



Naming taxa from cladograms: some confusions, misleading statements, and necessary clarifications

Alain Dubois*

Vertébrés: Reptiles et Amphibiens, USM 0602 Taxonomie and Collections, Département de Systématique and Evolution, Muséum national d'Histoire naturelle, 25 rue Cuvier, 75005 Paris, France

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Abstract

Hillis (2006) recently published a rebuttal of my analysis (Dubois, 2006c) of a paper by Hillis and Wilcox (2005) on the taxonomy and nomenclature of American ranid frogs. His paper consists not only in a reply to my paper, as it contains in fact three distinct kinds of statements: (1) an attempt to “save” the new generic nomina proposed by Hillis and Wilcox (2005) from being considered *nomina nuda* under the *Code*; (2) another plea for the superiority of the *Phylocode* over the *Code*, especially as regards the absence of a Rule of Coordination and the substitution of “phylogenetic definition” of nomina to the use of onomatophores for the allocation of nomina to taxa; (3) a plea for “taxonomic stability” in order not to upset the traditional use of nomina and to please users of electronic data bases. These three points are here commented, as follows: (1) even with the best goodwill, under the rules of the *Code* it is possible to “save” only three or four of the seven new nomina of Hillis and Wilcox (2005), the others being indeed *nomina nuda*; furthermore, three of these seven nomina are definitively useless and redundant, being junior objective synonyms of other generic nomina; (2) the well-known arguments against the *Phylocode* do not need to be repeated in detail once again, the most important one being that replacement of a secular nomenclatural system by another one, whose theoretical and practical superiority is highly questionable, would cause considerable chaos and detract taxonomists from their urgent task of accelerating the collection, study and description of the living species of our planet; (3) the claim for taxonomic and nomenclatural stability ignores the importance of the taxonomic impediment and sends a misleading message to the scientific community and to society as a whole: in the present situation of our knowledge, taxonomic stability is ignorance, and the science of taxonomy would have much to lose to adapt its concepts and practices to the needs of databases at the expense of scientific quality. It is once again stressed that, for the quality and accuracy of communication between evolutionary biologists, and above all with other biologists and non-biologists, it is urgent that scientific periodicals impose the use of different systems of notation of nomina following distinct nomenclatural systems, such as the *Code* and the *Phylocode*.

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We are now at the beginning of the “century of extinctions”, and the “biodiversity crisis” poses major challenges to all biologists (Dubois, 2003). At this stage of the history of science, the existence of several nomenclatural codes, based on different philosophies of biological nomenclature, is a source of confusion and chaos, and is not doing a service to the study of biodiversity and to actions aiming at understanding and conserving it

(Sluys et al., 2004). Even more damaging for the image of taxonomy outside the specialized milieu of taxonomists and phylogeneticists, is the confusion caused by the use in some publications of a “double nomenclature”, supposed to be valid under two distinct nomenclatural systems, the *Code* (Anonymous, 1999) and the *Phylocode* (<http://www.ohioi.edu/phylocode/>), but ignoring some of the basic rules of one of them. This had prompted me to propose (Dubois, 2006c) a detailed analysis of the nomenclatural problems raised by a recent publication (Hillis and Wilcox, 2005), which provides a very enlightening example of such problems. As clearly stated in the

*Corresponding author:

E-mail address: adubois@mnhn.fr

introduction of my paper, its purpose was “to address a specific question: can the same nomina be available and valid under both systems, and if so under which conditions?” (Dubois, 2006c, p. 318). It was therefore not meant to discuss again the respective merits of the *Code* and of the *Phylocode*, or propose a new taxonomy of American frogs traditionally referred to the genus *Rana*, as it is reasonable to consider that many more basic data must be obtained before a “final word” on this latter question can be written (Dubois, 2006b, p. 828, 2006c, pp. 320–321).

Hillis (2006) recently provided a reply to my paper. However, his work in fact consists of three distinct papers: one part replies indeed to some of my comments on the use of the *Code* in taxonomic publications, but another large part of this paper has nothing to do with this question, as it provides still another plea for the superiority of the *Phylocode* over the *Code*, whereas a third part discusses whether one or two distinct genera should be recognized for American ranid frogs. As these three distinct questions are largely intermingled in Hillis’s (2006) paper, confusion is likely in the minds of many readers. This compels me to clarify again some of these points. This is all the more necessary that Hillis’s (2006) paper once again illustrates the confusion between nomenclature and taxonomy, which is basic to the *Phylocode* philosophy and to the disagreements between the latter and that of the *Code* (see e.g., Dubois, 2005b).

My analysis of Hillis and Wilcox’s (2005) paper was based on the major theoretical distinction (Dubois, 2005b,d), which is crucial for any adequate discussion of the particularities of the *Code*, between the three distinct “storeys” of zoological nomenclature, *availability*, *allocation* and *validity* of nomina. I pointed to six genuine nomenclatural problems in the use in Hillis and Wilcox’s (2005) paper of a nomenclature supposed to be valid under the *Code*: (1) the need of characters (diagnoses or apognoses) for the *availability* of nomina; (2) the role of onomatophores for the *allocation* of nomina to taxa; (3) the permanent *invalidity* of junior homonyms; (4) the permanent *invalidity* of junior objective synonyms; (5) the conditional *invalidity* of junior subjective synonyms; (6) and the need of respecting the rank hierarchy recognized by the *Code* for *validity* of the nomina. Besides, (7) I pointed to minor problems in the formation of some of the new nomina proposed by Hillis and Wilcox (2005). Below, I first reply to the comments of Hillis (2006) on these seven points, then I address the two other questions raised in Hillis’s (2006) contribution, and that have nothing to do with a reply to my paper.

In this paper, the unambiguous term *nomen* is used to designate “scientific name” as defined in the *Code* (Dubois, 2000). As proposed elsewhere (Dubois, 2005b, 2006b,c,d) and to avoid confusion between the two kinds of nomina, in this paper nomina following the *Code* are written in the traditional way (e.g., *Amerana*), whereas nomina following the *Phylocode* proposed rules

are written between signs evoking cladogeneses: e.g., <AMERANA>. Nomina unavailable under the *Code* for being *nomina nuda* are written between quotation marks: e.g., “*Laurasiarana*”. Quotations from previous articles are printed in *italics* between quotes. Finally, the terms *taxon*, *diagnosis*, *apognosis* and *cladognosis* are used below with the following meanings:

1 A *taxon* is a class or group of organisms or of taxa recognized by a taxonomist following a philosophy of biological classification: nowadays, most taxonomists agree that taxa should only be recognized for groups that are considered monophyletic (holophyletic *sensu* Ashlock, 1971 and Dubois, 1988), i.e., considered to include all descendants of a single ancestral species. Three synonymous terms have been coined to designate this kind of taxa: *phylon* of Dubois (1991); *cladon* of Mayr (1995); *phylo-taxon* of Joyce et al. (2004).

2 A *diagnosis* (traditional term in taxonomy; Dubois, 2006a, p. 251) is a list of all known characters that are considered by a taxonomist to distinguish a taxon from all other taxa, especially those considered its most closely related.

3 An *apognosis* (Dubois, 1997, 2006a, p. 250) is a list of known or supposed apomorphies that are considered by a taxonomist to establish the fact that a taxon corresponds to a monophyletic group.

4 A *cladognosis* (new term) is a definition given for a taxon considered by a taxonomist to be monophyletic: this definition may be based on *characters* (apognosis as defined above, roughly equivalent to “apomorphy-based definition” in the terminology of the *Phylocode*), or on *inclusion* of some organisms or taxa in the group (roughly “node-based definition” in the terminology of the *Phylocode*), or on such an inclusion combined with *exclusion* of some other organisms or taxa from the group (roughly “stem-based definition” in the terminology of the *Phylocode*) (for more details on these matters, see Dubois, 2006d).

