over adherence to rules governing the naming of taxa, it is useful to consider the relevance of the

diagnosis in modern systematics. Diagnoses were not required by the ICZN prior to 1930, and they were apparently added to the rules to ensure that biologists who proposed names had (or thought they had) some evidence in support of the taxa they were naming. The diagnosis, however, harkens back to the age of essentialism in biology, when biologists tried to capture “the essence” of a taxon by listing its “essential” features. In contrast, evolutionary biologists today recognize that phylogenetic history, rather than a list of essential features, is what defines monophyletic groups, even if they have no “diagnostic” features. Even Dubois recognized this change in biological classification when he wrote: “Most biologists nowadays agree that biological classification should provide information on the phylogenetic relationships between organisms” (Dubois, 2006, p. 317). Clearly, we want biologists to discuss the evidence that they discover in support of particular clades, but what was considered appropriate evidence in 1930 would hardly be considered sufficient (or perhaps even relevant) by most biologists today. The ICZN rules do not even require that diagnoses be correct. If we wrote “the species of *Novirana* may be distinguished from other *Rana* because they are green,” that would be considered sufficient under ICZN rules to make the name available, even though the diagnosis is incorrect. We could also write “*Novirana* is defined by the presence of a thymine at position 200 of the small subunit mitochondrial rRNA gene,” and that would satisfy the ICZN rules, despite the absurdity of the phrase. Any base position is subject to further evolution, and the existence and definition of the taxon clearly does not depend on the presence of the supposedly “diagnostic” character. This fact does not detract from the use of such characters to infer phylogenetic relationships, however. But a phylogenetic analysis of the complete genomes of all the relevant species, and presentation of the phylogenetic analysis and the statistical support of all the clades in the paper where the taxon is described, would not be considered sufficient to make the taxon name available under ICZN rules. Clearly, there are some problems with the rules.

Part of the problem is that ICZN rules have not kept up with changes in modern biology, and part of the problem is that ICZN rules are designed more with the description of species in mind, rather than with the discovery and description of new clades. The ICZN rules do concern two major groups of ranks of supraspecific taxa, namely the genus-group and family-group, but the application of the ICZN rules to the genus-group ranks is highly problematic, as I will discuss in more detail below. But why are character diagnoses (even if not accurate) required for all new names, whereas a careful phylogenetic analysis of the relevant taxa is not considered sufficient evidence to propose a new name for a taxon? Surely most biologists recognize that it is phylogenetic history, not a list of characters, that defines a monophyletic group. We may say that “members of *Tetrapoda* may be diagnosed by the presence of four limbs,” but we readily recognize snakes and caecilians as members of *Tetrapoda*, despite their lack of limbs. Similarly, we do not

use diagnoses to “define” any monophyletic group. Rather, we define the group based on its phylogenetic history, which we infer from an analysis of characters, none of which are essential for group membership. Therefore, a character diagnosis should be considered neither necessary nor sufficient to establish a new clade name, especially since the diagnosis then has no role in how the name is subsequently applied.

One could argue that character diagnoses are useful to delimit how new names should be applied, but the *ICZN* rules do not use the diagnoses in this fashion. In fact, under *ICZN* rules, clade names have no definition that attaches them to taxa, other than by reference to the type species: the genus *Rana* is the genus to which the type species of *Rana* belongs. Each person who follows the *ICZN* is free to use the genus name *Rana* for virtually any group of species, as long as that group contains the type species of *Rana*.

This “freedom” of taxonomic application promoted by the *ICZN* rules comes at the cost of taxonomic chaos. As a result, most non-taxonomists think that taxonomists are out to make nomenclature and classification as confusing as possible, especially as names change according to the whims of each new taxonomic expert. Many phylogeneticists now see nomenclature and classification as largely irrelevant to phylogenetics (e.g., see Felsenstein, 2004, p. 145). Moreover, the *ICZN* rules require the same name to be used to apply to several different clades in the taxonomic hierarchy (as with the names of a genus and its nominotypical subgenus, such as genus *Rana* and subgenus *Rana*). It is hard to imagine a use of biological classifications where this would be considered helpful. Most taxonomic search engines use the names of taxa, but not their ranks. Therefore, in most searches of taxonomic databases, one would enter “*Rana*,” for example, rather than “subgenus *Rana*.” To make this approach useful, the name *Rana* must be defined to apply consistently and uniquely to a particular monophyletic group.

