

RESPONSE TO THE *POINT OF VIEW* OF GREGORY B. PAULY, DAVID M. HILLIS, AND DAVID C. CANNATELLA, BY THE ANURAN SUBCOMMITTEE OF THE SSAR/HL/ASIH SCIENTIFIC AND STANDARD ENGLISH NAMES LIST

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“Stultum facit Fortuna quem vult perdere”—Publius Syrus, Maxim 911

ABSTRACT: The *Point of View* by Gregory Pauly, David Hillis, and David Cannatella misrepresents the motives and activities of the anuran subcommittee of the Scientific and Standard English Names Committee, contains a number of misleading statements, omits evidence and references to critical literature that have already rejected or superseded their positions, and cloaks the limitations of their nomenclatural approach in ambiguous language. Their *Point of View* is not about promoting transparency in the process of constructing the English Names list, assuring that its taxonomy is adequately reviewed, or promoting nomenclatural stability in any global sense. Rather, their *Point of View* focuses in large part on a single publication, *The Amphibian Tree of Life*, which is formally unrelated to the *Standard English Names List*, and promotes an approach to nomenclature mistakenly asserted by them to be compatible with both the *International Code of Zoological Nomenclature* and one of its competitors, the *PhyloCode*.

Key words: Amphibia; *Bufo*; *Rana*; Species names; Taxonomic stability; Zoological nomenclature

In their *Point of View* (p. 115–128) Gregory B. Pauly, David B. Hillis, and David C. Cannatella (subsequently referred to as PHC) allege that the Society for the Study of Amphibians and Reptiles (SSAR), American Society of Ichthyologists and Herpetologists (ASIH), and Herpetologists' League (HL), which sponsor the *Scientific and Standard English Names of Amphibians and Reptiles of North America* (Crother, 2008), through their selection of committee members and endorsement of review procedures, deemed inadequate by PHC, have confounded and confused users of such lists, thereby engendering taxonomic chaos (their term). While some of PHC's points deserve careful consideration, their document is in fact an attack on the amphibian taxonomy proposed and the analytical methods used by Frost et al. (2006)⁵. PHC suggest that their criticisms of our anuran Scientific and Standard English Names subcommittee are elements of a widely-held taxonomic and nomenclatural

viewpoint. However, evidence from publications, including those of their own research group, suggests otherwise. As we will show, the PHC document contains an abundance of misinformation and misleading statements and reflects a pattern of omission or mis-citation of critically relevant literature, as well as exclusion of evidence where it serves their purpose.

PHC pose as disinterested scientists attempting to protect non-systematists from dangerous ideas. However, if their approach were to be applied generally the central principles of the *International Code of Zoological Nomenclature* (Dubois, 2006b, 2007;

⁵ Relevant to this discussion is that Hillis and Cannatella are two of the PI's on a major NSF grant, *AmphibiaTree*, funded in 2003, to produce a not-yet-published comprehensive tree and taxonomy of all amphibians. The amphibian biology website, *Amphibia-Web* (<http://amphibiaweb.org/aw/about/index.html>) is an extension of this same *AmphibiaTree* consortium and largely reflects the viewpoints promoted by PHC. The funded proposal, made available by NSF in redacted form, can be downloaded from <ftp://files8.cyberlynk.net> (username: NSF_grant; password: anonymous).

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ICZN, 1999), which regulate a nomenclatural system that has been universally accepted effectively for 250 years, must be substantially abandoned or modified.

But, regardless of what we, Pauly, Hillis, or Cannatella do at this moment in time, the amphibian systematics community will follow its own course, as it has for more than two centuries. The taxonomy it adopts and nomenclatural codes it follows will depend largely on the state of revisionary publications and perceptions of what is *useful*. No one gets to have the last word. Lifetimes are short, discoveries are effectively unlimited, and the intellectual and social fabric of systematics changes, not only with each scientific revolution (Kuhn, 1962), but with each retirement and subsequent hire.

AGREEMENT WITH PAULY, HILLIS,
AND CANNATELLA

Before we address the specific issues raised by PHC, let us first state that we agree with them that professional societies should not officially adopt scientific names. As discussed elsewhere (Crother, 2009: 133), the term "official" on the title page was used primarily to promote common usage of non-scientific names and to distinguish this list from an online list of English names produced by the Center for North American Herpetology (Collins and Taggart, 2009: <http://www.naherpetology.org>). Any implication of scientific names being official (whatever that might mean in practice) would obviate the intent of the SSAR-HL-ASIH annotated names list, which, beyond its primary objective of presenting a set of standardized English names for North American taxa, was to invite additional work on the species listed by pointing out lacunae in our knowledge of these taxa. PHC indicated that we should have discussed taxonomic levels above species more fully and commented on every change in nomenclature since 2001. Moreover, they wondered why we did not adopt or discuss conventions that they considered important, and they suggested why they thought this was so, including the allegation that we are legislating taxonomy. Obviously, additional discussion was warranted and we provide that here. Regardless, none of this would have

changed the scientific names we chose to adopt. Had we felt the need to justify the name changes more fully, we would simply have cited the literature (none of which was referenced by PHC) that had already rejected or superseded the positions advocated by PHC (e.g., Che et al., 2007; Dubois, 2006b, 2007; Frost et al., 2008a); these citations will appear in the *Standard English Names* list when it goes online.

We also agree with PHC about two goals of a taxonomy: to provide a reference system that (1) facilitates communication and (2) reflects evolutionary history. The first goal may be guided by the principle of stability and the second by the notion of monophyly. But, we think that PHC have missed a third goal of taxonomy, which is to promote cogent comparisons and to invite additional systematic work by bringing attention to previously overlooked taxonomic units. The traditional methods to this end have been the publication of sound taxonomic work with appropriate taxonomic partitions and nomenclatural designations. The history of taxonomy reflects a balancing act among these three goals, at different times tipping in different directions as progress is made. PHC lean strongly in favor of stability (part of goal 1) but completely neglect goal 3. In the short term this has merit, as do all three of the goals, but in the longer term, as discussed below, this makes for practical problems.

"TAXONOMIC CHAOS" - IS IT REAL?