Nomenclatural problems in Hillis and Wilcox (2005)

Availability of nomina

Although he rejected my statement that the new nomina proposed by Hillis and Wilcox (2005) were *nomina nuda*, Hillis (2006) agreed that, to be available under the *Code*, a new nomen must be published either associated with “a description or definition that states in words characters that are purported to differentiate the taxon”, or “a bibliographic reference to such a published statement”, or “be proposed expressly as a new replacement name (*nomen novum*) for an available name” (Article 13.1 of the *Code*). This is one of the main messages that I wanted to pass to all readers of Hillis and Wilcox’s (2005) paper regarding the publication of

new nomina. As this statement has now been repeated twice in the journal where it was published (Dubois, 2006c; Hillis, 2006), it is to be hoped that in the future this journal, as well as others, will care for this rule to be followed in all papers where a new nomen is proposed with the purpose of making it available under the rules of the *Code* (this comment is irrelevant for nomina intended for use only under the rules of the *Phylocode*). As I mentioned already (Dubois, 2003, 2006c), this simple rule is far from having been followed in all recent publications, especially in papers and journals dealing primarily with molecular cladistics or evolution, not with taxonomy.

Now, Hillis (2006) rejected my interpretation that Hillis and Wilcox's (2005) new nomina were *nomina nuda* on the basis of the presence, in the main body of this paper, of information that can be considered to provide diagnoses or apognoses for the new taxa. I maintain that this information happened to be associated "by chance" with most of the new nomina (see Dubois, 2006c, p. 322), but I admit that a purely formal analysis of their text can be used to consider some of these nomina as available and to "save" them. However, even if I am ready to accept, as has apparently also Darrel Frost (Hillis, 2006, p. 333), some of the nomina in Hillis and Wilcox (2005) as nomenclaturally available because of information cursorily provided in the main body of their paper, a careful study of this text proves that this is not possible for all of them, as is misleadingly alleged by Hillis (2006). In support of his "defense" of their new nomina, Hillis (2006) discussed some "examples" (*Torrentirana*, *Scurrilirana*, *Lacusirana*, *Nenirana*) only, but let us consider all the new nomina successively (in the order of their appearance in appendix B of their paper): this shows that the case of these "examples" cannot be generalized to the other nomina not mentioned by Hillis (2006).

1 "*Laurasiarana*". This nomen first appears on p. 305 of Hillis and Wilcox (2005), where the cladogram of fig. 2 shows it as designating a taxon including both the *Rana boylii* group (or <AMERANA>) and the *Rana temporaria* group. No definition, diagnosis or apognosis of this taxon, or bibliographic reference to such a statement, is provided there. The nomen "*Laurasiarana*" is formally defined in appendix B (p. 311), but this is only a "phylogenetic definition" (cladognosis based on inclusion of taxa), which mentions no character. It is therefore impossible to "save" this nomen, which must remain a *nomen nudum*. As pointed out already (Dubois, 2006c), however, this is of no consequence in nomenclature following the *Code*, as this nomen is redundant, being an objective junior synonym of *Aurorana* Dubois, 1992.

2 "*Novirana*". This nomen first appears on p. 305 of Hillis and Wilcox (2005), where the cladogram of fig. 2 shows it as designating the sister taxon of

"*Laurasiarana*", i.e., a taxon including all American frog species referred to *Rana* except the *Rana boylii* group (or <AMERANA>). No definition, diagnosis or apognosis of this taxon, or bibliographic reference to such a statement, is provided there. This taxon is defined in the text on p. 305 as "*the eastern and tropical groups of North American Rana*". Such a "definition" through geographic distribution, i.e., particularities extrinsic to the organisms themselves, is not acceptable under the *Code* as a diagnostic character making the nomen available (Dubois, 2006c, p. 322). The nomen "*Novirana*" is formally defined in appendix B (p. 311), but here again this is only a "phylogenetic definition", which includes no character. It is therefore also impossible to "save" this nomen, which remains a *nomen nudum*. As pointed out already, however (Dubois, 2006c), this is of no consequence in nomenclature following the *Code*, as this nomen also is redundant, being an objective junior synonym of *Pantherana* Dubois, 1992.

3 *Torrentirana*. As argued by Hillis (2006), the following sentence (Hillis and Wilcox, 2005, p. 308) can be considered diagnostic for the taxon designated by this nomen, thus making it nomenclaturally available: "*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.*" Under the *Code*, however, this nomen also is redundant, being an objective junior synonym of *Zweifelia* Dubois, 1992.

4 "*Stertirana*". This nomen first appears on p. 305 of Hillis and Wilcox (2005), where the cladogram of fig. 2 shows it as designating a taxon including both the species *Rana pipiens* and the *Rana montezumae* group (or *Lacusirana*). The nomen also appears in the text in this page, but no definition, diagnosis or apognosis of this taxon, or bibliographic reference to such a statement, is provided there. On p. 309, the nomen is also mentioned, but without characters unique to the taxon it designates. The following statement is given in this page: "*All species of Stertirana (including R. pipiens and Nenirana have a 'snore-like' mating call.*" As this character is common to two taxa (which furthermore are not considered sister taxa in the cladogram of fig. 2), it cannot be diagnostic of any of them, so its mention in appendix B (p. 312) cannot make it available. The nomen "*Stertirana*" is formally defined there but this is only again a "phylogenetic definition", which includes no character. This nomen is therefore also a *nomen nudum*.

5 *Lacusirana*. As mentioned by Hillis (2006), Hillis and Wilcox (2005, p. 309) stated that this nomen refers to the *Rana montezumae* group of the Alpha division of the *Rana pipiens* complex of Hillis et al. (1983, p. 137). The latter authors (Hillis et al., 1983, pp. 137, 143) had indeed provided a molecular apognosis (list of 11 synapomorphies) and a morphological one ("*the presence of small yellow spots on the posterior surfaces of the*

thighs”) for this group. In Hillis et al. (1983, p. 137), this group was considered to include four named species (*Rana chiricahuensis*, *R. dunni*, *R. megapoda*, *R. montezumae*). Hillis and Wilcox (2005, p. 312) added three species to this group, *R. fisheri*, *R. lemosespinali* and *R. subaquavocalis*, the last two of which were described after the paper of Hillis et al. (1983), and the first one had not been mentioned in this paper. In the absence of contrary indications, it can be supposed that, despite this addition of three species, the diagnosis of the taxon in Hillis et al. (1983) still applies to the taxon recognized in Hillis and Wilcox (2005). Under this interpretation, the nomen *Lacusirana* can be considered nomenclaturally available by virtue of Article 13.1.2 of the *Code*.

6 *Nenirana*. This case is similar to the preceding one. Hillis and Wilcox (2005, pp. 309, 312) stated that this nomen refers to the *Rana areolata* group of the Alpha division of the *Rana pipiens* complex of Hillis et al. (1983, p. 137). This group was apogonized in Hillis et al. (1983, pp. 137, 143) by six molecular synapomorphies and a morphological one (“*the presence of thick, glandular dorsolateral folds*”). In Hillis et al. (1983, p. 137), this group was considered to include three named species (*Rana areolata*, *R. capito*, *R. palustris*). Hillis and Wilcox (2005, p. 312) added a fourth species to this group, *R. sevosa*, which had not been mentioned in Hillis et al. (1983). Here also, in the absence of contradictory information, one can suppose that, despite this species addition, the diagnosis of the taxon in Hillis et al. (1983) still applies to the taxon recognized in Hillis and Wilcox (2005). Under this interpretation, the nomen *Nenirana* can be considered nomenclaturally available by virtue of Article 13.1.2 of the *Code*.

