



Taxonomy / Taxonomie

New proposals for naming lower-ranked taxa within the frame of the *International Code of Zoological Nomenclature*

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Abstract

The recent multiplication of cladistic hypotheses for many zoological groups poses a challenge to zoological nomenclature following the *International Code of Zoological Nomenclature*: in order to account for these hypotheses, we will need many more ranks than currently allowed in this system, especially in lower taxonomy (around the ranks genus and species). The current *Code* allows the use of as many ranks as necessary in the family-series of nomina (except above superfamily), but forbids the use of more than a few ranks in the genus and species-series. It is here argued that this limitation has no theoretical background, does not respect the freedom of taxonomic thoughts or actions, and is harmful to zoological taxonomy in two respects at least: (1) it does not allow to express in detail hypothesized cladistic relationships among taxa at lower taxonomic levels (genus and species); (2) it does not allow to point taxonomically to low-level differentiation between populations of the same species, although this would be useful in some cases for conservation biology purposes. It is here proposed to modify the rules of the *Code* in order to allow use by taxonomists of an indeterminate number of ranks in all nominal-series. Such an 'expanded nomenclatural system' would be highly flexible and likely to be easily adapted to any new finding or hypothesis regarding cladistic relationships between taxa, at genus and species level and below. This system could be useful for phylogeographic analysis and in conservation biology. In zoological nomenclature, whereas robustness of nomina is necessary, the same does not hold for nomenclatural ranks, as the latter are arbitrary and carry no special biological, evolutionary or other information, except concerning the mutual relationships between taxa in the taxonomic hierarchy. Compared to the *Phylocode* project, the new system is equally unambiguous within the frame of a given taxonomic frame, but it provides more explicit and informative nomina for non-specialist users, and is more economic in terms of number of nomina needed to account for a given hierarchy. These ideas are exemplified by a comparative study of three possible nomenclatures for the taxonomy recently proposed by Hillis and Wilcox (2005) for American frogs traditionally referred to the genus *Rana*. **To cite this article: A. Dubois, C. R. Biologies 329 (2006).**

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Résumé

Nouvelles propositions pour la nomenclature des taxons de rangs inférieurs dans le cadre du *Code international de nomenclature zoologique*. La multiplication récente d'hypothèses cladistiques pour de nombreux groupes zoologiques pose un défi à la nomenclature zoologique respectant le *Code international de nomenclature zoologique* : afin de rendre compte de telles hypothèses, il est nécessaire de disposer de bien plus de rangs que ceux actuellement autorisés par ce système, notamment en taxinomie inférieure (autour des rangs genre et espèce). Le *Code* actuel permet l'emploi d'autant de rangs que nécessaire dans la série-famille

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de nomina (sauf au-dessus de la superfamille), mais interdit l'emploi de plus de quelques rangs dans les séries genre et espèce. Il est ici soutenu que cette limitation n'a pas de justification théorique, ne respecte pas la liberté de pensée et d'action taxinomique, et est néfaste à la taxinomie zoologique de deux manières au moins : (1) elle ne permet pas d'exprimer dans le détail des hypothèses de relations de parenté entre taxons aux niveaux taxinomiques inférieurs (genre et espèce); (2) elle interdit d'exprimer taxinomiquement des différenciations à bas niveau, entre populations de la même espèce, alors que cela serait utile dans certains cas en biologie de la conservation. Il est ici proposé de modifier les règles du *Code* de manière à permettre la reconnaissance par les taxinomistes d'autant de rangs que nécessaire dans toutes les séries nominales. Un tel « système nomenclatural élargi » serait très flexible et susceptible d'adaptation à toute nouvelle découverte ou hypothèse concernant les relations cladistiques entre taxons, aux niveaux genre et espèce et en-dessous. Ce système serait utile pour les analyses phylogéographiques et en biologie de la conservation. En nomenclature zoologique, si une robustesse des nomina est nécessaire, il n'en va pas de même pour les rangs nomenclaturaux, car ces derniers sont arbitraires et n'apportent aucune information particulière en termes biologiques, évolutifs ou autres, sauf en ce qui concerne les relations mutuelles entre les taxons dans la hiérarchie taxinomique. Si on le compare avec le projet de *Phylocode*, le nouveau système permet de la même manière une expression non-ambigüe d'une taxinomie donnée, mais il procure des nomina plus explicites et informatifs, notamment pour les non-spécialistes, et il est plus économique en ce qui concerne le nombre de nomina nécessaires pour rendre compte d'une taxinomie donnée. Ces idées sont illustrées par une comparaison de trois nomenclatures possibles pour une même taxinomie, celle récemment proposée par Hillis et Wilcox (2005) pour les grenouilles américaines traditionnellement rapportées au genre *Rana*. **Pour citer cet article : A. Dubois, C. R. Biologies 329 (2006).**

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Mots-clés : Nomenclature élargie ; Rangs nomenclaturaux ; Taxinomie phylogénétique ; Phylogéographie ; Biologie de la conservation ; *Phylocode* ; Parcimonie nomenclaturale ; *Rana*

1. Introduction

Our planet is inhabited by billions of organisms. In order to be able to study them and deal with them, we need a system of biological classification or *taxonomy*. As the different kinds of organisms result from a historical process (biological evolution), most biologists nowadays agree that, to be meaningful, the taxonomic system should provide information on the evolutionary or phylogenetic relationships between organisms. Although details of the real tree of life will probably remain unknown, scientific methods exist to propose hypotheses regarding the structure of this tree. Such hypotheses (cladograms) can be used as a basis for taxonomies. Once distinguished and defined, taxonomic units or *taxa* (singular *taxon*) are usually designated by 'scientific names' or *nomina* (singular *nomen*) [1]. Although often confounded, the two processes are distinct [2,3]: taxa can be recognized but not named, and nomina can be created without designating taxa [4]. In order for nomina to allow efficient, unambiguous and universal communication among biologists, their allocation to taxa requires following precise and stringent rules. Several nomenclatural systems have been and still are used by biologists.