The issues addressed in the PHC paper surround the notion that by adopting a taxonomy that recognizes genera smaller than those preferred by PHC, the English Names anuran subcommittee promoted "taxonomic chaos," something we have not noticed in our heavy use of current systematic and conservation literature, and something we do not find evident in any other field of herpetology, either. In addition, Frost and McDiarmid are, in PHC's opinion, overly influential in promoting confusion, apparently because of their willingness both to support new, *useful* taxonomies and to work on taxonomic catalogs that serve to limit confusion among non-systematists (e.g., *Amphibian Species of*

the World [ASW; <http://research.amnh.org/herpetology/amphibia/index.php>]; *Integrated Taxonomic Information System* [ITIS; <http://www.itis.gov/>]). Neither Frost nor McDiarmid has any relationship with *AmphibiaWeb* (<http://amphibiaweb.org/>; associated with PHC's *AmphibiaTree* consortium), which did not adopt any of the Frost et al. (2006) taxonomy below the level of family-group, or with the *IUCN Red List* (<http://www.iucnredlist.org/>) which largely did adopt the taxonomy of Frost et al. (2006). So, the larger issue for PHC seems to be that for some taxa there is more than one message being provided among websites and in the literature. What PHC do not mention is that taxonomic practice by non-Austin members of the *AmphibiaTree* consortium does not meet PHC's current standard of taxonomic practice, either, so we can only conclude that PHC's point of view is not widely shared among workers within that work-group.

PHC apparently support the idea that nomenclatural changes, unless required to represent monophyletic taxonomies (but regardless of *any* other kind of utility, such as reflecting the age of a taxon or reducing a nomenclatural unit to a more manageable size), are bad if they affect species found in the United States, while identical classes of changes—such as those supported by their own *AmphibiaTree* grant—that affect the names of *severely* endangered species *outside* of the United States are good. Examples of “taxonomic chaos” laid by PHC at the feet of Frost et al. (2006) are (1) a redelimiting of the former genus “*Rana*” such that species in the Americas are now members of the either the genus *Lithobates* or a redelimited *Rana* (which was further partitioned in the Old World; see also Che et al., 2007), and (2) a partitioning of the former genus “*Bufo*” such that species in the Americas are now members of the genera *Anaxyrus*, *Incilius*, *Nannophryne*, *Rhaebo*, and *Rhinella* (and, like the former *Rana*, further partitioned in the Old World). Similarly, Hedges et al. (2008), in a publication arising from the *AmphibiaTree* grant, partitioned the formerly enormous genus *Eleutherodactylus* (>800 species) into four *families*: Brachycephalidae: *Ischnocnema* (part); Craugastoridae: *Craugastor* and *Haddadus*; Eleutherodactylidae: *Diasporus* and

Eleutherodactylus (redelimited); and Strabomantidae: *Pristimantis*, *Hypodactylus*, *Lynchius*, and *Strabomantis*. It may be that PHC do not approve of the taxonomic changes in Hedges et al.'s (2008) landmark revision because many of their changes go beyond the minimum required to render a monophyletic taxonomy. Cannatella, nevertheless, seems to have adopted these nomenclatural novelties (e.g., see Elmer and Cannatella, 2008).

Numerous major taxonomic revisions of recent years (e.g., Faivovich et al., 2005 [revision of Hylinae]; Glaw and Vences, 2006 [revision of Mantellidae]; Grant et al., 2006 [revision of Dendrobatoidea]; Hedges et al., 2008 [revision of former Brachycephalidae, now Brachycephalidae, Craugastoridae, Eleutherodactylidae, and Strabomantidae]) and their resulting nomenclatural changes have been rapidly and widely accepted by investigators who deal with the substantial amphibian biodiversity outside of the United States (of which at least 32% are threatened or extinct; Stuart et al., 2008). These revisions reduced the ambiguity resulting, in part, from extremely large genera. *Hyla*, *Mantidactylus*, *Colostethus*, and *Eleutherodactylus* were all partitioned beyond the minimal amount allowed under the PHC dictate, but these partitions have enhanced clarity, not promoted any substantial confusion. It is also clear that workers from biodiverse countries (e.g., Argentina, Brazil, China, Colombia, India, Mexico, South Africa, Sri Lanka) as well as those from newer centers of taxonomic expertise outside of the United States (e.g., Belgium, Germany, Spain) are now increasingly driving amphibian taxonomy, with the United States becoming less influential. A few contrary Americans are not going to hold back this tide.

The taxonomic changes in Bufonidae and Ranidae with which PHC take particular issue were published more than three years ago (Frost et al., 2006) and enjoy a healthy level of acceptance and professional discussion outside of the immediate *AmphibiaTree* work-group, by those who publish on the systematics of these groups (e.g., Caramaschi and Pombal, 2006; Chaparro et al., 2007; Che et al., 2007; Di Candia and Routman, 2007;

Fouquet et al., 2007; Goebel et al., 2009; Lehr et al., 2007; Lima et al., 2007; Maciel et al., 2007; Padiál et al., 2006; Pramuk et al., 2008). PHC provide no evidence to support their assertion that adopting scientific names in our English Names list that delimit groups smaller than they prefer promotes misunderstanding more than clarity. Moreover, if evolving taxonomies create such a fundamental problem, one wonders why ecologists, cell biologists, physiologists, government agencies, and conservation biologists, rather than the *AmphibiaTree* competitors of the Frost et al. (2006) team, are not calling for resolution.

PHC also cite several authors for support of taxonomic stability, which like mother and apple pie is tough to argue against when taken out of context. The authors cited by PHC predictably include, among others, the pre-phylogenetic authors George Gaylord Simpson and Ernst Mayr, one of the two authors of the *PhyloCode* (Philip D. Cantino), and Frost's colleague Eugene S. Gaffney. The Gaffney citation only tenuously supports the PHC view and appears to hinge on a single phrase within Gaffney's section *Classification: Stability is ignorance* (Gaffney, 1979: 103): "I hardly advocate change for its own sake ..." Nevertheless, Gaffney supports neither the methods of PHC nor their nomenclatural philosophy (e.g., see Gaffney et al., 2006). The paper by Godfray and Knapp (2004) also does not support the positions of PHC, even though PHC cited it as supporting their statement about taxonomies based on "poorly supported branches, or for issues unrelated to monophyly ..." and their statement, simply untrue, that Godfray and Knapp (2004) supported the view that changes have "brought the ire of many biologists ... and only promote the increasing disregard of the field."

Godfray and Knapp's (2004) paper warrants complete and careful reading; it is a great deal more textured than implied by PHC. A relevant quotation (pp. 561–562, see below) clarifies PHC's misleading citation, provides enormous irony, and suggests that PHC's proposed changes to the traditional practices of zoological nomenclature are fraught with new problems:

"There is intense competition for science funding today and any field seeking new or continuing monies is obliged both to point to its past history of success and list the enthusiastic end-users of its products. Taxonomy as currently practiced can do both, yet the adoption of PhyloCode or similar proposals risks both. Reinventing nomenclature suggests that the Linnaean system of the past 250 years is not the success we claim, but rather a blind alley. It also risks severely alienating most people who use taxonomy. You need only look at how taxonomists are sometimes portrayed by their colleagues in other fields: as scientists who do a valuable job yet have the irritating habit of changing names for no apparent purpose. The wholesale abandonment of the Linnaean naming system and its replacement by a new and untried method would destroy the support base for the field and imperil its survival. And it is not as if we cannot have our cake and eat it too. Especially today with modern Web technologies we can link Linnaean taxonomies with phylogenetic hierarchies and have the benefits of both."