Although the importance of a unique series of hierarchically nested names seems obvious from an information storage-and-retrieval standpoint, the *ICZN* rules do not permit such a classification. To illustrate the ambiguity created by application of the *ICZN* rules, consider the various taxa to which Dubois has applied the name *Lithobates*. This name was originally proposed by Fitzinger (1843), but it has rarely been used since then. The entire “description” of *Lithobates* in Fitzinger (1843, p. 31) consists of the following three entries in three columns of a table: “*Lithobates*” “Am.,” and “*Lithob. palmipes*.” In other words, Fitzinger (1843) proposed *Lithobates* as the genus for the American species he called *Lithobates palmipes*. Other authors quickly put Fitzinger’s species into the genus *Rana*, however, and the name *Lithobates* was virtually unused (except in lists of synonyms) until 1992. Then, Dubois (1992) applied the name *Lithobates* to two different paraphyletic groups: he recognized a subgenus *Lithobates* that consisted of *Rana bwana*, *R. palmipes*, and *R. vailanti*, and also a section *Lithobates* that consisted of these three species plus species in the subgenera *Sierrana*, *Trypherosis*, and *Zweifelia*. To my knowledge, the diagnoses of these

two taxa by Dubois (1992) were the first character diagnoses presented for *Lithobates* by any author. The analysis by Hillis and Wilcox (2005) showed that neither the subgenus nor the section called *Lithobates* by Dubois in 1992 was monophyletic, and so Dubois (2006) applied the name *Lithobates* to two more taxa: as a genus for all the New World species of ranid frogs except for the west coast *Amerana*, and as a subgenus of all of these except *Rana sylvatica* and members of the *R. catesbeiana* group, which he placed together in the subgenus *Aquarana*.

Although Dubois (1992, 2006) applied the name *Lithobates* to four different nominal taxa, two of them now considered paraphyletic, this has all been consistent with the application of *ICZN* rules. Moreover, the *ICZN* actually requires that one subgenus within every genus take on the same name as the genus (assuming that subgenera are recognized at all). Even if one were to use Dubois’ ranks in combination with the names, the names would still not apply unambiguously to a single taxon. For instance, one could say “subgenus *Lithobates*, in the sense of Dubois,” and that phrase would still apply to several different taxa. Even adding a citation to a particular paper does not necessarily restrict the meaning of the name to a single taxon.

The taxonomic chaos that is generated by this application of the *ICZN* rules can be ameliorated by phylogenetic definition of taxon names (e.g., de Queiroz and Gauthier, 1990, 1992, 1994). Already, the *PhyloCode* is the only set of rules that regulate many aspects of zoological names of clades above the level of the family-group, so anyone who uses names such as *Anura*, *Tetrapoda*, or *Vertebrata* is either following the *PhyloCode* or else not following any formal rules at all. However, there is some overlap between the two systems, as the *PhyloCode* seeks to regulate all clade names, whereas the *ICZN* seeks to regulate both species names as well as names in the genus and family groups. How can these systems be reconciled?

In defining the taxon names in Hillis and Wilcox (2005), we sought to maintain the long-standing meanings of names as they have been most widely applied, or in the case of little-used names, as they were intended by the original authors. For instance, we used the diagnoses provided by the original authors to identify the clades most closely associated with each of the taxon names, and then defined the names based on the principles of phylogenetic nomenclature (as in the *PhyloCode*). In most cases, the names we used follow both the *ICZN* rules as well as those of the *PhyloCode*. However, it is true that the *ICZN* rules do not allow the unambiguous naming of many monophyletic groups. Where the *ICZN* rules do not permit a clade to be named uniquely, we followed the *PhyloCode* rules to provide a usable and useful classification.