7 *Scurrilirana*. As mentioned in Dubois (2006c, p. 322), in appendix B of Hillis and Wilcox (2005, p. 312), after the “phylogenetic definition” of this taxon, the following sentence appears: “*Etymology: From the Latin words scurrilis, meaning ‘jesting’, and rana, meaning ‘frog’, in reference to the advertisement calls of most of the species in this clade, which sound like chuckling laughter*”. I had therefore outlined that, as this character was credited to “*most of the species*” of this taxon, it could not be considered “diagnostic”, not being considered common to all the species of the taxon. Hillis (2006, p. 332) stated that my statement was “inaccurate”, as if I had invented the quotation above, and he produced another quotation from Hillis and Wilcox (2005, p. 309), where these authors stated that “*the species of Scurrilirana all have some form of ‘chuckle-like’ mating call*”. Both quotations from Hillis and Wilcox (2005) are accurate, and the least that can be said is that they are not equivalent: in one case it is stated that “*most of the species*” of this group have this mating call, in the other that “*all*” of them have it. Hillis’s (2006, p. 333) statement that this character, like others, was “*clearly*

described as applying to all the species of the taxon and diagnosing it from other taxa”, suggests that, in this case, the information in the main body of the text (p. 309) is to be considered valid, but not that provided in appendix B, although the latter gives the formal “definitions” of the new taxa. If this interpretation is judged acceptable, then the nomen *Scurrilirana* can be considered nomenclaturally available. For more security in this respect, it would be important to have one or several references documenting the fact that, at least by the time when Hillis and Wilcox (2005) wrote their paper, *all* the 15 named and six unnamed species referred by them to this taxon and whose mating call had then been reliably described, were known to have a “chuckle-like” mating call. In the absence of such a reference in Hillis and Wilcox (2005), the question of availability of the nomen *Scurrilirana* is in fact formally unsettled, but I do not object to considering it to be available as an act of good faith, following the statement in Hillis (2006, p. 333).

In conclusion, of the seven new nomina created by Hillis and Wilcox (2005), four (in fact exactly those four that had been given as “examples” by Hillis, 2006) can be “saved” as nomenclaturally available (including one, *Scurrilirana*, for which this is possible only by “goodwill”), but the other three cannot in the least be so, and must still be considered *nomina nuda*, contrary to the misleading statement in Hillis (2006). If nothing more, this shows that more care should have been taken by Hillis and Wilcox (2005) when creating their new nomina, if their intention was to make the latter available under the rules of the *Code*. In fact, it is clear that these authors did not consider characters or diagnoses as necessary for the availability of their nomina. This interpretation is confirmed by the presence in Hillis’s (2006) paper of a long section 3, that has nothing to do with the question discussed in my paper (see below). It is the full right of Hillis to think that diagnoses are “obsolete” in “modern” taxonomy, but this is not what the *Code* says: the question is not whether one likes the *Code* or not, but that, if one intends to use nomina validly under the *Code*, then one must follow its rules. If the highway code states that cars must stop when the traffic light is red, then every car must stop, even if a driver thinks that the color blue would have been a better choice than red. Misunderstanding this is a basic misunderstanding of what a code, like any law, really is.

Allocation of nomina to taxa

This point deserves little discussion, as Hillis’s (2006) comments also amount to a criticism of the rules of the *Code*, not to showing that my analysis was wrong in the light of the actual *Code*. As discussed in detail elsewhere (e.g., Dubois, 2005b, 2006d) and briefly below, under

the *Code* the allocation of nomina to taxa is not made through definitions (be them “phylogenetic” or not) but through the use of onomatophores (so-called “types”). Therefore, under this system, two nomina based on the same onomatophore are definitively to be treated as objective synonyms, the junior one being permanently invalid. This does not depend in any respect on the original definitions or contents of the taxa for which these nomina had been initially coined.

Under the *Code* also, following the Rule of Coordination, the same nomen can designate different taxa at different ranks. Hillis (2006), after others, criticizes this (see below), but this criticism has no bearing on the fact that these are the rules of the current *Code*, and that using different nomina having the same onomatophore for different taxa of different ranks is forbidden. This is the only point I was making in this respect in my paper: if one claims to use a nomenclature acceptable under the *Code*, then one must follow the Rule of Coordination. So, it is beyond discussion that, under the rules of the *Code*, it is impossible to have a nomenclature in which all subgenera included in a genus bear different nomina from that of the genus: it is compulsory that one of them (the oldest named) bears the same nomen as the genus. Whether this is confusing or not is another question, that will be briefly discussed below, but this has no bearing on the fact that the current rules are what they are.

Validity of nomina

The permanent invalidity of junior homonyms

In his text, Hillis (2006) did not challenge my statement (Dubois, 2006c) that, being a junior homonym, the nomen *Ranula* Peters, 1859 is definitively invalid, both under the rules of the *Code* and those of the *Phylocode*, so one may think that he agreed with this statement. However, while still supporting his *Phylocode* nomenclature, he did not provide a replacement nomen for <RANULA [Peters, 1859] Hillis and Wilcox, 2005>, nor did he announce his intention to do so later. Furthermore, Hillis (2006, p. 336), while presenting a nomenclature alternative to his preferred one, wrote: “*The clade names Novirana, Laurasiarana, Levirana, Ranula, Stertirana, and Torrentirana are not used as subgenera under this solution.*” This suggests that, under his preferred solution, the nomen *Ranula* could still be used as a valid subgeneric nomen. He further wrote: “*This list includes all the names considered junior objective synonyms or homonyms by Dubois*”. However, contrary to what this sentence implies, this is not a question of interpretation. These nomina were not *considered* by me as junior homonyms or objective synonyms, they *are* so: whereas junior objective synonyms are so under the

Code only, as concerns junior homonyms they are so both under the *Code* and the *Phylocode*. As a matter of fact, Article 6.2 of the latter requires that, to be converted, a “preexisting name” be “potentially valid” under the *Code*, which is not the case of junior homonyms, as illustrated on p. 123 of the *Code*. This additional misleading statement illustrates again that Hillis (2006) did not really understand what a code is, or that he was not really prepared to follow completely the rules of any code.

The permanent invalidity of junior objective synonyms

This point simply results from the second point above (role of onomatophore for nomen allocation). Whatever the taxonomy adopted, three of the seven new generic nomina created by Hillis and Wilcox (2005) are definitively invalid under the *Code*, being redundant as junior objective synonyms of generic nomina created previously: “*Laurasiarana*”, which has the same type-species (*Rana aurora*) as *Aurorana* Dubois, 1992; “*Novirana*”, which has the same type-species (*Rana pipiens*) as *Pantherana* Dubois, 1992; and *Torrentirana*, which has the same type-species (*Rana tarahumarae*) as *Zweifelia* Dubois, 1992. Even if the nomen *Torrentirana* is considered nomenclaturally available as argued by Hillis (2006) and accepted above, it will never have to be used as the valid nomen of any taxon under the *Code*. As for the two former nomina, they are currently *nomina nuda*, as discussed above, and my suggestion is that no effort should be done to make them nomenclaturally available under the *Code* (e.g., in publishing them again, but then associated with a diagnosis or apognosis), as they would nevertheless remain forever invalid, as junior objective synonyms.

The conditional invalidity of junior subjective synonyms

Hillis and Wilcox’s (2005) nomenclature also includes one case of subjective synonymy, between the nomina *Lacusirana* and “*Stertirana*”. The type-species of the former is *Rana megapoda*, and that of the latter *Rana montezumae*, and both these species are members of the same taxon (the former *Rana montezumae* group), so under the *Code* only one nomen would be acceptable in a generic taxonomy, even if the *Code* was modified in order to allow two or more different ranks below genus (see below and Dubois, 2006b). This synonymy is, however, conditional and thus labile: if a new taxonomic arrangement was proposed, where *Rana megapoda* and *Rana montezumae* would be placed in different taxa, then two different nomina could be necessary. However, for the time being, this is not the case, and the nomen “*Stertirana*” being a *nomen nudum*, as shown above, my suggestion again is that no effort should be done to make it nomenclaturally available, as it would be redundant with *Lacusirana* under the current taxonomic arrangement.