In zoology, the traditional nomenclatural system is ruled by the *International Code of Zoological Nomenclature* [5,6], designated below as 'the *Code*'. Many

alternative systems have been unsuccessfully proposed all along the last 250 years, but most of them have been forgotten by now. In the recent years, several new alternative systems have been developed under different lines [7–13], that all have in common to have been called 'phylogenetic' by their proponents. Among them, the system known as *Phylocode*, derived from the original proposal of de Queiroz and Gauthier [8,9], has elicited a number of comments, both favourable (review and references in [14]; recent references in [15–18]) and unfavourable (review and references in [2]; recent references in [19–21]). An important point, however, is the contention that, because of its underlying 'typological' philosophy, the *Code* would not be appropriate for naming taxa under a phylogenetic taxonomic system has been rejected, both in zoology [2,12,13] and in botany [22]. Possibly the most important reasons for keeping the current *Code* are not theoretical, but practical, with two major points at stake: (1) the co-existence of two nomenclatural systems is already, and might become growingly, a cause of confusion and of communication problems with the rest of the community of biologists as well as with all members of the society [19]; (2) the working time and energy that have already, and that might still, be involved in the implementation of the *Phylocode*, at the beginning of the *century of extinctions* [23], by the small scientific community of taxonomists, would be better used to collect,

study and describe the many species of our planet that are still unknown [2], and not doing so can be viewed as “a criminal operation against the study of biodiversity” [24].

No taxonomic principles and no nomenclatural rules will ever be ‘perfect’, at least from a pure theoretical point of view, as it is impossible to account for the very complex processes of organismic evolution in a one-dimensional classificatory and nomenclatural scheme. However, the theoretical foundations of the current *Code* are no doubt very sound [1,2,6,20,21,25–38]. Importantly, these rules respect a large independence between taxonomy and nomenclature. They have therefore allowed nomenclature to follow the changes in the paradigms of taxonomy that have occurred during the history of systematics [39–41], and are susceptible to adapt to still further changes that might occur in the future [2]. Thus, they largely respect the following statement of the *Preamble* of the zoological *Code*: “The objects of the Code are to promote stability and universality in the scientific names of animals and to ensure that the name of each taxon is unique and distinct. All its provisions and recommendations are subservient to those ends and none restricts the freedom of taxonomic thought or actions.” It is important to maintain the current nomenclatural system and not embark into an adventure for the search of a ‘theoretically better’ system, as the harm to taxonomy would be much larger than the expected benefit [2 (pp. 396–398)]. However, this does not mean that the current *Code* is perfect and final and should not change. The *Code* would have much to gain to evolve, in particular to take into account the recent developments of taxonomy that followed the expansion of cladistic studies in most animal groups.

One of the problems of the current *Code*, perhaps its major one, is its incomplete covering of taxonomic hierarchy. In this respect, the *Code* is inferior to other recently proposed systems like the *Phylocode*, which do not have such limitations. The *Code* does not regulate all nomina, but only those from the rank subspecies to the rank superfamily, excluding those of taxa above the rank superfamily and below the rank subspecies (such as forms and varieties, although these ranks are recognized by the botanical code [42]). Furthermore, even within the span covered between subspecies and superfamily, the *Code* limits the number of authorized ranks. The hierarchy of ranks recognized by the *Code* is not a continuum, but is divided in three ‘groups’, or better *series* [1,2] of nomina, the *species-*, *genus-* and *family-series*. Two additional nominal-series, the *class-series* and the *variety-series*, are currently not regulated by the

Code, but this situation might change in the future [24, 43–48].

Nomina within each nominal-series interact concerning coordination, priority, synonymy and homonymy, but the interactions between nomina belonging to different series are limited, being mostly restricted to nomina of higher series relying on ‘types’, or better *onomatophores* [2], that are nomina (more exactly ‘nominal taxa’ or *taxomina* [2]) of lower series. The Rule of Coordination insures that, whenever a taxon includes several subordinate taxa referred to the same nominal-series, the first named of the latter, called ‘nominotypical’ in the *Code*, bears the same nomen (with the same onomatophore, author and date) as the superordinate taxon.

In each nominal-series recognized by the *Code*, several distinct ranks are allowed. The situation is however different in the three series. In the family-series, the number of potential ranks is virtually unlimited, except above superfamily, as this series “encompasses all nominal taxa at the ranks of superfamily, family, subfamily, tribe, subtribe, and any other rank below superfamily and above genus that may be desired” (Art. 35.1). In contrast, in the other two series, the number of ranks recognized by the *Code* is strictly limited, as the genus-series “encompasses all nominal taxa at the ranks of genus and subgenus” (Art. 42.1), and the species-series “encompasses all nominal taxa at the ranks of species and subspecies” (Art. 45.1). Despite this formal definition given in Art. 45.1, two additional ranks are allowed in the *Code* in the latter series, those of “aggregates of species” and of “aggregates of subspecies”, whose nomina may be interpolated in parentheses between the genus and species nomina or between the species and subspecies nomina (Art. 6.2) and are submitted to the Principle of Priority (Art. 23.3.3). Nomenclatural ranks below subgenus and below subspecies are not recognized by the *Code*, which means that nomina proposed for taxa at such lower ranks in these two series are not nomenclaturally valid. A striking fact is that the number of ranks allowed by the botanical code is much higher than in zoology, as it includes ranks such as section and series below genus, and variety and form below species, and also subsidiary ranks such as subsection, subseries, etc. This is all the more strange that the number of known species and other taxa is much lower in botany than in zoology.