4. How much of the Tree of Life do the *ICZN* rules allow to be named?

Dubois (2006) takes issue with the point made by Hillis and Wilcox (2005) that the supraspecific names for the

various clades of *Rana* are all treated as subgenera by the *ICZN*, even though they are hierarchically arranged. This is what the *ICZN* states about this issue:

“10.4. Availability of names for divisions of genera. A uninominal name proposed for a genus-group division of a genus, even if proposed for a secondary (or further) subdivision, is deemed to be a subgeneric name even if the division is denoted by a term such as ‘section’ or ‘division’.”

The wording of this rule makes it clear that secondary (and further) subdivisions of genera are possible under the *ICZN* rules, but that the names of all such divisions are treated as the names of subgenera for the purposes of availability, as stated by Hillis and Wilcox (2005, p. 304):

“[A]ll of the clade names within *Rana* that are defined in Appendix B are subgenera under *ICZN* rules, even though the clades are nested hierarchically within one another ... We recommend that *Rana* still be the primary clade name used with species epithets to promote nomenclatural stability; the other clade names, in turn, are useful for discussing historical groups of species within *Rana*. Therefore, the species names in this paper ... are identical under either Linnean binomial nomenclature (as binomials), or following Option M for species names as suggested by Cantino et al. (1999).”

This is the only claim made in Hillis and Wilcox (2005) about the application of *ICZN* rules to our classification of New World *Rana*, and I maintain that our statement was then, and remains now, accurate.

Dubois (1992) clearly also believed that multiple subgeneric divisions were possible under the *ICZN*, as he named and diagnosed subgenera within subsections within sections within genera. The *ICZN* makes it clear that these multiple subdivisions of genera are possible, but that the name of each division is deemed to be the name of a subgenus under the *ICZN* rules for availability, no matter what it was called by the original author. Dubois (2006) makes the claim that although the *ICZN* treats all names for divisions below genus as subgenera for the purposes of availability, and allows that multiple subdivisions of a genus may exist, that only one hierarchical level can be treated as a subgenus (the only formal taxonomic division recognized by the *ICZN*). I see that argument as inconsistent with the wording of the *ICZN* rules.

Despite my disagreement with Dubois (2006) about what the *ICZN* actually says with regard to subgenera, I agree with Dubois that this provision of the *ICZN* is illogical and inconsistent with other aspects of the *ICZN* rules (however, the wording is interpreted). The treatment of subgenera by the *ICZN* also has the unfortunate problem that multiple nominotypical subdivisions below the generic level (i.e., a section *Lithobates*, subsection *Lithobates*, and subgenus *Lithobates*, for instance) are all deemed to have the same rank (as well as the same name) by the *ICZN*. Hillis and Wilcox (2005) chose to provide different names

(defined phylogenetically) for the various “subgeneric” divisions, and to follow the *PhyloCode* recommendations for these names. It is true that several of these names are considered junior objective synonyms of other names under the *ICZN* rules, whenever the type species is the same. This is another undesirable feature of the *ICZN*: even though one species is simultaneously a member of many nested hierarchical taxa, it may only be the type species for one name within the genus-group series. However, even if we had designated different type species for each “subgeneric” division in the hierarchy, Dubois would consider all of these to be junior subjective synonyms of other subgenera, so it makes no difference in application under the *ICZN* rules. The *ICZN* rules do not permit unambiguous naming of these clades in any case, so it makes little difference how the *ICZN* treats these phylogenetically defined names. Fortunately, none of this is problematic under the *PhyloCode* rules, so a reasonable classification can still be constructed. As we stated, our proposed clade names are “useful for discussing historical groups within *Rana*,” which largely can not be said for whichever classification is proposed under the *ICZN* rules (where the names are tied to ranks rather than to taxa).