The need of respecting the rank hierarchy recognized by the Code

There is little to add also on this point, as Hillis (2006) still did not make a clear distinction between *availability* and *validity* of nomina, i.e., between floors 1 and 3 of the “nomenclatural house” (Dubois, 2005b,d). As explained in detail in Dubois (2006c, p. 324), one first point is that, regarding *availability*, following Article 10.4 of the *Code* (in its chapter 4, “Criteria of availability”), the nomen of any genus-series division of a genus, whatever its original designation, is deemed to have been created at rank subgenus. But this does not mean that, regarding *validity*, several subgenera can be “*nested hierarchically within one another*”. This would be equivalent to stating that several genera can be nested hierarchically within one another, or several species within one another, several families within one another, etc., a course that would be completely contradictory with the hierarchical structure of zoological nomenclature as implemented in the *Code*. Under the *Code*, if a family includes two or more subordinate family-series taxa, these have the rank subfamily, then the rank below is tribe, then subtribe, etc., without limitation. Particular problems exist in the genus-series and in the species-series of nomina because of the restriction in the number of ranks allowed by the *Code* in these nominal-series (see below and Dubois, 2006b), but Hillis and Wilcox (2005) ignored these problems. As for Hillis (2006), he was not yet convinced by my analysis, and wrote: “*Readers are welcome to read the rules and decide for themselves which interpretation is correct.*” This is easy, as no problem of “interpretation” exists. Article 42.1 of the *Code* (in its chapter 9, “Genus-group nominal taxa and their names”) reads as follows: “*The genus group, which is next below the family group and next above the species group in the hierarchy of classification, encompasses all nominal taxa at the ranks of genus and subgenus*”. That is all, and no further rank is allowed by the *Code* below subgenus. This is further confirmed by the following definitions in the *Glossary* of the *Code*:

“**rank**, *n.* The level, for nomenclatural purposes, of a taxon in a taxonomic hierarchy (e.g., all families are for nomenclatural purposes at the same rank, which lies between superfamily and subfamily).” (p. 114).

“**genus group**, *n.* In the hierarchy of classification the group of taxa ranked between the family group and the species group. The genus group includes taxa at the ranks of genus and subgenus [Art. 42.1].” (p. 105).

“**genus** (*pl. genera*), *n.* (1) The rank within the genus group next below the family group and above subgenus. (2) A taxon at the rank of genus.” (p. 105).

“**subgenus** (*pl. subgenera*), *n.* (1) The genus-group rank below genus. (2) A taxon at the rank of subgenus.” (p. 117).

In order to support his interpretation, Hillis (2006, p. 335) wrote: “*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.” This is simply a misleading presentation of my paper, where I had written: “*I give provisionally to these units the statute of subgenera of the genus Rana. (...) Furthermore, in order to facilitate the forthcoming practical work on this group [the genus Rana], these subgenera have been provisionally distributed here in nine ‘sections’ of the genus Rana, which are artificial and purely phenetic groups. These sections are not for the time being, contrary to the subgenera, formal taxonomic units. It is likely that subsequent research will result in affording a taxonomic status (genus or subgenus) to some of them, and in dismantling others*” (Dubois, 1992, p. 309, translated). In table 4 at the end of this paper (Dubois, 1992, pp. 337–338), where a proposed provisional taxonomy of ranoid frogs was presented, the genus *Rana* was listed with its provisional 33 subgenera, but not its sections and subsections. It is therefore clear that in this paper, as well as in all my other publications, I never suggested the use of more than one formal genus-series rank below the rank genus.

After a discussion of this “interpretation” problem, Hillis (2006) proceeded to a discussion of alternative proposals to the rules of the *Code* concerning infrageneric nomenclature. This point is distinct from, and has no bearing on, that of the validity of the nomenclature used in Hillis and Wilcox (2005) under the current *Code*. It will be briefly discussed below.

Problems in the formation of some nomina

This is very minor point that only deserves very brief comment. Contrary to the preceding points, my comments were not meant to correct a mistake but to make a suggestion, namely that it would be “*certainly preferable*” that new nomina, when derived from classical Greek or Latin words, be correctly formed relative to their etymology, more precisely relative to the stems of the words from which they may have derived. The *Code* does not provide precise guidelines for the formation of generic nomina, but regarding family-series nomina, Art. 29.3.1 states that the stem of a generic nomen being or ending in a Greek or Latin word “*is found by deleting the case ending of the appropriate genitive singular*”. Thus the stem of the genus *Homo* is not *Hom-* or *Homo-*, but *Homin-*, as the genitive of the Latin word *homo* is *hominis*: so, the family nomen based on the genus *Homo* is *HOMINIDAE*, not *HOMIDAE* or *HOMOIDAE*. The same guidelines can be applied to the generic nomen *Lacusirana*, which is derived from the Latin word *lacus* (lake), the genitive of which is *lacus*, not *lacusis*, so that its stem is *lac-*. Deriving a generic nomen from the stem of the Latin word *lacus* combined with the word *rana* would thus give nomina like “*Lacrana*”, “*Lacirana*” or “*Lacorana*”, but not “*Lacusirana*”. However, my personal preference, for

reasons of euphony and clarity, would go to “*Lacunirana*”, derived from the stem *lacun-* of the Latin word *lacuna* (genitive *lacunae*), for which the dictionaries (e.g., Simpson, 1968, p. 334), give the following meanings: “*cavity, hollow, dip; esp. a pool, pond*”, the last two of which clearly designate standing water bodies as those inhabited by these frogs. In Latin, “frog of the lake” would write “*rana lacus*” or “*lacus rana*”, and “frog of the pool” “*rana lacunae*” or “*lacunae rana*”, i.e., if both words were fused, still different spellings from those discussed above, but it is more usual to derive a nomen from a Latin stem than from an unmodified Latin formula. Finally, concerning *Scurrilirana*, my suggestion was simply to use the shorter Latin noun *scurra* (“*a jester, buffoon*”), conveying exactly the same meaning as the longer adjective *scurrilis* (“*like a buffoon, mocking, jeering*”), as stem for the generic nomen, and to further shorten it by fusion with the nomen *rana* to produce the shorter nomen “*Scurrana*”.

Although I offered these brief comments in my paper, I clearly stated that these were not formal proposals of new nomina, but merely *suggestions* in case it would later prove necessary to formally create new nomina for the taxa designated by Hillis and Wilcox (2005) by nomina that according to my analysis were *nomina nuda*. In other words and in precise nomenclatural terms, the two new spellings I had suggested were only “conditional proposals”. According to Article 15.1 of the *Code*, a new nomen proposed conditionally and published after 1960 is not thereby made available, so the two spellings “*Lacunirana*” and “*Scurrana*” are nomenclaturally unavailable. They cannot therefore qualify as “*unjustified emendations of the original names*”, as stated by Hillis (2006, p. 336), because an unjustified emendation is an available nomen, with its own author and date (Articles 19.1 and 33.2.3 of the *Code*). This may appear to some as useless quibbling, but the use in a scientific publication of precise technical nomenclatural terms such as “unjustified emendation” must conform to the definitions and concepts of the *Code*. Be it as it may, according to Article 11.8 of the *Code*, any spelling is acceptable for a new generic nomen, provided it contains two or more letters and is, or can be treated as, a noun in the nominative singular. Any nomen incorrectly derived from its stated etymology can be simply treated as an “arbitrary combination of letters” (Article 11.3) and does not have to be emended. This is an additional reason to be careful in the creation of new nomina, and my brief remark was only meant at calling attention to this point, not at opening a useless debate.