The current rules of the *Code* therefore forbid the use of a nomenclatural hierarchy of more than two ranks within the genus-series and more than four in the species-series. Is there any theoretical justification for this limitation? None that I ever heard of. The major reason of this restriction seems to be ‘tradition’. At lower

taxonomic level, probably the fact that many ‘varieties’ and ‘forms’ of the earlier taxonomists were in fact only ‘atypical’ specimens, exhibiting unusual mutations, or hybrids, or rare variants found in sympatry with other more ‘normal’ specimens, has played a role: such specimens clearly did not qualify as members of distinct taxa, and suppression of these lower ranks was probably meant to extirpate these ‘non-taxonomic’ ranks from zoological taxonomy. But nowadays the distinction between taxon and individual variant is clear for most zoologists and this historical reason does not hold any more.

The arbitrary restrictions that exist in the genus- and species-series can legitimately be considered as an unacceptable restriction of “freedom of taxonomic thought or actions”. The only justification for these restrictions is ‘tradition’. Maintaining these unwarranted restrictions in our days where many cladistic analyses are produced, which result in an increase in the number of taxa that need to be recognized, may become a reason for some zoologists to abandon the *Code* to shift to an alternative nomenclatural system devoid of these limitations.

The purpose of the present paper is to address two specific questions: are these restrictions harmful to zoological taxonomy, and should this be changed? It will be shown below that the reply to both questions is yes, for two reasons at least: (1) the current rules do not allow us to express in detail hypothesized cladistic relationships among taxa at lower taxonomic levels (around genus and species); (2) they do not allow to point to low-level differentiation between populations of the same species, although this would be useful in some cases for conservation biology purposes.

Full understanding of the text below requires a few preliminary clarifications.

(1) A distinction is made between *taxa* and *clades*. Although the aim of taxonomy is to provide a classificatory scheme based on the patterns of phylogeny of organisms, a distinction is made here between these patterns or clades, and taxa. Taxa are concepts or models used in biological classification, which account for some particularities of the organisms. Under a cladistic approach of taxonomy, a taxon can be recognized only for a group of organisms that is considered holophyletic, a concept for which the synonymous terms *phylon* [49], *cladon* [50] and *phylo-taxon* [51] have been coined. Such taxa are hypotheses about the real clades of the real world, but not these clades themselves, which are unknown. Thus, if clades may be viewed ontologically as individuals, it is not the case of taxa, which are

classes of organisms, defined by scientific criteria such as characters.

(2) Further distinctions are made between *taxa* and *nomina*, and between *nomina* and *ranks*. Taxa are taxonomic classes of organisms, whereas *nomina* are ‘just’ labels given to these taxa to designate them unambiguously and universally, but without any explanatory, descriptive or other role or value by themselves [2,24,46]. Ranks as used in the *Code* are distinct from *nomina*. The same nomen can be used (either unchanged or slightly modified) to designate distinct (i.e., more or less inclusive) taxa at different ranks in the nomenclatural hierarchy. This is because of the existence in the *Code* of the Rule of Coordination.

(3) In the text below, for reasons explained in detail elsewhere [4], the two nomenclatural systems mentioned above are qualified by neuter designations, respectively ‘onomatophore-based’ for the *Code* and ‘definition-based’ for the *Phylocode*. Besides, generic and specific *nomina* following the *Code* are written below as they have been in most publications for more than one century, i.e. in small characters italics: *Lithobates* or *Lithobates* Fitzinger, 1843. In contrast, *nomina* following the *Phylocode* are written as follows: <LITHOBATES>, <LITHOBATES Hillis and Wilcox, 2005> or <LITHOBATES [Fitzinger, 1843] Hillis and Wilcox, 2005>. These conventions avoid possible confusion between both kinds of *nomina*, which follow widely different and incompatible nomenclatural philosophies [2,4].

2. Do we need nomenclatural ranks?

Nomenclatural ranks are nothing but *levels* in a *hierarchical* arrangement of taxa: taxa of higher ranks are composed of taxa of lower ranks. Ranks tell us nothing more than this information on the *structure* of taxonomy. The usefulness of nomenclatural ranks in zoological taxonomy has recently been challenged by several authors [12,14,52–54], mostly among supporters of the *Phylocode*. They claimed that ranks should be abandoned as they are subjective and arbitrary, and do not warrant comparisons between taxa of same rank in different groups. The latter is indeed true: taxa ascribed to a given rank in different groups are rarely equivalent by various biological standards, as well illustrated by the case of the taxa of birds as compared to those of other vertebrates, discussed in detail in [55]. However, the fact that nomenclatural rank has been used by some authors to make invalid comparisons is not a good reason for rejecting ranks [2]: “Just because some doctors misprescribe a particular drug, should other doctors be

banned from prescribing it?” [36 (p. 13)]. As aptly discussed, e.g. in [56], taxonomic hierarchies as reflected in nomenclatural ranks are “organizational models of relationships” that are useful for keeping track of inter-level relationships among entities. Abandoning ranks in zoological nomenclature would make it much less efficient as a tool for communication about taxonomies, its basic purpose.