Although I disagree with Dubois’ (2006) interpretation of the *ICZN* with regard to how many subgeneric divisions are allowed, I do not think the point matters much. Readers are welcome to read the rules and decide for themselves which interpretation is correct. But, as the *ICZN* rules require redundant names to be used below the level of genus in any case, I do not recommend that biologists attempt to follow the *ICZN* rules for subgeneric taxa, no matter how this aspect of the *ICZN* is interpreted. As subgeneric names do not affect the names of species binomials in any case (under any rules), and since the *ICZN* is incapable of providing non-redundant classifications at this level, biologists will likely find little usefulness in the subgeneric categories governed by the *ICZN*, whether or not more than one subdivision is allowed. If Dubois’ (2006) interpretation is judged to be correct, then this provides an additional reason for biologists to ignore the *ICZN* rules for naming taxonomic groups within genera, as the rules apparently would not allow most of these clades to be named in any fashion. In this case, I agree with Dubois (2006), who argues that the *ICZN* rules unnecessarily restrict “freedom of taxonomic thought or actions” and that “[i]n this respect, the *PhyloCode* is no doubt superior to the [*ICZN*] *Code*.” Dubois (2006) states that he has submitted a proposal to fix this odd aspect of the *ICZN*. Hopefully, the *ICZN* rules will eventually follow more closely those of the *PhyloCode*. Until then, phylogenetic taxonomists may prefer to use the *PhyloCode* rules for clade names, and restrict the use of the *ICZN* rules to naming species.

Biologists who wish to follow only the *ICZN* for the names of subgenera can still follow the recommendations of Hillis and Wilcox (2005), but only recognize the smallest clades defined by these authors as subgenera. Under this system, one

would simply not use any names for taxa between the ranks of genus and subgenus. Thus, the subgenera for New World *Rana* would be the groups defined as *Amerana*, *Aquarana*, *Trypheropsis*, *Lithobates*, *Zweifelia*, *Lacusirana*, *Nenirana*, and *Scurrilirana* by Hillis and Wilcox (2005). One could also recognize the monotypic subgenera *Pantherana* (for *Rana pipiens*) and *Sierrana* (for *Rana sierramadrensis*), although these subgeneric names would then be used in a different sense than recommended by Hillis and Wilcox (2005). Under this system, none of these subgeneric names are synonyms (either objective or subjective), and all are available and valid under *ICZN* rules. The clade names *Novirana*, *Laurasiarana*, *Levirana*, *Ramula*, *Stertirana*, and *Torrentirana* are not used as subgenera under this solution. Under this system, the taxa represented by these names would be between the genus and subgenus levels, and therefore would not be formally namable taxa under the *ICZN* rules according to Dubois. This list includes all the names considered junior objective synonyms or homonyms by Dubois.

5. Are the clade names in Hillis and Wilcox (2005) incorrectly formed?

Dubois (2006) suggests alternative spellings for two of the names created by Hillis and Wilcox (2005): “*Scurrana*” for *Scurrilirana*, and “*Lucunirana*” for *Lacusirana*. Under any of the rules, these are unjustified emendations of the original names. The original spellings are correct (and correctly formed), and cannot be changed because of personal preferences for another spelling. This is what the *ICZN* rules says about this point:

“32.1. Definition. The ‘original spelling’ of a name is the spelling used in the work in which the name was established.

32.2. Correct original spelling. The original spelling of a name is the ‘correct original spelling’, unless it is demonstrably incorrect as provided in Article 32.5.”

“32.5.1. If there is in the original publication itself, without recourse to any external source of information, clear evidence of an inadvertent error, such as a lapsus calami or a copyist’s or printer’s error, it must be corrected. Incorrect transliteration or latinization, or use of an inappropriate connecting vowel, are not to be considered inadvertent errors.”

In the case of the names we proposed, the names are not even incorrectly Latinized, nor are Dubois’ alternatives preferable from an etymological perspective. *Lacusirana*, for instance, is derived from the Latin *lacus* (lake), whereas *Lucunirana* seems more clearly derived from the Latin word *lacuna* (hollow or cavity). Since the members of *Lacusirana* are lake frogs, and that was the basis of the name, the reasons for Dubois’ preference are unclear. In any case, Dubois (2006) merely prefers an alternative form. Such changes are expressly disallowed by both the *ICZN* and *PhyloCode* rules.