We think that Godfray and Knapp (2004) are correct (see also Godfray et al., 2007; Sluys et al., 2004) and that PHC have underestimated the power of the web and online nomenclators to ameliorate "the irritating habit of changing names for no apparent purpose", but readers should realize that PHC are the ones casting aspersions on systematists, not Godfray and Knapp (2004), and that PHC should be pointing to their past history of success and to the enthusiastic end-users of their products, not deriding Frost et al. (2006) and certainly not criticizing the anuran subcommittee of the *Names* list. We concur with Godfray and Knapp's (2004) that replacing one system of nomenclature with another, the *PhyloCode* (or the related approach asserted by PHC to represent a compromise), which has its own problems of instability (see see Dominguez and Wheeler, 1997, and Frost et al., 2006: 144, and footnote 26 therein), may be ill-advised, especially if the change is promoted through misleading statements and misrepresentations, and contrary evidence is ignored, as was pointedly noted by Dubois (2006b, 2007).

PHC's misrepresentation of the Godfray and Knapp (2004) article goes further—it is an overview article that refers to Mace (2004; in the same journal issue) regarding the tension between taxonomy and conservation. Mace (2004) clearly focuses the problem of taxonomic confusion at the species level, because issues such as species boundaries, subspecies (whatever this term may mean), and Evolutionarily Significant Units may cause significant confusion in the process of formal conservation listings and in courts of law. Mace (2004) makes no mention of any possible taxonomic chaos above the species level. Indeed, the IUCN adoption of the generic taxonomy so criticized by PHC indicates that the realm of conservation embraces, rather than decries, taxonomic efforts above the species level. Mace (2004) makes an elegant plea for conservationists and taxonomists to work together on matters related to species concepts and relevant taxonomic issues. Ironically, by presuming they understood the basic issue at hand and neglecting the primary literature, PHC have nominated themselves as another example of Ivory-Tower elitism with respect to the increasingly crucial field of amphibian conservation.

In this day of web-based sources of information (e.g., *AmphibiaWeb* [maintained by D. B. Wake and supported, in part, at least historically by the University of California, Berkeley and in part, by NSF funds awarded to the *AmphibiaTree* work-group] and *Amphibian Species of the World* [maintained D. R. Frost and supported by the American Museum of Natural History]), no one has to wonder to which natural population a particular amphibian name applies. Therefore, the justification for authoritarian nomenclatural stability, never strong, has evaporated, and systematists have increased freedom to ramp up the rates of discussion, naming of taxa, testing of hypotheses, and promotion of research advocating new taxonomies. Indeed, taxonomists are not confused by nomenclatural changes and see them for what they are, aspects of the discussion among systematists that promote work on various taxonomic groups, shed light on new questions, compel irritated systematists to write *Points of View*

and to defend their territories with new data and larger studies, and respond to the notions of what taxonomists think are *useful* within the canon of monophyly.

As noted above, non-systematists in the conservation world are not confused by changing nomenclature, as evidenced by IUCN's adoption, through its *Red List of Threatened Species* (<http://www.iucnredlist.org/amphibians>) (also supported by Conservation International and NatureServe) of the taxonomy criticized by PHC at the first possible opportunity (well before *ITIS*, and with *AmphibiaWeb* as a counter-example). Like *Amphibian Species of the World* and *AmphibiaWeb*, the online *IUCN Red List* can be searched by common synonyms (all synonyms in *Amphibian Species of the World*) so as to obviate any possibility of the confusion that PHC suggest is such a serious problem. In addition, the ongoing revolution in amphibian taxonomy has made its way into textbooks written by critical scientists knowledgeable about the ongoing issues (e.g., Vitt and Caldwell, 2009), which assures that an unfamiliar taxonomy will not remain unfamiliar for long.

We recognize that PHC may regard *Amphibian Species of the World* and the *IUCN Red List* as inherent sources of confusion, inasmuch as having adopted the Frost et al. (2006) taxonomy, they are not consistent with the taxonomy employed by *AmphibiaWeb*, which largely adheres to their viewpoint in “*Rana*” and “*Bufo*”, although it does not formally address subgenera nor allow for them to be searched for explicitly. Presumably, *AmphibiaWeb* will evolve to better meet PHC's approach in the near future. If so, then we will have to question whether employing two nomenclatural systems (ICZN, 1999; *PhyloCode*) in a single database that does not reveal to the user which system governs what names will reduce or increase taxonomic confusion (Sluys et al., 2004). Regardless, suppose that *Amphibian Species of the World*, *AmphibiaWeb*, and the *IUCN Red List* never are totally in agreement. Can that be demonstrably bad when differences of opinion are what drive the whole scientific process (Hull, 1988)?

Regardless of the points made by PHC and discussed more fully below, we expect that

large genera (such as *Rana* and *Bufo*, sensu PHC) will continue to be partitioned in an effort to render tractable units that invite additional work and that will guide non-systematically-informed comparative biologists toward cogent comparisons much more effectively than do arcane cladograms. For recent examples, see the partition of *Mantidactylus* (Glaw and Vences, 2006); redelimitation of several genera of Ranidae, including “*Rana*” (Che et al., 2007); the continuing struggle to understand relationships within Rhacophoridae, resulting in generic redelimitations (e.g., Grosjean et al., 2008); recent attempts to develop generic naming conventions that are congruent with the age of a taxon (e.g., *Hydromantes*, *Atylodes*, and *Speleomantes* partitioned out as genera from 2007—a partition supported by *AmphibiaTree* funds and co-authored by one of the PIs, but not reflected in *AmphibiaWeb*); and changes in family-groups, such as the partition of the monophyletic groups Hylidae and Microhylidae based on taxon age (Bossuyt and Roelants, 2009). Partitioning has been a *useful* standard practice for the entire history of systematics and is the reason that there are more than three amphibian genera (i.e., *Rana* Linnaeus, 1758, *Salamandra* Laurenti, 1768, and *Caecilia* Linnaeus, 1758), the minimum required to provide for named monophyletic genera for frogs, salamanders, and caecilians, rather than the >500 genera of living amphibians currently recognized (Frost, unpublished data). The putative confusion resulting from taxon partitioning decried by PHC has been part and parcel of systematics since its beginning, reflects the growth of systematics as it deals with more and more species, and has not presented any credible impediment to communication.