A major function of biological classifications [39–41] is to provide a universal system of storage and retrieval of information. In order to play this role, a taxonomic system must have a hierarchical structure. Without such a structure, all taxa having the same ‘level’, scoring of millions of items would be necessary before finding the proper one. To be efficient and coherent, a hierarchy must be unique, each taxon at a lower level being referred to a single taxon at the next higher level. This can be rigorously defined in mathematical terms (e.g., [57 (p. 11)]) and was more simply called by Gould [58 (p. 66)] “irrevocable branching without subsequent amalgamation”. The hierarchical structure of the nomenclatural system of the *Code* allows taxonomy to play the practical role of an indexation system of information, just like the hierarchical structure of keywords in an index or a database. In such systems, keywords at a given level are only roughly equivalent (in terms of information content or diversity, or of number of subordinate keywords) but are nevertheless quite useful to find the information. A nomenclature without ranks would be most inconvenient and poorly informative.

However, some confusion has long been maintained in zoological taxonomy between *taxonomic categories* and *nomenclatural ranks*. It is highlighted by the recent use of the formula ‘categorical ranks’ [3,12]. The distinction between the two concepts, recently emphasized [2 (p. 412)], helps to clarify the current debate on ranks. Nomenclatural ranks, discussed above, are subsequent levels in a hierarchy of taxa that are considered to be more or less inclusive. In any phylogenetic taxonomy, they carry by themselves no information apart from hierarchical cladistic relationships. In contrast, taxonomic categories are classes of taxa that may coincide only partially with ranks. They may, or not, be given biological definitions, and may, or not, be ranked. In higher taxonomy, categories usually coincide with nomenclatural ranks and strictly reflect the structure of the cladogram: no biological definition of the categories ‘order’ or ‘class’ has ever been proposed. The only convincing criterion ever suggested to standardize the use of such categories over the whole of zoology is the absolute age of taxa [59–61], 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. In lower taxonomy, however, biological definitions have been proposed for a number of taxonomic categories, either at genus [55,62] or at species level [49,63]. Several distinct taxonomic categories can be ascribed the same rank in the nomenclatural hierarchy. For example, the same nomenclatural rank ‘species’ can be ascribed to the taxonomic categories ‘bisexual species’, ‘parthenogenetic species’, and ‘hybridogenetic species’ [49]. Many of the criticisms recently published about the non-equivalence between taxa of the same nomenclatural ranks are irrelevant, as they do not make this distinction. It is quite true that taxa of the same nomenclatural rank are not equivalent by any biological criterion. But taxa allocated to some taxonomic categories for which biological (or historical, e.g. [61]) definitions have been provided, may be equivalent under these criteria.

Any taxonomy can exist without a nomenclature. It can be expressed as a list of taxa, whose hierarchical relationships can be shown by successive indentations from the margin. But pure indentation without any designation of ranks, either by terms or by codes or numbers, is unpractical, as it does not allow us to know which taxa are at equivalent levels, e.g., ‘sister-taxa’ (e.g., [7 (pp. 203–204)]). To avoid this difficulty, a mode of notation has to inform on the relative levels of taxa. In a given taxonomic hierarchy, the relation of *ordination* (from the Latin *ordo*, ‘series, order, rank’) between any two taxa can be referred to one of the following situations: both taxa may be *parordinate* (sharing the same level in the hierarchy; from the Latin *par*, ‘equal’) or *imparordinate* (occupying different levels in the hierarchy; from the Latin *impar*, ‘unequal’). In the latter case, there are two possibilities: they may be *coordinate*, when they have a topotaxic relation of *peritaxy* [2], i.e., one of the two taxa, called *subordinate*, is included in the other one, called *superordinate*; or they may be *xenordinate*, when they have a topotaxic relation of *xenotaxy* [2], i.e., none of the two taxa is included in the other.

In nomenclature following the *Phylocode*, no device is used to indicate the relationships of ordination in the nomina of taxa or even in terms designating the ranks, as ranks, although allowed, are not involved in the process of naming taxa. In contrast, under the *Code*, ranks are part of the naming process, although slightly differently in the three nominal-series. In the family-series, the same nomen takes different spellings to designate different coordinate taxa: thus, superfamily *Ranoidea*, family *Ranidae*, subfamily *Raninae*, tribe *Ranini*. In the genus- and species-series, the spelling of the nomen does not change when it designates different coordinate taxa:

genus *Rana*, subgenus *Rana*; species *Rana temporaria*, subspecies *Rana temporaria temporaria*. The nomen of any taxon that includes at least two subordinate taxa must also be given to one of the latter: thus, if the family *Ranidae* includes subfamilies, one needs to be named *Raninae*, and if containing subgenera the genus *Rana* needs to have a subgenus *Rana*. In the *Code*, the subordinate taxon that bears the same nomen as its superordinate taxon is designated as *nomi-notypical*. To complete the extirpation of the term *type* and of its derivatives from zoological nomenclature, advocated elsewhere [2], the latter term could be replaced by the adjective *eponymous* (from the Greek *epi*, ‘above’), or by its substantive *eponym*, but I propose that these terms be used in a wider sense than in common language, i.e., to designate identity or subidentity between coordinate nomina in *both* direction of the hierarchy. Thus, all three nomina *Ranoidea*, *Ranidae* and *Raninae* are eponyms. Two kinds of eponyms can be distinguished: a subordinate eponym can be called a *hyponym*, and a superordinate eponym an *epinym* [4]. Thus, *Ranoidea* is an epinym of *Ranidae*, and *Raninae* a hyponym of the latter.

The system of ranks as used in the *Code* provides a convenient and workable system of indexation of taxonomic information and it would simply be destructive and ‘masochist’ for zoologists to abandon it. This is why, in strong contrast with the authors who recently suggested abandoning ranking, it is here argued that ranking in zoological nomenclature should not only be *kept*, but even *expanded*, to become more general and more useful, for reasons that require now explanation.