6. What species names should be used with New World true frogs?

The *ICZN* rules are used most often by biologists to provide the valid names of species. However, because the application of ranks to the names of higher taxa (including genera) is subjective under the *ICZN* rules, many different binomial names for the same species may be recognized by different authors. Hillis and Wilcox (2005) sought to provide some stability for the binomial names of New World true frogs by using the convention of designating a clade name to be used in the binomial combinations that is consistent with prior widespread usage. Thus, we recommended that *Rana* be used as the “clade address” for all the New World species of true frogs, as this name has been almost universally used as the first part of the binomial names of these species. Under this recommendation, the names of the species would remain stable and would not change with each subjective shift in generic allocation. In addition, since *Rana* is a valid genus-group name under the *ICZN* rules, this recommendation has the advantage of being completely consistent under both sets of existing nomenclatural rules. The same species names can be used by followers of the *PhyloCode*, as well as followers of the *ICZN* rules, without any widespread confusion or massive changes in taxonomic databases.

In contrast to this approach of promoting taxonomic stability, Frost et al. (2006) and Dubois (2006) recommended subjective changes to the species names of New World true frogs, even though there was no phylogenetic justification. Examples of the specific names suggested by each of these authors are compared in Table 1, along with the arrangement proposed by Dubois (1992). All of these suggested species names are consistent with the *ICZN* rules, as are many other possibilities. However, the names proposed for use by Hillis and Wilcox (2005) follow the *ICZN* rules, do not violate any phylogenetic definitions of clade names, and also maintain the traditional usages. Thus, contrary to critic’s allegations, the *PhyloCode* can be used as a tool to stabilize scientific names. In this case at least, it is the promoters of the *ICZN* rules (Frost et al., 2006; Dubois, 2006) who recommend the massive subjective changes of species names.

Under the *ICZN* rules, any generic-rank taxon that includes the type species of *Rana*, and no older generotype of a valid genus, can be called *Rana*, whether it is monophyletic or not. Nowadays, when biologists conduct a new phylogenetic analysis, they often modify the content of genera so that the genera will represent monophyletic groups. However, in the case of the recommendations of Frost et al. (2006) and Dubois (2006), the restriction of the name *Rana* to a small subset of European and American true frogs was not necessitated by new phylogenetic findings. Frost et al.’s (2006) study confirmed the findings of Hillis and Davis (1986) and Hillis and Wilcox (2005), and showed that all the New World true frogs, together with the *Rana temporaria* group of Eurasian frogs, form a monophyletic group.

Table 1
Recommended species names for selected species of New World true frogs

	Hillis and Wilcox (2005)	Frost et al. (2006)	Dubois (1992)	Dubois (2006)
Follows <i>ICZN</i> rules	Yes	Yes	Yes	Yes
Follows phylogenetic definitions of clade names	Yes	No	No	No
Supraspecific names for monophyletic taxa only	Yes	Yes	No	Yes
Retains existing binomials	Yes	No	Yes	No
Retains existing meaning for supraspecific names	Yes	No	Yes	No
Examples:				
<i>Rana aurora</i>	<i>Rana aurora</i>	<i>Rana aurora</i>	<i>Rana (Amerana) aurora</i>	<i>Rana (Amerana) aurora</i>
<i>Rana catesbeiana</i>	<i>Rana catesbeiana</i>	<i>Lithobates catesbeianus</i>	<i>Rana (Aquarana) catesbeiana</i>	<i>Lithobates (Aquarana) catesbeianus</i>
<i>Rana sylvatica</i>	<i>Rana sylvatica</i>	<i>Lithobates sylvaticus</i>	<i>Rana (Rana) sylvatica</i>	<i>Lithobates (Aquarana) sylvaticus</i>
<i>Rana pipiens</i>	<i>Rana pipiens</i>	<i>Lithobates pipiens</i>	<i>Rana (Pantherana) pipiens</i>	<i>Lithobates (Lithobates) pipiens</i>
<i>Rana palmipes</i>	<i>Rana palmipes</i>	<i>Lithobates palmipes</i>	<i>Rana (Lithobates) palmipes</i>	<i>Lithobates (Lithobates) palmipes</i>

Frost et al. (2006) and Dubois (2006) simply chose to apply the genus name *Rana* to a different monophyletic group than that recommended by Hillis and Wilcox (2005), thus necessitating many changes in the binomial names of common American species.