The standard familial classification of amphibians prior to Frost et al. (2006) was formulated in the 1970’s (e.g., Duellman, 1975; Heyer, 1975; Heyer and Liem, 1976; Kluge and Farris, 1969; Laurent, 1980 “1979”, 1986; Liem, 1970; Lynch, 1971, 1973; McDiarmid, 1971) when the number of species of amphibians known was less than half of that known today. For instance, in the 1970’s Dendrobatidae contained approximately 70 species, but by the time of Grant et al.’s

(2006) revision, the number had grown to about 250. Such growth without taxonomic restructuring makes for unwieldy groups that do not invite additional work. Ranks such as subgenus are rarely encountered and easily misunderstood by non-systematists and are unlikely to be commonly used or reflected in secondary literature; as a result they will have little impact on non-systematic comparative literature. Therefore, we think the recommendation by PHC to extensively employ the subgenus category to ameliorate the discomfort of name changes for English-speaking North Americans is doomed to failure, first, because taxonomic nomenclature is an international endeavor played on a global field without national preference, and second, because this use of subgenera in practice equates to concealing diversity from the non-systematics community.

PHC may assert that phylogenetic definition of name placement is an important part of the answer to the problem that they perceive, but even they have not been able to stick to their own definitions. For example, if the definition of Hylidae of Ford and Cannatella (1993) and Cannatella and Hillis (2004) is applied to our current understanding of the phylogeny of frogs (e.g., Frost et al., 2006; Grant et al., 2006), minimally the following must be placed within Hylidae (to the serious distortion of any traditional understanding of that taxon): Aromobatidae, Bufonidae, Centrolenidae, Ceratophryidae, Cycloramphidae, Dendrobatidae, Hylodidae, Leiuperidae, and Leptodactylidae. But, Darst and Cannatella (2004) saw this coming and redefined Hylidae by implication to exclude Hemiphractinae because they showed the latter taxon to be far from other nominal hylids. This kind of redelimitation is necessary if one is concerned about keeping content and diagnosis as stable as possible with respect to the traditional use of the term Hylidae. This one example suggests to us that the efforts of PHC to stabilize nomenclature through definition of names will largely be obviated by what the future will bring: an onslaught of new people, new ideas, epistemological considerations, and ever denser taxon sampling.

PHC also suggest that an extremely broad external review of the scientific names to be

used in a *Names* list would prevent such lists from being controversial and therefore, in their view, make them much more useful. Of course, being noncontroversial would militate against *any* kind of change (and certainly would retard the adoption of new approaches, such as Phylogenetic Taxonomy, which PHC are promoting). This is similar to the implication by Hillis (2007) who noted that the name *Rana pipiens* had enormously more hits in *Google* than did *Lithobates pipiens* and that this was evidence of how confusion could be propagated by name changes and critical literature lost. However, Dubois (2007: 399–400) provided evidence that this superficially reasonable viewpoint, if applied for more than a brief period would have severely negative effects (citation dates modified to reflect our Literature Cited):

“I had the curiosity to repeat his Google searches and I found different, but similar results for the same nomina (e.g., about 369 000 results for *Rana pipiens* versus 151 for *Lithobates pipiens*), but I also obtained other interesting results with other nomina: e.g., about 20 900 references for *Rana kuhlii* versus 1130 for *Limnonectes kuhlii*; about 18 700 results for *Rana limnocharis* versus 858 for *Fejervarya limnocharis*; or about 19 400 references for *Rana breviceps* versus 403 for *Sphaerotherca breviceps*. However, the three latter species, first removed from *Rana* by Dubois (1981, 1987 “1986”, 1992), are now universally accepted as belonging, not only in other genera, but also in other subfamilies (Dubois, 2005a) or even families (Frost et al., 2006). Following Hillis’ (2007) suggestion would require to come back to the obsolete, although long prevalent, ranid taxonomies of Boulenger (1918, 1920a, b), Inger (1954, 1966, 1968) and many others. As another example, a Google search for *Tomopterna breviceps* produced 1550 results, i.e., much more than *Sphaerotherca breviceps*, which, to please Google users, would require ignoring the works of Glaw et al. (1998) and Vences et al. (2000), as well as all subsequent works, which confirmed their main results.”

In our view the PHC viewpoint in application would likely help retard progress in the

United States compared to the forward motion of the rest of the amphibian biologist community. The international community of amphibian conservation biologists and systematists are getting species and monophyletic groups named and nomenclaturally sorted (e.g., Alam et al., 2008; Antunes et al., 2008; Barrio-Amorós et al., 2008; Biju and Bossuyt, 2009; Bossuyt and Dubois, 2001; Chaparro et al., 2008; Cruz et al., 2008; Das, 2008; Fei et al., 2008; Günther, 2008; Köhler et al., 2008; Kuzmin, 2008; Li et al., 2008; Manamendra-Arachchi and Pethiyagoda, 2005; Padial et al., 2008) at an increasing rate compared to that of the USA. Further, we doubt if imposing an additional level of social inertia by English-speaking North Americans on international nomenclature would be seen by the international community as positive. Would Chinese authors who recognize *Lithobates* (ca. 50 species), thereby underscoring the distinctiveness of *Rana* (the *Rana temporaria* group and close relatives, ca. 50 species) from its close Asiatic relative, *Pseudorana*, (2 species) (see Che et al., 2007), want their taxonomy judged by people who have no substantive knowledge of the systematic issues in Asian ranids? We doubt it. Moreover, progress is rapid, due to the increasingly easy acquisition and analysis of large amounts of data and the availability of rapid publication outlets such as *Zootaxa*.

TAXONOMIC PROBLEMS OF SPECIAL CONCERN

PHC singled out two of our taxonomic treatments (Frost et al., 2008b) as problems of special concern: one regarding American bufonids and the other concerned with American ranids. They suggested specific nomenclatural remedies to reduce the taxonomic confusion that they asserted was created by our treatment of these groups, which we here address in some detail. We apologize to the general reader at this point because to answer adequately the accusations in PHC requires very specific and technical responses regarding phylogenetic reconstruction and evidence (both of which PHC have played fast and loose) and the *PhyloCode*. Moreover, the questions raised by PHC cannot be restricted to North America, although that is PHC’s preferred arena,

inasmuch as revisionary name changes have global effects.