3. Limitations in the number of ranks allowed by the *Code*: an enlightening example

In order to facilitate this discussion, it may be better to start from a concrete example. A good one is provided by the phylogeny and taxonomy of American frogs referred to the genus *Rana* recently published by Hillis and Wilcox [64]. These authors provided an analysis of the cladistic relationships between 58 species, based on sequences from the mitochondrial genome of most known species of this group. Although this study is certainly not the ‘final word’ on this question [4], for the sake of discussion of nomenclatural problems we will consider the cladograms given in this work [64 (fig. 1–2)] as an acceptable working hypothesis. On the basis of these cladograms, these authors distributed all American species referred to the genus *Rana* and the European species *Rana temporaria* into 24 taxa. Interestingly, they provided a ‘double nomenclature’, under both the *Code* and the *Phylocode*, for these taxa. Under the *Phy-*

locode, they used an unranked taxonomy with taxa that were all designated by uninomina, but without formal ranks. For 16 of these taxa, they provided nomina with their node-based ‘phylogenetic definitions’, but they left four plurispecific taxa unnamed pending further data supporting or rejecting their validity, or ascertaining their specific content. Furthermore, following the taxonomic principles of the *Phylocode* against ‘taxonomic redundancy’, they did not provide nomina for four identified taxa that are currently believed to include only one species and for one that is considered to include only non-American species. They also provided nomina meant to be usable under the *Code* for these taxa, but, as analysed in detail elsewhere [4], in this respect their paper contains several distinct misinterpretations of the *Code* and other nomenclatural mistakes: thus, all their seven new nomina are *nomina nuda*, a junior homonym and several junior synonyms are treated as valid nomina, and up to six ranks are recognized in the genus-series below the rank genus, although this is not allowed by the *Code*. The problems in this paper regarding availability, homonymy and synonymy can be solved, but the last problem, regarding ranks, cannot be satisfactorily solved within the frame of the current *Code*.

Table 1 presents the hierarchical relationships proposed in [64] for the 24 supraspecific taxa recognized in American ranid frogs. Ranks under the *Code* have by themselves no special meaning: they are purely arbitrary conventions, usually given according to the taxonomic tradition in the zoological group concerned, and their role is simply to provide information on the structure of the taxonomic hierarchy used. Following [13], the two major taxa disclosed by this analysis are here given the rank genus, and following [4] their immediate subordinate taxa are afforded the rank subgenus. In order to recognize taxonomically all nodes of the trees in [64], four additional levels must be distinguished below subgenus. In Table 1, the levels or ranks of the taxa are simply expressed by numerical codes, without using nomina: parordinate taxa are designated by codes with the same number of numerals, and a superordinate taxon has less numerals than any of its subordinate taxa. Taxa at rank genus are designated by one numeral (e.g., T 1), those at rank subgenus by two numerals (e.g., T 1.1), and lower subordinate ranks are designated by three (e.g., T 1.1.1) to six (e.g., 1.2.2.1.1.1) numerals. These four latter ranks are subordinate to subgenus and superordinate to species.

Basic information on the nomenclatural status under the *Code* of all genus-series nomina ever published for the taxa of Table 1 was provided elsewhere [4 (Table 1)]. This information is necessary for the proper and auto-

Table 1

Supraspecific and infrageneric taxonomy of American frogs referred to the genera *Lithobates* (T1) and *Rana* (T2, including also the European type-species of the latter, *Rana temporaria*), according to the cladistic hypothesis of [64], the generic taxonomy of [13] and the subgeneric taxonomy of [4]

T 1.	
T 1.1.	
T 1.1.1.	<i>Lithobates (Aquarana) catesbeianus</i> (Shaw, 1802)
	<i>Lithobates (Aquarana) clamitans</i> (Latreille, 1801)
	<i>Lithobates (Aquarana) grylio</i> (Stejneger, 1901)
	<i>Lithobates (Aquarana) heckscheri</i> (Wright, 1924)
	<i>Lithobates (Aquarana) okaloosae</i> (Moler, 1985)
	<i>Lithobates (Aquarana) septentrionalis</i> (Baird, 1854)
	<i>Lithobates (Aquarana) virgatipes</i> (Cope, 1891)
T 1.1.2.	<i>Lithobates (Aquarana) sylvaticus</i> (LeConte, 1825)
T 1.2.	
T 1.2.1.	
T 1.2.1.1.	
T 1.2.1.1.1.	<i>Lithobates (Lithobates) vibicarius</i> (Cope, 1894)
	<i>Lithobates (Lithobates) warszewitschii</i> (Schmidt, 1857)
T 1.2.1.1.2.	<i>Lithobates (Lithobates) melanosoma</i> (Günther, 1900)
T 1.2.1.2.	<i>Lithobates (Lithobates) bwana</i> (Hillis & de Sá, 1988)
	<i>Lithobates (Lithobates) juliani</i> (Hillis & de Sá, 1988)
	<i>Lithobates (Lithobates) palmipes</i> (Spix, 1824)
	<i>Lithobates (Lithobates) vaillanti</i> (Brocchi, 1877)
T 1.2.2.	
T 1.2.2.1.	
T 1.2.2.1.1.	
T 1.2.2.1.1.1.	<i>Lithobates (Lithobates) chiricahuensis</i> (Platz & Mecham, 1979)
	<i>Lithobates (Lithobates) dunni</i> (Zweifel, 1957)
	<i>Lithobates (Lithobates) fisheri</i> (Stejneger, 1893)
	<i>Lithobates (Lithobates) lemosespinali</i> (Smith & Chiszar, 2003)
	<i>Lithobates (Lithobates) megapoda</i> (Taylor, 1942)
	<i>Lithobates (Lithobates) montezumae</i> (Baird, 1854)
	<i>Lithobates (Lithobates) subaquavocalis</i> (Platz, 1993)
T 1.2.2.1.1.2.	<i>Lithobates (Lithobates) pipiens</i> (Schreber, 1782)
T 1.2.2.1.2.	
T 1.2.2.1.2.1.	
T 1.2.2.1.2.1.1.	<i>Lithobates (Lithobates) areolatus</i> (Baird & Girard, 1852)
	<i>Lithobates (Lithobates) capito</i> (LeConte, 1855)
	<i>Lithobates (Lithobates) palustris</i> (LeConte, 1825)
	<i>Lithobates (Lithobates) sevosus</i> (Goin & Netting, 1940)
T 1.2.2.1.2.2.	
T 1.2.2.1.2.2.1.	<i>Lithobates (Lithobates) berlandieri</i> (Baird, 1854)
	<i>Lithobates (Lithobates) blairi</i> (Mecham, Littlejohn, Oldham, Brown & Brown, 1973)
	<i>Lithobates (Lithobates) brownorum</i> (Sanders, 1973)
	<i>Lithobates (Lithobates) chichicuahutla</i> (Cuellar, Méndez-DeLaCruz & Villágran-Santa Cruz, 1996)
	<i>Lithobates (Lithobates) forreri</i> (Boulenger, 1883)
	<i>Lithobates (Lithobates) macroglossa</i> (Brocchi, 1877)
	<i>Lithobates (Lithobates) magnaocularis</i> (Frost & Bagnara, 1976)
	<i>Lithobates (Lithobates) miadis</i> (Barbour & Loveridge, 1929)
	<i>Lithobates (Lithobates) neovolcanicus</i> (Hillis & Frost, 1985)
	<i>Lithobates (Lithobates) omiltemanus</i> (Günther, 1900)