Although Frost et al. (2006) and Dubois (2006) recommended massive changes in the species names for New World true frogs, nothing in the *ICZN* rules compels biologists to follow their recommendations. The recommendations of Hillis and Wilcox (2005) with regard to the specific names of these frogs are equally valid and consistent with the *ICZN* rules. Moreover, I argue that most biologists will see clear advantages to maintaining the traditional species names for these frogs. Consider the consequences of the subjective change from *Rana pipiens* to *Lithobates pipiens*, as recommended by Frost et al. (2006) and Dubois (2006). If one conducts a Google search on the World Wide Web for “*Rana pipiens*,” about 300,000 pages are returned. A search for “*Lithobates pipiens*,” in contrast, returns 13 pages. Likewise, a search of GenBank (<http://www.ncbi.nlm.nih.gov/entrez/query.fcgi>) using “*Rana catesbeiana*” returns 593 sequences, whereas a search using “*Lithobates catesbeianus*” returns none. A search in Web of Science for published scientific papers on “*Rana catesbeiana*” produces a list of 1867 references, whereas a search on “*Lithobates catesbeianus*” returns none. Using Dubois’ recommended long form, *Lithobates (Aquarana) (group clamitans) catesbeianus* Shaw, 1802, is not likely to improve the situation for any of these searches. The name *Lithobates* is in the GenBank classification, but it is used as the name is defined phylogenetically, not in one of the various other senses of the name as used by Frost et al. (2006) or Dubois (2006). Indeed, the multiple meanings of the same taxon names recommended by Dubois (2006) is highly problematic for taxonomic search engines in general.

7. Conclusions

It is worth noting that the differences in taxonomic recommendations among Hillis and Wilcox (2005), Frost et al. (2006), and Dubois (2006) have nothing to do with issues of

the phylogenetic relationships of the relevant species. The phylogenetic hypotheses of true frogs presented by Hillis and Wilcox (2005) and Frost et al. (2006) are virtually identical (and Dubois also accepted these phylogenetic hypotheses in making his taxonomic recommendations). The species of New World true frogs analyzed by Frost et al. (2006) were a small subset of the species analyzed by Hillis and Wilcox (2005), but the minor differences in species placement between these two studies do not affect any of our recommendations. We have all recommended species-level taxonomies that are consistent with the *ICZN* rules. The differences come only in whether to retain widely used species names, and whether and how to recognize names for clades discovered in our respective analyses.

I suspect that most readers of this journal will wonder what the fuss is all about, since none of this discussion revolves around differences of opinion about molecular data, or phylogeny, or evolution. Thus, it may seem odd to have this discussion in a journal called *Molecular Phylogenetics and Evolution*. Many phylogeneticists feel as Felsenstein (2004) did when he advocated the “It-Doesn’t-Matter-Very-Much school of classification.” Felsenstein (2004, p. 145) noted that evolutionary biologists “... use phylogenies a great deal. But, having an estimate of the phylogeny in hand, they do not make use of the classification.” The problem, however, comes not from evolutionary biologists who know how to use phylogenetic information, but from the far greater number of biologists who only see phylogenetic information as it is reflected in a classification. Most users of GenBank, for instance, are far more likely to be exposed to the GenBank classification than they are to the phylogenetic analyses upon which the classification is based. Therefore, the systems we use to translate phylogenetic findings into systems of words are important, if only to ensure that all our phylogenetic studies do not go for naught. Many phylogenies get used only to the extent that they are translated effectively into a classification.