Back to comparing the respective merits of the *Code* and the *Phylocode*

In his section 3, Hillis (2006) criticized again the use of diagnoses or apognoses under the *Code*. This criticism

stems back from the oft-repeated (e.g., De Queiroz and Gauthier, 1990, 1994; Pennisi, 2001; Joyce et al., 2004), but wrong, statement that, under the *Code*, the function of diagnoses is to provide *definitions* of taxa (second storey of the nomenclatural house, *allocation* of nomina), whereas this function is indeed to provide *availability* of nomina (first storey). The role of diagnoses is “simply” to make sure that the new nomen is based on one or several actual and identifiable specimen(s) from the real world, and not proposed for unidentifiable specimens or taxa, not to say for “hypothetical concepts” like the yeti or the Loch Ness monster (Dubois and Ohler, 1997; Dubois and Nemésio, 2007). Under the *Code*, nomina are not “defined”, but *attached* to taxa by the mean of onomatophores (Dubois, 2005b, 2006d). The onomatophore allocates a nomen to a taxon as a label that allows to designate and find it, but not in any way to define or describe its characters, biological peculiarities, phylogenetic relationships, etc. Under the *Code*, such actions are considered to be a matter of taxonomy, not of nomenclature, but the confusion between the two fields is consubstantial with the *Phylocode*. Regarding taxa definition, the *Code* is *theory-free* and as such it is misleading to state that it is linked to a pre-evolutionary approach of taxonomy. The *Code* does not deal with the way taxa are defined, it only provides clear, stringent and universal rules for the allocation of a given nomen to a given taxon within the frame of a given taxonomy. This is why there exist no such things as “ICZN-taxa” (Joyce et al., 2004). There is no point in appealing to Darwin in a liminar citation to promote the idea that the *Phylocode* is “modern” because it is “evolutionary”, and the *Code* “out of date” because it is “pre-evolutionary”!¹ Being theory-free regarding taxonomy, the *Code* is fully compatible not only with all current taxonomic schools, including “phylogenetic” ones, but also potentially with other paradigms of taxonomy that might develop in the future (Dubois, 2005b, p. 374). In contrast, being linked to a theory of taxonomy, the *Phylocode* does not have this flexibility and would have to be abandoned if such a new paradigm was to become prevalent. Under the current *Code*, nothing impedes supporters of “phylogenetic taxonomy” to define their *taxa* in the way they are under the *Phylocode*, but to allocate *nomina* to these taxa through onomatophores. Under such a course, taxa (but not nomina) could be defined following “phylogenetic definitions”, or more briefly cladognoses. As mentioned above, cladognoses can be either based on included and excluded taxa (“node-based definitions” and “stem-based definitions”), or on characters (“apomorphy-based defini-

¹It may be ironically reminded that that the so-called “Strickland’s code” (Strickland et al., 1843), from which the current *Code* is directly derived (Dubois, 2006c,d), was written by a group of 12 British zoologists and paleontologists, which included Charles Darwin himself!

tions”). In the latter case only, the cladognosis is equivalent to an apognosis as can be used to provide availability of a nomen under the *Code*, but in the first two cases the cladognosis would not provide nomen availability. Such a course would provide fully unambiguous allocation of nomina to taxa, and avoid the complete disruption of zoological nomenclature, which would follow a shift from a nomenclatural system used in millions of publications to a brand new one (Stuessy, 1997; Stevenson and Davis, 2003; Godfray and Knapp, 2004; Dubois, 2005b).

Under the *Code*, the need of diagnoses based on characters for the availability of genus-series nomina is not compulsory for older zoological nomina. According to Article 12 of the *Code*, a new genus-series nomen published before 1930 may be available simply if associated with an “indication”, such as the inclusion in this genus of one or more species designated by available nomina. In such a case, the *Code* does not require the existence of a diagnosis of the genus for availability of its nomen. This is the case for *Lithobates* Fitzinger, 1843, simply published with the indication of the nominal species *Rana palmipes* Spix, 1824 as its “type-species” by original designation (Dubois, 1981, 1992, 1999). It is therefore normal and fully acceptable if no definition or diagnosis of the subgenus or genus *Lithobates* was proposed for long, even when the nomen was used as valid. Actually this was done for the first time by Hillis himself (Hillis and de Sá, 1988, p. 16), i.e., before Dubois (1992, p. 329), but this did not raise any problem then: under the *Code*, diagnoses are useful only for allowing the availability of a nomen at the time of its creation, but not for its subsequent allocation to taxa (which is made through its onomatophore). Therefore, Hillis’s (2006) surprise about the fact that character diagnoses for *Lithobates* were not published before 1992 is not justified: in this case, because the nomen was published prior to 1931, the absence of diagnosis was not a problem. Frost et al. (2006, p. 254) gave a so-called morphological apognosis for their genus *Lithobates* (“absence of an outer metatarsal tubercle”), but even if they had not, their use of this nomen would be valid under the *Code*, as they did not create it. This clearly shows that under the *Code* diagnoses or apognoses do not play the important role which Hillis (2006) seemed to believe they have, and which in his mind disqualifies the *Code* in “modern” taxonomy.

In the same paragraph, Hillis (2006) complained about the fact that, under the *Code*, the same nomen may be used for different more or less inclusive taxa, with different definitions, and he considered this as a source of nomenclatural ambiguity. He came back in more detail to this point in his section 4. His idea is shared by all supporters of the *Phylocode*: according to this philosophy, a given nomen should apply only to a single taxon, and it should be impossible to use the same nomen to

designate different taxa. Although he did not mention this technical term of the *Code*, this means that Hillis (2006), after others, thought that the existence of the Rule of Coordination is a great weakness of the *Code*. There is a genuine theoretical debate here. Supporters of the *Code* think that nomina are just labels to designate and trace taxa, without meaning and content, and that one strength of the Rule of Coordination is that it allows “nomenclatural parsimony” (Dubois, 2006b, p. 838, 2006c, p. 327), i.e., the need of a lower number of nomina to express a given taxonomic scheme. Such a system has been in use for decades in innumerable publications by high numbers of taxonomists, who have apparently had no difficulty in mastering it and who did not find it “ambiguous”. However, it is true that recent developments of communication between taxonomists and various users, in particular through the use of the World Wide Web, is likely to modify this situation. The example of “genus *Rana*” versus “subgenus *Rana*”, given by Hillis (2006), could be complemented by examples like “*Rana temporaria*” versus “*Rana temporaria temporaria*”, or “family *RANIDAE*” versus “subfamily *RANINAE*”. No ambiguity exists for the use of the nomina of the *Code* when (1) the rank of the taxon is indicated, and (2) the taxonomic scheme used as a reference is provided. If these two pieces of information are not given, then ambiguity may exist, as discussed by Hillis (2006), but the exact content of a taxon named according to the *Phylocode* is equally ambiguous if no reference phylogeny or taxonomy is provided (Dubois, 2005b, pp. 383–384, 389–391).

Hillis (2006) seemed to think that the only possible solution to this problem is through the rules of the *Phylocode*, i.e., through “phylogenetic definition of nomina” and abandonment of the onomatophore system. However, the latter is the major strength of the *Code*, as it maintains an objective link between the world of language and the real world of organisms, and as it is theory-free, thus susceptible of adaptation to new taxonomic paradigms (Dubois and Ohler, 1997; Dubois, 2005b). Hillis’s (2006) statement is simply not true. As shown in detail in Dubois (2006d), there exist several possibilities to adapt the system of onomatophores in order for a given nomen to designate unambiguously one, and only one, taxon in a given taxonomy. Implementation of one of these possibilities in the *Code* would require to abandon the Rule of Coordination. According to the analysis provided (Dubois, 2006d), the most efficient of them, first presented in Dubois (2004a, 2005a,d, 2006a), is that using a double system of onomatophores and onomatostases. It was proposed to incorporate higher-ranked taxa nomina into the *Code*, without disturbing the current use of nomina of higher taxa. However, although this would be theoretically possible, it does not appear appropriate to adapt this system to the nomenclature of species-series, genus-series

and family-series taxa, for the same practical reason, which may be the main one for not accepting the shift from the nomenclatural system of the *Code* to that of the *Phylocode*. “Redefining” millions of nomina would require an enormous amount of manpower, time, energy and money, and this would be at the expense of a much more urgent need for taxonomy: that of accelerating the work of collection, study and description of the millions species of our planet that are still unknown to science, a large proportion of which will become extinct in the coming decades. For this simple reason, modifying the rules of the *Code* in order for all subgenera of a genus to bear nomina different from that of the genus, but also, for simple consistency, all subspecies of a species, all subfamilies of a family, all tribes of a subtribe, etc., in the same way, would be “a criminal operation against the study of biodiversity” (Dubois, 2005d, p. 208), and this idea should not be supported.