(continued on next page)

Table 1 (Continued)

T 1.2.2.1.2.2.	<i>Lithobates (Lithobates) onca</i> (Cope, 1875)
	<i>Lithobates (Lithobates) spectabilis</i> (Hillis & Frost, 1985)
	<i>Lithobates (Lithobates) sphenoccephalus</i> (Cope, 1889)
	<i>Lithobates (Lithobates) sphenoccephalus sphenoccephalus</i> (Cope, 1889)
	<i>Lithobates (Lithobates) sphenoccephalus utricularius</i> (Harlan, 1825)
	<i>Lithobates (Lithobates) taylori</i> (Smith, 1959)
	<i>Lithobates (Lithobates) tlaloci</i> (Hillis & Frost, 1985)
	<i>Lithobates (Lithobates) yavapaiensis</i> (Platz & Frost, 1984)
T 1.2.2.2.	
T 1.2.2.2.1.	
	<i>Lithobates (Lithobates) johni</i> (Blair, 1965)
	<i>Lithobates (Lithobates) psilonota</i> (Webb, 2001)
	<i>Lithobates (Lithobates) pueblae</i> (Zweifel, 1955)
	<i>Lithobates (Lithobates) pustulosus</i> (Boulenger, 1883)
	<i>Lithobates (Lithobates) tarahumarae</i> (Boulenger, 1917)
	<i>Lithobates (Lithobates) zweifeli</i> (Hillis, Frost & Webb, 1984)
T 1.2.2.2.2.	
	<i>Lithobates (Lithobates) sierramadrensis</i> (Taylor, 1939)
T 2.	
T 2.1.	
	<i>Rana (Amerana) aurora</i> (Baird & Girard, 1852)
	<i>Rana (Amerana) boylei</i> (Baird, 1854)
	<i>Rana (Amerana) cascadae</i> (Slater, 1939)
	<i>Rana (Amerana) draytonii</i> (Baird & Girard, 1852)
	<i>Rana (Amerana) luteiventris</i> (Thompson, 1913)
	<i>Rana (Amerana) muscosa</i> (Camp, 1917)
	<i>Rana (Amerana) pretiosa</i> (Baird & Girard, 1853)
T 2.2.	
	<i>Rana (Rana) temporaria</i> (Linnaeus, 1758)

Supraspecific taxa are designated by a simple nomenclature based on the letter T followed by strings of numerals expressing hierarchical relationships: taxon T 1.2.1 is parordinate to T 1.2.2, subordinate to T 1.2 and superordinate to T 1.2.1.1.

matic establishment of the valid nomina under the *Code*: availability of nomina requires several conditions to be fulfilled, including publication of a diagnosis based on characters for the taxon designated by the nomen [4]; allocation of genus-series nomina to taxa is made through their onomatophores ('type-species'); and validity of nomina among synonyms and homonyms is determined by priority of publication or, if necessary, by first-reviser action.

Table 2 shows three different nomenclatures that account for the taxonomy of Table 1. As discussed in detail in [4], allocation of nomina to taxa is made following completely different rules under the *Code* and the *Phylocode*, which results in widely different nomina being applied to the same taxa in both systems, even if, through 'conversion' of nomina from one system to the other, the 'same' nomina, or more exactly nomina 'looking the same', are used in both cases. Hence the need to use strikingly different ways of writing the nomina in both systems [2,4].

In the nomenclature N1, following the *Phylocode* and coined in [64], nomina are allocated to taxa through

'phylogenetic definitions', not through onomatophores. In this system, each nomen designates a single taxon, but in the present case some taxa were not given nomina, for reasons given above. Therefore, 16 taxa only have definition-based nomina (one of which is invalid, having been converted from a junior homonym under the *Code*; see [4]), and eight remain unnamed. The 16 taxa for which nomina were proposed under the *Phylocode* [64] are not equally inclusive, some being subordinate to others, but there is strictly nothing in these nomina themselves to inform a reader in this respect: this information must be obtained by looking at the original cladograms, or at the indented taxonomy of Table 1.