“BUFO”

First, we (Frost et al., 2008b) erred in listing one generic name for some North American toads. The seniority of *Incilius* Cope, 1863, over *Ollotis* Cope, 1875 “1876”, and *Cranopsis* Cope, 1875 “1876” is clear and was independently discovered by PHC, Frost et al. (2009), and Jeff Boundy (pers. comm. to DRF). We regret the error. However, errors happen unless one never makes any taxonomic changes—seemingly the position taken by Pauly and Cannatella and close associates. This was the case with “*Bufo*” in which the obvious and documented paraphyly of “*Bufo*”, sensu lato (Graybeal and Cannatella, 1995; Pauly et al., 2004) went unaddressed, at least until Frost et al. (2006).

PHC’s discussion of “*Bufo*” taxonomy revolves around a reanalysis of the Frost et al. (2006) data purporting to provide PHC with the basis to consider *Rhinella* (sensu Chaparro et al., 2007), *Incilius*, and *Anaxyrurus* as subgenera, along with the *Bufo bufo* group (Eurasian) within a redelimited *Bufo*. Analysis of evolutionary tree structure rests on (a) assumptions and concomitant operations of analysis (e.g., transformation cost functions); (b) data; and (c) selection of terminal taxa. Minor changes in any of these three categories can have major effects, so what constitutes a test of a phylogenetic hypothesis is epistemologically an important area of discussion. In our view if an analytical technique is being discussed, b and c must remain constant, or be augmented, not reduced. In this case Pauly and Cannatella have changed all three, called it a reanalysis of the data from Frost et al., 2006, and then made a big deal of the differences between the two analyses. Cannatella and Pauly’s unpublished reanalysis is based on reducing the amount of evidence under consideration from that employed by Frost et al. (2006) to just 12S and 16S mtDNA data; the exclusion of the problematic *Rhinella margaritifera* (discussed by Pauly et al., 2004); not looking for the best overall solution of the two nested NP-complete problems; and, seemingly not basing their analysis on denser taxon sampling

nor including all the relevant data available (e.g., data from Chaparro et al., 2007; Clarke, 2001; Cunningham and Cherry, 2004; Frost et al., 2006; Graybeal, 1997; Graybeal and Cannatella, 1995; Matsui et al., 2007; Mendelson et al., 2005; Pramuk, 2000, 2002, 2006; Pramuk et al., 2001; Pramuk and Lehr, 2005; Pramuk et al., 2008; Wasonga and Channing, 2007). A reanalysis of a *subset* of Frost et al.’s data and terminals does not constitute a scientific test of the Frost et al. (2006) hypothesis. Moreover, it is not evident how the Cannatella-Pauly analysis extends beyond the studies of Pramuk (2006, 2008) and Chaparro et al. (2007), who provided far more evidence. PHC do not explain this nor how fewer data are better than more, particularly given that increasingly dense taxon sampling is needed to apprehend additional homoplasy (Wheeler, 1992; Zwickl and Hillis, 2002). Perhaps the Cannatella and Pauly manuscript, which we have not seen, contains substantially more substance than implied by PHC and we have misunderstood the intent of their critique. We hope that their new bufonid manuscript will address a number of genera not sampled by Frost et al. (2006) that appear to be nested within traditional “*Bufo*” (i.e., *Adenomus*, *Altiphrynoidea*, *Andinophryne*, *Bufoidea*, *Churamiti*, *Crepidophryne*, *Laurientophryne*, *Nimbaphrynoidea*, *Parapelophryne*, *Pseudobufo*, and *Sabahphrynus*, as well as the hugely interesting and unallocated “*Bufo stomaticus*” and “*Bufo orientalis*” groups). The inclusion of all of these diverse taxa within *Bufo*, together with substantial amounts of new data, could significantly alter the names of the species associated with those genera as well as the traditional concept of *Bufo* as a similarity cluster.

PHC misrepresent Frost et al. (2006) regarding the partition of *Bufo* (sensu lato), in part by not presenting the entire Frost et al. (2006) tree of bufonids, which is reproduced in Fig. 1. It shows in dark gray what Frost et al. would have had to call *Bufo* in order to meet PHC’s criterion of United-States-first taxonomic stability. The difference between PHC’s tree (their Fig. 1A) and the original Frost et al. tree, is that an African clade composed of *Capensibufo*, *Stephopaedes* (now in *Mertensophryne*), and various groups of