How should we deal with the facts that there are competing systems for the formation of scientific names, and that the oldest and most widely used systems (for animals, the *ICZN*) predates (and even sometimes excludes) evolution-

ary and phylogenetic advances? My recommendation is that we strike a compromise, and attempt to live with both systems, at least until the *ICZN* and its sister codes are amended to allow biologists to name the various parts of the Tree of Life. Biologists can follow the *PhyloCode* to name the clades of life, and provide a direct and unique system of names to describe the monophyletic groups that we discover. In following the *PhyloCode*, I advocate using *ICZN*-based names wherever possible, to minimize any taxonomic confusion. At the same time, biologists can follow the *ICZN* rules to name the species of animals (and the other traditional codes to name the species of other groups), and use the *PhyloCode* definitions to stabilize usage of the binomials. By following these compromises, we can stabilize nomenclature (by preventing subjective changes in species names), and make nomenclature consistent with modern phylogenetic analyses at the same time.

What are the alternatives? Dubois (2006) claims that there is no formal way to name multiple hierarchical groups of taxa below the level of genus under the *ICZN* rules. If one accepts his conclusion, then there need be no significant conflict between the *ICZN* and *PhyloCode* names in this case. Biologists who wish to retain existing usage of species names, and follow either system of nomenclatural rules, can use the species names recommended by Hillis and Wilcox (2005), and continue using the name *Rana* in association with New World true frogs. Biologists who want to use names to refer to the various monophyletic groups within *Rana* can use the classification suggested by Hillis and Wilcox (2005). Or, biologists may choose to accept the recommendations of Dubois (2006), in which case they will have to accept that no names can be used to refer to most of the monophyletic groups of true frogs, and they will have to learn new names for most the species (and live with the fact that the new names are largely disconnected to the vast lit-

erature of these species). Fortunately, biologists are free to make these decisions for themselves.

Acknowledgments

I thank David Cannatella, Kevin de Queiroz, Jacques Gauthier, Greg Pauly, and David Wake for suggestions on the manuscript. My work on amphibian phylogeny is supported by an grant from the National Science Foundation's Assembling the Tree of Life Program (EF-0334952).

References

- Cantino, P.D., Bryant, H.N., de Queiroz, K., Donoghue, M.J., Eriksson, T., Hillis, D.M., Lee, M.S.Y., 1999. Species names in phylogenetic nomenclature. *Syst. Biol.* 48, 790–807.
- de Queiroz, K., Gauthier, J., 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Syst. Zool.* 39, 307–322.
- de Queiroz, K., Gauthier, J., 1992. Phylogenetic taxonomy. *Ann. Rev. Ecol. Syst.* 23, 449–480.
- de Queiroz, K., Gauthier, J., 1994. Toward a phylogenetic system of biological nomenclature. *Trends Ecol. Evol.* 9, 27–31.
- Dubois, A., 1992. Notes sur la classification des Ranidae (Amphibiens Anoures). *Bull. Société Linnéenne de Lyon* 61, 305–352.
- Dubois, A., 2006. Naming taxa from cladograms: a cautionary tale. *Mol. Phylogenet. Evol.* 42, 317–330.
- Felsenstein, J., 2004. *Inferring Phylogenies*. Sinauer, Sunderland, MA.
- Fitzinger, L., 1843. *Systema Reptilium*. Vienna.
- Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M., Wheeler, W.C., 2006. The amphibian tree of life. *Bull. Am. Mus. Nat. Histol.* 297, 1–370.
- Hillis, D.M., Davis, S.K., 1986. Evolution of ribosomal DNA: fifty million years of recorded history in the frog genus *Rana*. *Evolution* 40, 1275–1288.
- Hillis, D.M., Frost, J.S., Wright, D.A., 1983. Phylogeny and biogeography of the *Rana pipiens* complex: a biochemical evaluation. *Syst. Zool.* 32, 132–143.
- Hillis, D.M., Wilcox, T.P., 2005. Phylogeny of the New World true frogs (*Rana*). *Mol. Phylogenet. Evol.* 34, 299–314.