To apply nomina to taxa under the *Code*, no role is played by 'definitions' of the taxa, be them 'phylogenetic' or not, as allocation of nomina to taxa in this nomenclatural system is made through onomatophores, i.e., biological specimens, not through definitions, i.e. concepts and words. In this case, the nomenclatural status of all the nomina concerning this group of frogs must be examined, in order to establish which ones are nomenclaturally available and unavailable and which ones are

Table 2

Three nomenclatures corresponding to the taxonomy of Table 1

Taxonomic hierarchy	(N1) Definition-based nomenclature following the <i>Phylocode</i> [64]	(N2) Current onomatophore-based nomenclature following the <i>Code</i> [4]	(N3) Proposed expanded onomatophore-based nomenclature
T 1	<NOVIRANA Hillis & Wilcox, 2005>	Genus <i>Lithobates</i> Fitzinger, 1843	Genus <i>Lithobates</i> Fitzinger, 1843
T 1.1	Unnamed taxon	Subgenus <i>Aquarana</i> Dubois, 1992	Subgenus <i>Aquarana</i> Dubois, 1992
T 1.1.1	<AQUARANA [Dubois, 1992] Hillis & Wilcox, 2005>	Group <i>clamitans</i> Latreille, 1801	Infragenus <i>Aquarana</i> Dubois, 1992
T 1.1.2	Unnamed taxon	Group <i>sylvaticus</i> LeConte, 1825	Unnamed infragenus A
T 1.2	<SIERRANA [Dubois, 1992] Hillis & Wilcox, 2005>	Subgenus <i>Lithobates</i> Fitzinger, 1843	Subgenus <i>Lithobates</i> Fitzinger, 1843
T 1.2.1	<“RANULA [Peters, 1859] Hillis & Wilcox, 2005”>	Group <i>palmipes</i> Spix, 1824	Infragenus <i>Lithobates</i> Fitzinger, 1843
T 1.2.1.1	<LEVIRANA [Cope, 1894] Hillis & Wilcox, 2005>	Unnamed subgroup A	Casta <i>Trypheropsis</i> Cope, 1868
T 1.2.1.1.1	<TRYPHEROPSIS [Cope, 1868] Hillis & Wilcox, 2005>	Unnamed infragroup A1	Subcasta <i>Trypheropsis</i> Cope, 1868
T 1.2.1.1.2	Unnamed taxon	Unnamed infragroup A2	Unnamed subcasta B
T 1.2.1.2	<LITHOBATES [Fitzinger, 1843] Hillis & Wilcox, 2005>	Unnamed subgroup B	Casta <i>Lithobates</i> Fitzinger, 1843
T 1.2.2	Unnamed taxon	Group <i>pipiens</i> Schreber, 1782	Infragenus <i>Sierrana</i> Dubois, 1992
T 1.2.2.1	<PANTHERANA [Dubois, 1992] Hillis & Wilcox, 2005>	Unnamed subgroup C	Casta <i>Pantherana</i> Dubois, 1992
T 1.2.2.1.1	<STERTIRANA Hillis & Wilcox, 2005>	Unnamed infragroup C1	Subcasta <i>Pantherana</i> Dubois, 1992
T 1.2.2.1.1.1	<LACUSIRANA Hillis & Wilcox, 2005>	Unnamed hypogroup C1a	Unnamed infracasta C
T 1.2.2.1.1.2	Unnamed taxon	Unnamed hypogroup C1b	Infracasta <i>Pantherana</i> Dubois, 1992
T 1.2.2.1.2	Unnamed taxon	Unnamed infragroup C2	Unnamed subcasta D
T 1.2.2.1.2.1	<NENIRANA Hillis & Wilcox, 2005>	Unnamed hypogroup C2a	Unnamed infracasta D1
T 1.2.2.1.2.2	<SCURRILIRANA Hillis & Wilcox, 2005>	Unnamed hypogroup C2b	Unnamed infracasta D2
T 1.2.2.2	<TORRENTIRANA Hillis & Wilcox, 2005>	Unnamed subgroup D	Casta <i>Sierrana</i> Dubois, 1992
T 1.2.2.2.1	<ZWEIFELIA [Dubois, 1992] Hillis & Wilcox, 1985>	Unnamed infragroup D1	Subcasta <i>Zweifelia</i> Dubois, 1992
T 1.2.2.2.2	Unnamed taxon	Unnamed infragroup D2	Subcasta <i>Sierrana</i> Dubois, 1992
T 2	<LAURASIARANA Hillis & Wilcox, 2005>	Genus <i>Rana</i> Linnaeus, 1758	Genus <i>Rana</i> Linnaeus, 1758
T 2.1	<AMERANA [Dubois, 1992] Hillis & Wilcox, 1985>	Subgenus <i>Amerana</i> Dubois, 1992	Subgenus <i>Amerana</i> Dubois, 1992
T 2.2	Unnamed taxon	Subgenus <i>Rana</i> Linnaeus, 1758	Subgenus <i>Rana</i> Linnaeus, 1758

See text for explanation. The nomen <“RANULA”> is invalid under the *Phylocode*, being based on an invalid junior homonym under the *Code* (see [4 (Table 1)]).

definitively invalid for being junior homonyms or junior objective synonyms [4]. The remaining nomina must be confronted with the proposed taxonomy of Table 1, and, through use of the onomatophores and of the publication dates, the rules of the *Code* allow finding automatically which nomen should be used for each taxon.