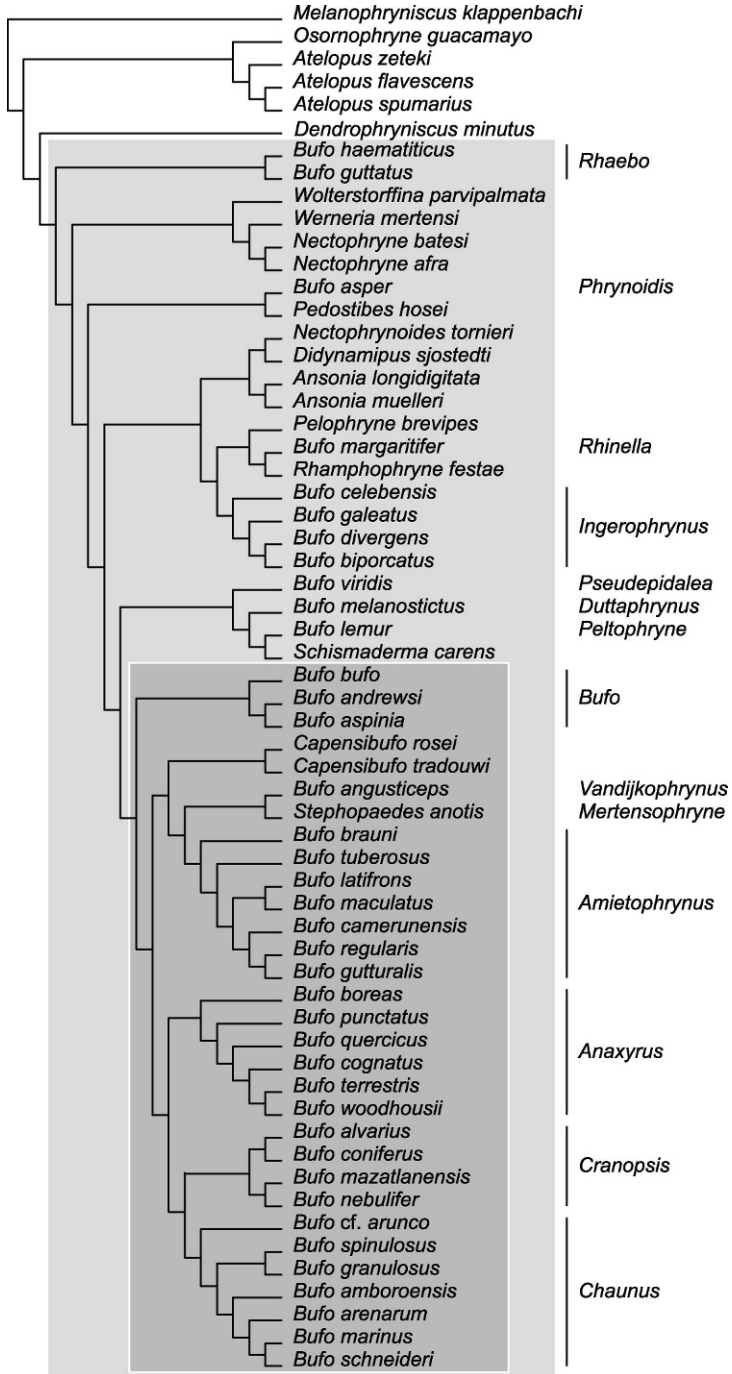


FIG. 1.—Bufonid section of the Frost et al. (2006) tree, modified to show in light gray what taxa would minimally have to be included within *Bufo* to retain all former members of *Bufo* within that taxon (Cranopsis of Frost et al., 2006, is now *Incilius*). The dark gray polygon represents the smallest group of taxa that would have to be included to retain all North American bufonid taxa within nominal *Bufo*. Note the placement of “*Bufo*” *margaritifer*, the type species of *Rhinella*, and excluded from the reanalysis of PHC. The status of *Chaurus* with respect to *Rhinella* is covered in text.

African “*Bufo*” (e.g., including what are now *Vandijkophrynus* and *Amietophrynus*) intrudes between *Bufo* sensu stricto and the American clade composed of *Anaxyrus*, *Incilius*, and *Chaunus*, with “*Bufo*” *margaritifer*, far from the *Anaxyrus*–*Incilius*–*Chaunus* clade in the Frost et al. (2006) tree. As noted above, “*Bufo*” *margaritifer* (the type species of *Rhinella*) was excluded from PHC’s rework of Frost’s data (their Fig. 1A), an astonishing omission that likely allowed PHC to obtain the results they did from their reanalysis (see discussion by Pauly et al., 2004, regarding this terminal taxon). Had Frost et al. (2006) wished to retain North American bufonids as *Bufo*, they minimally would have had to make *Capensibufo* and *Stephopaedes* synonyms or subgenera, a taxonomic change that Frost et al. (2006) did not believe would be embraced by those working with the African taxa. Further, Frost et al. (2006) considered American “*Bufo*”, with about 130 species, to be unwieldy. Had Frost et al. (2006) wished to retain all former “*Bufo*” as *Bufo* (as they noted in their 2006 paper they would have had to include every taxon they studied, as well as those reasonably placed there on the basis of other literature, within the lighter gray polygon, effectively placing all bufonids other than the atelopodines, *Melanophryniscus*, *Dendrophryniscus*, and likely *Truebella*, within an extremely large genus *Bufo*).

Beyond the peevish and arguable criticisms of the methods employed by Frost et al. (2006), the PHC reanalysis provides PHC with the tree that they apparently prefer, i.e., a monophyletic group composed of *Anaxyrus*, *Incilius*, and *Rhinella*, with *Bufo* (sensu stricto) as its sister taxon. They go on (Pauly et al., 2009: p. 124) to write:

“Similarly, results from Pauly et al. (2004), Pramuk (2006), and Pramuk et al. (2008), indicate that (1) the New World Clade sensu Pauly et al. (2004) is very strongly supported; this clade includes all of the North American species of the list; and (2) the New World Clade is closely related to, or the sister-group of, the *Bufo bufo* species group.”

We agree that the papers they cite suggest that the American taxa *Rhinella*, *Incilius*, and

Anaxyrus form an inclusive group. We cannot agree that all of the relevant papers (including Chaparro et al., 2007, not mentioned by PHC) signal that the Eurasian *Bufo* (sensu stricto) is the sister taxon to this inclusive group, or even especially closely related to it without a simultaneous analysis of all evidence and taxa so far presented.

The topology presented by Pauly et al. (2004) on the basis of ca. 2.5 kb of mtDNA suggests that minimally the sub-Saharan African taxon *Amietophrynus* (38 species) would fall into their redelimited *Bufo* as well. (This is substantially similar to what would be required in the Frost et al., 2006, tree [Fig. 1], formulated on the basis of many more data, assuming that Chaparro et al., 2007, are correct in nesting *Rhinella margaritifer* within former *Chaunus*.)

The preferred topology of Pramuk (2006), on the basis of 4 kb of nuDNA (POMC; RAG-1) and mtDNA (12S, tRNA^{val}, 16S) as well as 83 morphological characters suggested that the tropical Asian *Phrynoidis* (2 species), but not *Amietophrynus*, would have to be included in this group. Importantly, the topology reported by Chaparro et al. (2007), but not cited by PHC, based on about 4 kb of mtDNA (12S mtDNA) and nuDNA (POMC and RAG-1) suggested that *Phrynoidis* (2 species), the Indonesian *Ingerophrynus* (11 species), tropical Asian *Duttaphrynus* (6 species), and African *Schismaderma* (1 species) would have to be included in that group.

The only topology that corroborates the narrow conclusion of PHC, based on a subset of the data provided by Frost et al. (2006), is the topology of Pramuk et al. (2008), based on 2.5 kb of mtDNA (12S, tRNA^{val}, 16S) and nuDNA (RAG-1, CXCR-4) but excluding the morphology and one nuDNA gene (POMC) from Pramuk (2006). Normally, we would assume that analyses based on the most data and with the fewest assumptions would be best; PHC do not specify the optimality criterion they used to judge goodness of trees.

This example illustrates PHC’s lack of concern for “taxonomic chaos” in any global sense. Rather, they seem to want to stabilize names of United States’ amphibians without regard to effects that their action may have on names of species on the rest of the planet.

Had they really been interested in maintaining net-positive nomenclatural stability for all of the species previously in *Bufo*, they would have opted for placing *all* taxa that fall into the lighter polygon into *Bufo* (Fig. 1) as was previously suggested by Smith and Chiszar (2006). That still would have necessitated placing many taxa unfamiliar to most North Americans and Europeans into *Bufo*, such as *Ansonia*, *Nectophryne*, *Didynamipus*, *Nectophrynoidea*, *Pedostibes*, *Pelophryne*, *Schismaderma*, and *Wolterstorffina*, a taxonomy that likely would have been rejected by the workers from Middle and South America, Africa, and tropical Asia, outside of PHC's audience of concern.