Hillis (2006) expressed agreement with the statement (Dubois, 2006c) that the limitation by the *Code* in the number of ranks allowed below genus in the genus-series to one (subgenus) is an unwarranted restriction to the “freedom of taxonomic thought or actions” (Anonymous, 1999, p. 2). As I had mentioned submission to the International Commission of Zoological Nomenclature of a manuscript dealing with this problem (Dubois, 2006e), Hillis (2006) imagined that I was suggesting that the rules of the *Code* “follow more closely” those of the *Phylocode*. In fact, my proposals were exactly the opposite of this idea, as I suggested to suppress all limitations in the number of potential ranks, not only in the genus-series, but also in the species-series (Dubois, 2006b). This proposal was made in the frame of the current *Code* system, using nominal-series and a Rule of Coordination within each of these series. This change would bring minor disturbance in the current nomenclatural system, would not require to “redefine” any nomen, but would allow taxonomists who may wish so to express in a much more detailed way hypothesized cladistic relationships at lower taxonomic level, as suggested by Hillis and Wilcox (2005). Examples of application of the proposed system to the taxonomy of American ranids proposed by Hillis and Wilcox (2005) were given (Dubois, 2006b).

Although he also questioned the importance of taxonomy and nomenclature in evolutionary biology, Hillis (2006) used *Molecular Phylogenetics & Evolution* as a forum to promote his ideas on the *Phylocode*. Publication of the complete discussion on this topic by this journal would have been very useful, as taxonomy and nomenclature play a great role, although often ignored or underestimated, in all biology, and particularly in evolutionary biology. As well explained, e.g., by Wiley (1981, pp. 203–204), cladograms alone, or lists of taxa showing subordination by pure indentation, cannot conveniently be used by evolutionary biologists themselves, and even less by users from other

disciplines, and we need classifications and nomenclatures to communicate about organisms and their relationships. However, there are several ways to express the same phylogenetic hypotheses under taxonomies and nomenclatures, and this has been a matter of hot debate among taxonomists and phylogeneticists in the recent decades. It would be fully relevant and useful for the readers of journals dealing with phylogenetics to open these journals to papers discussing the theory and practice of modern taxonomy and nomenclature. But if they did so, these journals should take care for allowing all different opinions to be expressed and discussed, in order to become true forums of free public discussion, not one-sided forums at the service of a single group of biologists, as several other journals already are, where opinions adverse to those of one “school” are systematically “silenced”.

Should taxonomy be drastically modified in order to please the users of the World Wide Web?

Section 6 of Hillis’s (2006) paper addresses a completely different question, that has nothing to do with my nomenclatural comments on the paper by Hillis and Wilcox (2005): he suggested that all American ranid species should be maintained in the genus *Rana*, mostly in order not to disturb users of online databases. Although unrelated with my initial work, and in fact mostly meant as a criticism of Frost et al.’s (2006) taxonomic proposals, this statement, which once again relies on a confusion between taxonomy and nomenclature, deserves comment, especially as the philosophy behind it is likely to carry a very misleading message, not only to taxonomists, but also to other biologists and to society as a whole.

As mentioned above, my paper was addressing only nomenclatural questions, not phylogenetic or taxonomic ones. It was not at all discussing the relationships and classification of ranoid frogs, as I think that we are still missing too much information, even after Frost et al.’s (2006) work, both on characters and on species, to be close to a robust hypothesis of detailed relationships among the many species of this group, and hence a robust taxonomy (Dubois, 2005c, 2006b,c). In the meanwhile, we will long have to use for this group provisional “working taxonomies” (Dubois, 1999) or “ergotaxonomies” (Dubois, 2005a,b,c). Regarding American species of this assemblage, their phylogenetic relationships will be more firmly established only when many more data are available on many more Asian and Oriental species (based on well-identified specimens), and in the meantime prudence is in order—as well illustrated by the recent unexpected discovery in Korea of the salamander genus *Karsenia* (Min et al. 2005).

This is why, in a recent ergotaxonomy of recent amphibians (Dubois, 2005c), many groups were still provisionally kept in the genus *Rana*. This was also the opinion of Hillis and Wilcox (2005). In contrast, recently Frost et al. (2006) proposed to raise the group recognized by Hillis and Wilcox (2005) as <NOVIRANA> to the rank of genus.

Both Hillis and Wilcox (2005) and Frost et al. (2006) agreed on the following hypotheses: the group (G1), including *Rana temporaria*, *R. boylei* and many other species (<LAURASIARANA Hillis and Wilcox, 2005>), is monophyletic; the group (G2), including *Rana palmipes*, *R. pipiens* and many other species (<NOVIRANA Hillis and Wilcox, 2005>), is monophyletic; the group (G3), including both these groups, is monophyletic. If these hypothesized relationships are accepted as a basis for a taxonomy, several arrangements are possible, including one where group (G3) is considered a genus, with two subgenera (G1) and (G2), and one where both groups (G1) and (G2) are treated as genera. This is not at all a matter of nomenclatural rules, but a matter of taxonomy.

As of today, nobody is able to say what a genus “is”. The term “genus” may both designate a nomenclatural rank and a taxonomic category (for the distinction between these two concepts, see Dubois, 2005b, 2006b). Taken as a nomenclatural rank, genus is “simply”, according to the *Code*, the rank between subtribe (or tribe, if no subtribes are recognized, or subfamily, or family) and subgenus (or species group, if no subgenera are recognized, or species): it only provides information on the hierarchical structure of the taxonomy, but not on any biological or other characteristics of the organisms. In contrast, if considered a taxonomic category, the term genus would designate a “kind” of taxa, which can be considered equivalent by some biological, historical or other criteria. Dubois (1988, pp. 66–73) provided a detailed discussion of possible criteria of equivalence between taxa in zoological taxonomy. Few such criteria have been proposed for the category genus, and only two of them may appear convincing today: that of absolute age of taxa (Hennig, 1950, 1966; Avise and Johns, 1999), which would appear an excellent criterion but whose implementation will be possible only when much more robust information is available on the ages of most zoological groups; and that of interspecific hybridizability (Dubois, 1988, 2004b), which currently is also marginally applicable, as few data are available in many zoological groups. Furthermore, as of today, none of these two criteria has been largely adopted by practicing taxonomists. Regarding the criterion of hybridizability, in the case of the frogs here at stake, no successful hybridization until adult stage has yet been reported between two species belonging, respectively, to groups (G1) and (G2), although such successful hybrids are known within both of these groups (Moore, 1955),

so this criterion is of no use here to stabilize generic taxonomy (for more details, see Dubois, 1988, 2004b). Therefore, in the present state of knowledge, genera in ranid frogs can correspond only to taxa ascribed to the same nomenclatural rank. As nomenclatural ranks carry no biological, historical or other information, the choice of the rank given to a set of sister taxa is largely arbitrary. As argued in detail in Dubois (2006b, p. 838), “the only, and relatively minor, constraint in this respect is that very-well known taxa, whose nomina are used in many textbooks and papers, should, as far as possible, be ascribed primary key ranks” as defined in Dubois (2006a). For this reason, Dubois (2006b, p. 838) had written that keeping *Rana* as a genus was “probably the best attitude for today, but in the future this genus will probably have to be dismantled, although probably not along the lines of the previous subgeneric classifications of this huge group”. So in the end I tend to agree with Hillis (2006) on this question, although not for the same reasons.