The approach suggested by PHC and putatively supported by their reanalysis of a subset of the Frost et al. (2006) data and taxa, requires, minimally, that *Duttaphrynus*, *Epidalea*, *Ingerophryne*, *Nannophryne*, *Phrynoidea*, *Pseudepidalea*, *Peltophryne*, and *Rhaebo* remain distinct from *Bufo* in order to achieve the narrow objective of constructing an exclusive group named *Bufo* (i.e., <BUFO>⁶), composed of *Rhinella* (sensu Chaparro et al., 2007), *Incilius*, *Anaxyrus*, and the *Bufo bufo* group.

If Cannatella and Pauly can demonstrate that *Rhinella*, *Incilius*, and *Anaxyrus* form an exclusive monophyletic group with *Bufo* (sensu stricto), the group will contain at least 145 species (including *Anaxyrus*: 22 species; *Bufo*: >13 species; *Incilius*: 33 species; *Rhinella*: 77 species). We are skeptical that Spanish- and Portuguese-speaking America will employ this taxonomy, even if it is used by some *AmphibiaTree* North Americans. South American workers will still have *Nannophryne* (the former *Bufo cophotis* group) and *Rhaebo* (the former *Bufo guttatus* group), so preservation of *Bufo* (sensu PHC) will not meet any perceived need in that productive academic community. We expect them to continue to use *Rhinella* for that geographically meaningful unit, likely even partition it into more tractable monophyletic

units, which will require English-speaking North Americans, who possess only a fraction of the entire New World bufonid fauna, either to employ *Anaxyrus* and *Incilius*, or to stubbornly retain a taxonomy that countenances paraphyly and disregards South American scientific viewpoints.

“RANA”

The discussion by PHC of *Rana* and *Lithobates* represents Hillis' third attempt (see also Hillis and Wilcox, 2005, and Hillis, 2007) to convince the systematics community that his heterodox approach to ranid nomenclature is compatible with both Phylogenetic Classification (de Queiroz and Gauthier, 1990, 1992, 1994; i.e., the *PhyloCode* [www.phylocode.org]) and the *International Code of Zoological Nomenclature* (ICZN, 1999). PHC do not mention that Dubois (2006b, 2007) already demolished Hillis' claims of meaningful compatibility, nor do they reference Dubois' papers in their *Point of View*, but his criticisms are serious and have merit, and Hillis' nomenclatural recommendations are clearly outside of the realm of standard nomenclatural practice. Consequently, the anuran English names subcommittee did not think Hillis' recommendations required discussion in the *English Names* list.

Moreover, PHC did not mention Che et al.'s (2007) phylogenetic analysis and revision of Ranidae (sensu Frost et al., 2006), which strongly influenced discussions of ranid taxonomy within the anuran English names subcommittee. In large part, that work supersedes the results of Frost et al. (2006) and Hillis and Wilcox (2005). Che et al. (2007) recognized *Lithobates* (sensu Frost et al.) because to do otherwise requires the distinctive Chinese genus *Pseudorana* to be placed in synonymy or treated as a subgenus of *Rana*. Stuart (2008), studying a different gene, subsequently confirmed this phylogenetic result. With the exception of his coauthorship with Bossuyt et al. (2006), in which no definite name changes were made, Hillis has repeatedly focused just on the New World species to the exclusion of the global ranid fauna. Because the anuran English names subcommittee judged that the optimal taxonomy should be based on large, global, phylogenetic

⁶ We employ Dubois' (2007) method of denoting names applied under the Phylocode and restrict the traditional italics for those generic and species names applied under the International Code of Zoological Nomenclature (ICZN, 1999). Because these names are applied under different and mutually incompatible rules, they need to be distinguished.

studies pertaining to the entire group, rather than on studies of smaller geographic components (e.g., just the Americas) we were led to adopt the taxonomy of Che et al. (2007; which strongly modified the Frost et al., 2006, taxonomy, at least in the Old World), which is reflected in Frost et al. (2008b), in the online *Amphibian Species of the World* (2009), and in the *IUCN Red List*—but not in *AmphibiaWeb*.

The PHC-suggested subgeneric classification (their Fig. 2A) is a direct descendant of the taxonomy proposed by Hillis and Wilcox (2005); we reproduce that here in our Fig. 2. Names in that system were attached not only to near-terminal subtaxa within American *Rana*, but also to other interior stems. Hillis and Wilcox explicitly stated (2005: 303) that "... the clade names presented in Appendix B are all unranked (i.e., they are not assigned to categories such as section or subgenus)", but now these clade names are proposed as subgenera (PHC's Fig. 2). Originally these names were to be construed, either implicitly or explicitly, within Phylogenetic Nomenclature, which is predicated on naming groups by various methods of pointing to ancestral stems, and thereby formulating a rule (a "definition") for placement of a name on a particular monophyletic part of a larger cladogram. In this system, groups are not delimited by content or particular synapomorphies. Further, taxon-ranks, as regulated by the *International Code of Zoological Nomenclature* (ICZN, 1999) are excluded.

Hillis and Wilcox (2005) asserted that use of these names was consistent with the *International Code*. Dubois (2006b) disagreed citing incompatibility in principle and also suggested that none of Hillis and Wilcox's (2005) new names was available for zoological taxa under the *Code*. Hillis (2007) countered with evidence for the legitimacy of names coined by Hillis and Wilcox (2005) under the *International Code* (ICZN, 1999)—except for the ones that remained unavailable for zoological nomenclature under even the most generous reading of the *Code* (i.e., <LAURASIARANA>, <NOVIRANA>, and <STERTIRANA>) which Hillis (2007) neglected to report (Dubois, 2007). Moreover, Dubois (2007) explained in great detail that even though identical names

might be applied in both systems to taxa that were identical in content, neither system required this.

In response to the criticisms of Dubois (2006b), and as noted by Dubois (2007), Hillis (2007) formulated the taxonomy currently accepted by PHC for North American ranids, simply by dumping the more interior clade names that were problematic (i.e., unavailable under the *Code*: <LAURASIARANA>, <NOVIRANA>, <RANULA>); or junior synonyms of other "subgeneric" names employed by Hillis: <TORRENTIRANA> = *Zweifelia*).

Rana has a long history of partition, from being the only genus of frogs (Linnaeus, 1758) to being the fourth largest group of ranid frogs (Che et al., 2007; Frost, 2009). Surprisingly, neither Hillis and Wilcox (2005), nor Hillis (2007), nor PHC defined <RANA> within Phylogenetic Nomenclature, presumably because the bulk of Old World "*Rana*" (e.g., at least in the last 15 years what is now partitioned among *Babina*, *Clinotarsus*, *Glandirana*, *Huia*, *Hylarana*, *Meristogenys*, *Odorrana*, *Pelophylax*, and *Pseudorana*) of other authors (e.g., Cai et al., 2007; Che et al., 2007) was beyond the scope of their studies. This raises the question of whether or not PHC also intend to include these taxa among their subgenera in order to preserve *Rana* as it was conceived of in the late 20th and early 21st centuries. One presumes that PHC would restrict <RANA> to Raninae sensu Bossuyt et al. (2006), but even this would allow most contained groups other than *Stauroides*, such as the large genera *Pelophylax* (22 species), *Odorrana* (51 species), and *Hylarana* (86 species), as well as the distinctive *Pseudorana* (2 species), all non-North American taxa, to be included within <RANA>. *AmphibiaWeb* lists under *Rana* various species that are currently in *Babina*, *Clinotarsus*, *Glandirana*, some *Hylarana* [e.g., *Rana milneana* and *R. waliaesa*], some *Odorrana*, *Pelophylax*, and *Pseudorana*, so we suspect that the intention is to consider these to be in *Rana* as well, although the message from *AmphibiaWeb* is mixed and may not reflect PHC's intention. Fortunately, the limits of *Rana* have been recently delimited by Che et al., (2007: 12) in their global study of ranids as the taxa subtended (or implied to be subtended) by their Stem G.

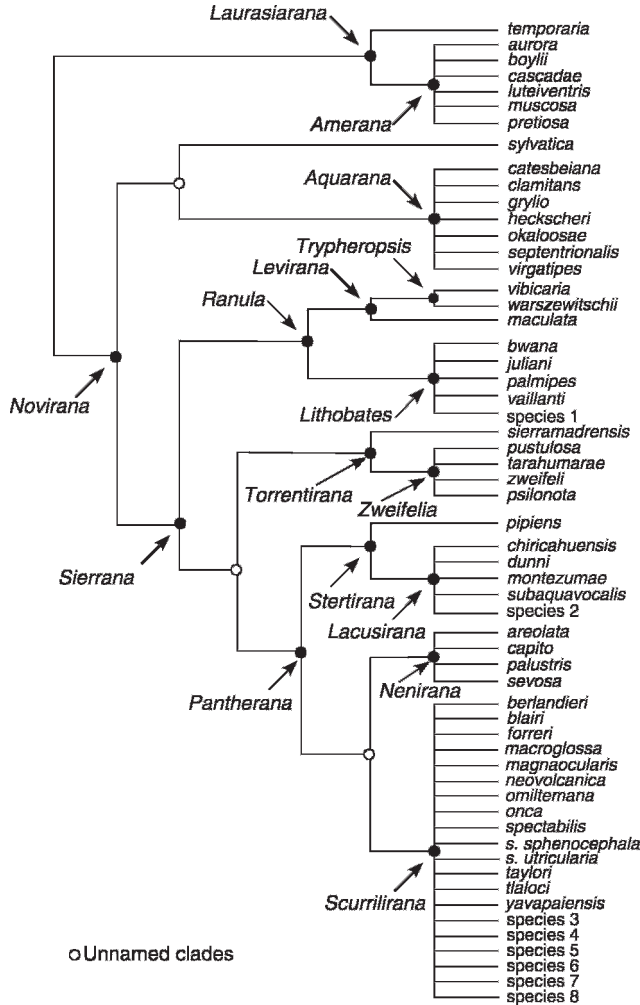


FIG. 2.—The original taxonomy tree of Hillis and Wilcox (2005) showing all taxa named by them and incorrectly suggested to be consistent with the *International Code of Zoological Nomenclature* (1999).

(The following will unavoidably confuse readers not firmly grounded in both the *ICZN* and *PhyloCode*.) We follow Che et al. (2007) in this determination and define the converted taxon name <RANA> as applying to the smallest monophyletic group including both *Rana temporaria* Linnaeus, 1758, and *Rana aurora* Baird and Girard, 1852. This renders both <RANA> (*PhyloCode*) and *Rana* (*ICZN*) subjective synonyms of Hillis and Wilcox’s (2005) <LAURASIARANA> (which under the *Code* is a nomen nudum and an objective synonym of *Aurorana* Dubois, 1992, through the shared type species). This renders the name *Rana*/*<RANA>* valid and of coextensive

content (sensu Frost et al., 2006) and Che et al., 2007) under both the *International Code* and the *PhyloCode*.

This leaves a conundrum which we do not resolve (and which illustrates the inherent conflict of the *ICZN* and the *PhyloCode*) with respect to the content equivalency of *Lithobates* and <NOVIRANA> and <LITHOBATES> and *Zweifelia*. Hillis and Wilcox (2005) defined <LITHOBATES> as applying to the *Rana palmipes* group (now the *Lithobates palmipes* group), but Frost et al. (2006) and Che et al. (2007) applied the name *Lithobates* to the largest endemic clade of American ranids, coextensive in content with <NOVI-

RANA> of Hillis and Wilcox (2005), although this name is, unfortunately, an objective synonym of *Zweifelia* Dubois, 1992, under the ICZN.

As is obvious from the previous paragraph, clarity in all future discussion of nomenclature requires that workers state clearly which rules of nomenclature they are following (e.g., see Marjanovic and Laurin, 2008). In particular, we agree with Dubois (2007: 400–401) that the use of systems of nomenclature alternative to the hugely dominant *International Code* (see Frost et al., 2006: 143) should be clearly noted in publications. That should prevent anyone from thinking that authors have complied with the *International Code*, given that the conflation of the different systems can result in such serious misunderstanding (Sluys et al., 2004). We therefore endorse Dubois' (2005*b*, 2006*a*, *b*, *c*) practice of giving all names applied under the *PhyloCode* an appearance different from that of names applied under the *International Code* (e.g., <PANTHERANA> versus *Pantherana*, respectively). The *PhyloCode* deserves careful and reasoned consideration, and while it does have some properties that we find attractive, inherent stability is not one of them. Any compromise between the *PhyloCode* and the ICZN that is not based on clear principles will result in something less satisfactory than either. We hope that editors of biological publications will adopt this approach as well, thereby avoiding the taxonomic confusion that can occur when alternative systems of nomenclature use identical names in fundamentally different ways to the detriment of communication. Further, we encourage Hillis and Cannatella to adopt a single nomenclatural system for their future publications and a format for the names that will identify that system and thereby eliminate (or greatly diminish) the risk of any misunderstanding and taxonomic confusion that we find evident in their *Point of View*. The decision to embrace the *International Code of Zoological Nomenclature* in subsequent editions of *Scientific and Standard English Names* lists or to abandon it for an alternative nomenclatural system must be made by the governing boards of the SSAR, HL, and ASIH.

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