My choice to follow Frost et al.’s (2006) generic taxonomy with two distinct genera *Rana* and *Lithobates* in my two papers discussing nomenclatural problems in this group (Dubois, 2006b,c) was not a taxonomic choice, but a pedagogical one: with two distinct genera, more nomina could be used in the two possible infrageneric taxonomies presented (Dubois, 2006b, table 2; Dubois, 2006c, table 2), and less taxa remained “unnamed”, which was no doubt clearer for the reader. This did not mean in the least that I was “supporting” any of these taxonomies, or even the phylogenetic hypothesis on which they were based, as shown by the sentences: “For the sake of discussion of nomenclatural problems, let us just consider the cladograms provided by Hillis and Wilcox (2005; figs 1 and 2) as an acceptable working hypothesis” (Dubois, 2006c, p. 321), and “Following Frost et al. (2006), the rank genus is given here in table 2 to the taxa *Rana* and *Lithobates*” (Dubois, 2006c, p. 327).

At any rate, the decision whether *Rana* and *Lithobates* should be treated as genera or subgenera is a taxonomic one, which has nothing to do with nomenclatural rules or with the nomenclatural flaws in Hillis and Wilcox (2005). Because of the need of “freedom of taxonomic thought or actions”, such a decision cannot be imposed by any kind of rules but must be left to the personal appreciation of taxonomists and to free discussions among them. In the long run, as has always been the case in the history of taxonomy, a consensus will no doubt appear among practitioners of the taxonomy of any given group. This matter should be left in the hands of specialists, not of laymen outsiders of the discipline of taxonomy.

In this respect, Hillis (2006, p. 337) proposed a very strange, and potentially very dangerous, approach, that can be briefly designated as a plea for “Google taxonomy”. He suggested that taxonomists should not

change the nomina of taxa in order not to upset users of electronic databases such as Google. 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 *Sphaerotheca breviceps*. However, the three latter species, first removed from *Rana* by Dubois (1981, 1987, 1992), are now universally accepted as belonging, not only in other genera, but also in other subfamilies (Dubois, 2005c) or even families (Frost et al., 2006). Following Hillis, (2006) suggestion would require to come back to the obsolete, although long prevalent, rapid 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 *Sphaerotheca 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 fact, although this is surprising from someone who has largely contributed to the progress of our knowledge in phylogeny and taxonomy, Hillis's (2006) comments on this point seem to give support to a very widespread, although completely wrong, opinion, namely that most of the biodiversity of our planet is "relatively well known", and that our taxonomies are "almost final". This ignores the "taxonomic impediment" (Anonymous, 1994) and the fact that only about 10–20% of the living species of our planet (or possibly even much less) have been collected, studied, described and named by taxonomists, and that even among the named ones, only a very small proportion can be considered relatively well known (Dubois, 2003, references therein). In no other research field, would our society consider it acceptable to have a percentage of missing data of 80–90%, as the rate of mistakes usually considered acceptable in science is below 5%. It would seem that the duty of every taxonomist or evolutionary biologist would be to pass this message to our society. The misleading idea that "final lists of species" or "final taxonomies" are available, and that, in order not to disturb the peace of mind of non-taxonomist users of data on biodiversity (including conservation biologists), no significant changes should be brought to the classifications and nomina, is not doing a service to the discipline of taxonomy and to our knowledge of our planet's biodiversity: "Rather than trying to comply with the requests for 'final lists' that are often presented to them, taxonomists should explain the reasons for this instability, and should try and convince our 'social partners' that, rather than asking for a 'freezing' of the scientific activity of

exploration and analysis of biodiversity, they should support and encourage it. In the long run, it may prove more interesting and useful to better understand the biodiversity on our planet than to have 'final' and 'stable', i.e., wrong and incomplete, lists of this biodiversity for the peace of minds of administrators and technocrats." (Dubois, 1998, p. 22). At the stage now reached by our knowledge of biodiversity, there is no doubt that "taxonomic stability is ignorance" (Gaffney, 1977, 1979; Dominguez and Wheeler, 1997; Benton, 2000; Padial and De la Riva, 2006), and evolutionary biologists should not even consider it a laudable aim in the short run. "Google taxonomy" is not a solution for the future of systematics.

Conclusions

At the end of his section 4, Hillis (2006, pp. 335–336) proposed another taxonomy and nomenclature of American ranids, indeed acceptable under the rules of the *Code*, which only recognizes, below the rank genus, "the smallest clades" defined by Hillis and Wilcox (2005) as subgenera. In this taxonomy, subgenera are recognized for all groups of species considered monophyletic but for which the data produce an unresolved polytomy. More exactly, all such groups except two. As a matter of fact, following the rules of the *Code*, Hillis (2006) accepted to recognize two "monotypic" (or, more exactly, currently considered so) genera, *Pantherana* for *Rana pipiens* and *Sierrana* for *Rana sierramadrensis*. However, if this course was followed, there would be no reason for not recognizing also two additional subgenera for two other "monotypic" (or currently considered so) groups, including, respectively, *Rana maculata* and *Rana sylvatica*. However, in both these cases, no existing genus-series nomen is available (Dubois, 2006c, table 1), so that new nomina should be coined (and published with a diagnosis or an apogonosis) to designate them.

Discussing this new possible taxonomic arrangement, Hillis (2006, p. 336) noted that some of these nomina "would then be used in a different sense than recommended by Hillis & Wilcox (2005)". This is indeed the case, and is fully unavoidable, as shown in table 2 in Dubois (2006b,c) and fully illustrated by the discussions in Hillis (2006) and here above. Because the rules of allocation of nomina to taxa are fully different under the *Code* and under the *Phylocode*, in many cases the "same" nomen under both systems will designate different taxa (even with the same taxonomic arrangement), so that it cannot be considered the "same" nomen. This was in fact the main and final message of my paper (Dubois, 2006c), a point that Hillis (2006) did not tackle in his reply, but which is however fully confirmed again by this long discussion. To avoid chaos in communication, I therefore reiterate my statement that it is urgent that all biological journals take

steps to make compulsory the use of different modes of writing for the nomina that follow these two nomenclatural schools. The system that I already advocated (Dubois, 2005b, 2006b,c,d), where the two kinds of nomina are very clearly distinguished (*Pantherana* versus <PANTHERANA>), would indeed fully play this role.

References

- Anonymous [Systematics Agenda 2000], 1994. Charting the Biosphere: a Global Initiative to Discover, Describe and Classify the World's Species. Technical Report. American Museum of Natural History, American Society of Plant Taxonomy, Society of Systematic Biologists and the Willi Hennig Society, New York.
- Anonymous [International Commission on Zoological Nomenclature], 1999. International Code of Zoological Nomenclature, 4th edn. International Trust for Zoological Nomenclature, London.
- Ashlock, P.D., 1971. Monophyly and associated terms. *Syst. Zool.* 20, 63–69.
- Avise, J.C., Johns, G.C., 1999. Proposal for a standardized temporal scheme of biological classification for extant species. *Proc. Natl Acad. Sci. USA* 96, 7358–7363.
- Benton, M.J., 2000. Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? *Biol. Rev.* 75, 633–648.
- Boulenger, G.A., 1918. Aperçu des principes qui doivent régir la classification des espèces du genre *Rana*. *Bull. Soc. Zool. Fr.* 43, 111–121.
- Boulenger, G.A., 1920a. A monograph of the South Asian, Papuan, Melanesian, and Australian frogs of the genus *Rana*. *Rec. Indian Mus.* 20, 1–226.
- Boulenger, G.A., 1920b. A monograph of the American frogs of the genus *Rana*. *Proc. Am. Acad. Arts Sci.* 55, 413–480.
- 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., 1994. Toward a phylogenetic system of biological nomenclature. *Trends Ecol. Evol.* 9, 27–31.
- Dominguez, E., Wheeler, Q.D., 1997. Taxonomic stability is ignorance. *Cladistics* 13, 367–372.
- Dubois, A., 1981. Liste des genres et sous-genres nominaux de Ranoidea (Amphibiens, Anoures) du monde, avec identification de leurs espèces-types: conséquences nomenclaturales. *Monit. Zool. Ital.* 15, 225–284.
- Dubois, A., 1987. *Miscellanea taxinomica batrachologica* (I). *Alytes* 5, 7–95.
- Dubois, A., 1988. The genus in zoology: a contribution to the theory of evolutionary systematics. *Mem. Mus. Nat. Hist. Nat.* 140, 1–123.
- Dubois, A., 1991. Nomenclature of parthenogenetic, gynogenetic and “hybridogenetic” vertebrate taxons: new proposals. *Alytes* 8, 61–74.
- Dubois, A., 1992. Notes sur la classification des Ranidae (Amphibiens, Anoures). *Bull. Mens. Soc. Linn Lyon* 61, 305–352.
- Dubois, A., 1997. An evolutionary biologist's view on the science of biology. *Alytes* 15, 133–136.
- Dubois, A., 1998. List of European species of amphibians and reptiles: will we soon be reaching “stability”? *Amphibia-Reptilia* 19, 1–28.
- Dubois, A., 1999. *Miscellanea nomenclatorica batrachologica*. 19. Notes on the nomenclature of Ranidae and related groups. *Alytes* 17, 81–100.
- Dubois, A., 2000. Synonymies and related lists in zoology: general proposals, with examples in herpetology. *Dumerilia* 4, 33–98.
- Dubois, A., 2003. The relationships between taxonomy and conservation biology in the century of extinctions. *C. R. Biol.* 326, S9–S21.
- Dubois, A., 2004a. The higher nomenclature of recent amphibians. *Alytes* 22, 1–14.
- Dubois, A., 2004b. Developmental pathway, speciation and supraspecific taxonomy in amphibians. 2. Developmental pathway, hybridizability and generic taxonomy. *Alytes* 22, 38–52.
- Dubois, A., 2005a. Propositions pour l'incorporation des nomina de taxons de rang supérieur dans le *Code International de Nomenclature Zoologique*. *Biosystema* 23, 73–96.
- Dubois, A., 2005b. Proposed Rules for the incorporation of nomina of higher-ranked zoological taxa in the *International Code of Zoological Nomenclature*. 1. Some general questions, concepts and terms of biological nomenclature. *Zoosystema* 27, 365–426.
- Dubois, A., 2005c. *Amphibia Mundi*. 1.1. An ergotaxonomy of recent amphibians. *Alytes* 22, 1–24.
- Dubois, A., 2005d. Proposals for the incorporation of nomina of higher-ranked zoological taxa into the Code. *Bull. Zool. Nomencl.* 62, 200–209.
- Dubois, A., 2006a. Proposed Rules for the incorporation of nomina of higher-ranked zoological taxa in the *International Code of Zoological Nomenclature*. 2. The proposed Rules and their rationale. *Zoosystema* 28, 165–258.
- Dubois, A., 2006b. New proposals for naming lower-ranked taxa within the frame of the *International Code of Zoological Nomenclature*. *C. R. Biol.* 329, 823–840.
- Dubois, A., 2006c. Naming taxa from cladograms: a cautionary tale. *Mol. Phylogenet. Evol.* 42, 317–330.
- Dubois, A., 2006d. Incorporation of nomina of higher-ranked taxa into the *International Code of Zoological Nomenclature*: some basic questions. *Zootaxa* 1337, 1–37.
- Dubois, A., 2006e. Should the Code limit the number of nomenclatural ranks in zoology? *Bull. Zool. Nomencl.*, submitted on 23 February 2006.
- Dubois, A., Nemésio, A., 2007. Does nomenclatural availability of nomina of new species or subspecies require the deposition of vouchers in collections? *Zootaxa* 1409, 1–22.
- Dubois, A., Ohler, A., 1997. Early scientific names of Amphibia Anura. I. Introduction. *Bull. Mus. Nat. Hist. Nat.* 4, 297–320.
- Frost, D.R., Grant, T., Faivovich, J., Bazin, 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. Hist.* 297, 1–370.
- Gaffney, E.S., 1977. The side-necked turtle family Chelidae: a theory of relationships using shared derived characters. *Am. Mus. Novit.* 2620, 1–28.
- Gaffney, E.S., 1979. An introduction to the logic of phylogeny reconstruction. In: Cracraft, J., Eldredge, N. (Eds.), *Phylogenetic Analysis and Paleontology*. Columbia University Press, New York, pp. 79–111.
- Glaw, F., Vences, M., Böhme, W., 1998. Systematic revision of the genus *Aglyptodactylus* Boulenger, 1919 (Amphibia: Ranidae), and analysis of its phylogenetic relationships to other Madagascan ranid genera (*Tomopterna*, *Boophis*, *Mantidactylus*, and *Mantella*). *J. Zool. Syst. Evol. Res.* 36, 17–37.
- Godfray, H.C.J., Knapp, S. (Eds.), 2004. Taxonomy for the twenty-first century. *Philos. Trans. R. Soc. Lond. (B)* 359, 559–739.
- Hennig, W., 1950. *Grundzüge Einer Theorie der Phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin.
- Hennig, W., 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana, IL.
- Hillis, D.M., 2006. Constraints in naming parts of the tree of life. *Mol. Phylogenet. Evol.* 42, 331–338.
- Hillis, D.M., de Sá, R., 1988. Phylogeny and taxonomy of the *Rana palmipes* group (Salientia: Ranidae). *Herpetol. Monogr.* 2, 1–26.

- 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.
- Inger, R.F., 1954. Systematics and zoogeography of Philippine Amphibia. *Fieldiana Zool.* 33, 181–531.
- Inger, R.F., 1966. The systematics and zoogeography of the Amphibia of Borneo. *Fieldiana Zool.* 52, 1–402.
- Inger, R.F., 1968. Amphibia. *Explor. Parc. Natl. Garamba* 52, 1–190.
- Joyce, W.G., Parham, J.F., Gauthier, J.A., 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *J. Paleontol.* 78, 989–1013.
- Mayr, E., 1995. Systems of ordering data. *Biol. Philos.* 10, 419–434.
- Min, M.S., Yang, S.Y., Bonett, R.M., Vieites, D.R., Brandon, R.A., Wake, D.B., 2005. Discovery of the first Asian plethodontid salamander. *Nature* 435, 87–90.
- Moore, J.A., 1955. Abnormal combinations of nuclear and cytoplasmic systems in frogs and toads. *Adv. Genet.* 7, 139–182.
- Padial, J.M., De la Riva, I., 2006. Taxonomic inflation and the stability of species lists: the perils of ostrich's behaviour. *Syst. Biol.* 55, 859–867.
- Pennisi, E., 2001. Linnaeus's last stand? *Science* 291, 2307.
- Simpson, D.P., 1968. *Cassell's Latin-English English-Latin Dictionary*, 5th edn. Continuum, London.
- Sluys, R., Martens, K., Schram, F.R., 2004. The PhyloCode: naming of biodiversity at a crossroads. *Trends Ecol. Evol.* 19, 280–281.
- Stevenson, D.W., Davis, J.I. (Eds.), 2003. *Säg bara Nej till fylokoden!* *Bot. Rev.* 69, 1–120.
- Strickland, H.E., Henslow, J.S., Phillips, J., Shuckard, W.E., Richardson, J., Waterhouse, G.R., Owen, R., Yarrell, W., Jenyns, L., Darwin, C., Broderip, W.J., Westwood, J.O., 1843. Series of propositions for rendering the nomenclature of zoology uniform and permanent, being the Report of a Committee for the consideration of the subject appointed by the British Association for the Advancement of Science. *Ann. Mag. Nat. Hist.* 1, 259–275.
- Stuessy, T.F., 1997. Classification: more than just branching patterns of evolution. *Aliso* 15, 113–124.
- Vences, M., Glaw, F., Kosuch, J., Das, I., Veith, M., 2000. Polyphyly of *Tomopterna* (Amphibia: Ranidae) based on sequences of the mitochondrial 16S and 12S rRNA genes, and ecological biogeography of Malagasy relict amphibian groups. In: Lourenço, W.R., Goodman, S.M. (Eds.), *Diversité et Endémisme de Madagascar*, Mémoires de la Société de Biogéographie. Société de Biogéographie, Paris, pp. 229–242.
- Wiley, E.O., 1981. *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*. Wiley, New York.