The second nomenclature (N2) presented in Table 2 is the only one possible under the *Code* that would recognize intermediate ranks between genus and species. Under the *Code*, all taxa considered valid in any taxonomy should be named, including those that are currently considered to include a single species. The taxonomic scheme of Table 1 uses six ranks below genus. In two different papers, Hillis and co-workers [64,65] thought that Art. 10.4 of the *Code* allowed them to use subgeneric nomina for taxa at several ranks below subgenus, but, as explained in detail in [4], this is not true. The *Code* only allows two such ranks: one (subgenus) below genus in the genus-series, and one ('aggregate of species' or species-group) above species in the species-series. Therefore, with the *Code* currently in force, the only possible way to express nomenclaturally in detail the taxonomy of Table 1 would be to raise the ranks of most taxa in this taxonomy: thus, if the lowest hierarchic supraspecific level in this taxonomy (e.g., T 1.2.2.1.1.1) is given the rank species-group, the next superordinate ranks would be subgenus, then genus, subtribe, tribe and subfamily. This would mean raising the genus *Rana* to the rank subfamily *Raninae*. However, this would not be a good solution to the problem, as, in order to keep a 'balanced' taxonomy of the *Ranoidea*, a similar rank upgrading should concern all or most other genera and other taxa of this superfamily, a virtually endless process.

If taxa T1 and T2 of Table 1 are left at the rank genus, applying strictly the rules of the current *Code* to this taxonomy results in the nomenclature N2 of Table 2, in which 6 out of the 24 taxa, at ranks genus and subgenus, can receive genus-series nomina, and 4, at rank species-group, receive species-series nomina [4]. These 10 taxa have therefore nomina that inform on their mutual relationships in the taxonomic hierarchy, but unfortunately this must end here. Under the *Code*, the 14 remaining taxa must remain unnamed, or be only given 'informal nomina' without 'official' nomenclatural existence, and that cannot therefore be regulated by the usual rules of the *Code* (onomatophores, priority, homonymy, coordination, etc.). This is not a good situation concerning the universality of zoological nomenclature, and in this case the *Phylocode* allows us to name more taxa of the tree and could appear superior for this reason.

This problem could be solved if the *Code* simply allowed the use of many more ranks in the genus-series [46]. The use of four additional ranks below subgenus in the genus-series would allow us to name all taxa recognized in this taxonomy. Under such rules, establishment of the valid nomen of each taxon recognized in this taxonomy would be a simple and fully automatic process relying upon objective criteria: type-species of nomina confronted with the allocation of species to taxa, and publication dates of nomina. In a few cases (*Amerana* vs. *Aurorana*, *Sierrana* vs. *Pantherana* and *Zweifelia*), simultaneous nomina (nomina created at the same date) would be in competition to designate a given taxon. According to the *Code*, in such cases precedence of one nomen over the other relies on the first-reviser action [4 (Table 1)].

Nomenclature N3 in Table 2 presents the result of such a process, recognizing additional ranks designated as infragenus, casta, subcasta and infracasta, following the proposals of [46] (see below), and simply using the genus-series nomina already available for these taxa in zoological nomenclature [4 (Table 1)]. All 24 taxa of the taxonomy at stake should be named. In the present case, nomina are already available to designate unambiguously 18 of the 24 taxa recognized in [64]. The other six taxa are designated in Table 2 by the letters A to D, D1 and D2, and nomina should be coined for these taxa, as the seven new nomina provided in [64] are *nomina nuda* and cannot be used [4]. Because of the Rule of Coordination, two of these unnamed taxa (subcasta D and one of its two infracastae) would be eponymous. On the whole, to name the 24 taxa, only 13 distinct nomina would be necessary, as all other 11 taxa would bear nomina hyponymous to those of superordinate taxa.

4. Why should we increase the number of nomenclatural ranks?

Let us come back now to the problem of ranks in onomatophore-based nomenclature under a more general approach. There are two major reasons for supporting the idea of increasing the number of nomenclatural ranks allowed by the *Code* in zoology: (1) to allow a better, finer nomenclatural expression of taxonomic data and hypotheses, especially of cladistic relationships hypothesized in many recent studies; (2) to allow a better support of taxonomy to conservation biology.

4.1. Cladistic relationships and nomenclatural ranks

Most zoologists nowadays acknowledge that taxonomy must be based on hypothesized cladistic relationships between organisms, as expressed, e.g., under the

form of cladograms. More and more such hypotheses have been produced recently, based on both morphological and molecular data, in all zoological groups and at all taxonomic levels, and this trend will certainly go on. Some of these hypothesized cladistic relationships are quite detailed and, in order to account for them in taxonomies, more and more ranks need to be used, even if not all nodes deserve to be recognized taxonomically. This poses no problem at high taxonomic levels, as the current *Code* does not regulate nomina above the family-series (but see [2,24,43–47]) and few problems for taxa whose nomina are part of the family-series, as the *Code* allows us to use as many ranks as needed at these levels, except (inexplicably) above the superfamily. But problems occur at lower levels, where the *Code* restricts the number of ranks that can be used. These restrictions are more and more difficult to accept, as they make it less efficient than other alternative nomenclatural systems, such as the *Phylocode*. If the *Code* does not evolve in this respect, these limitations may act as a factor of rejection of this set of rules by zoologists working on the tree of life, and of adhesion to such alternative systems by taxonomists wishing to express detailed cladistic hypotheses in their taxonomies. This is true both for detailed relationships among species within genera, and for infraspecific relationships among populations, a domain of research that is particularly useful in fine phylogeographic analyses. At these lower taxonomic levels, the prohibition of additional ranks has led in the recent years to two major developments, which had to be invented as ‘solutions’ to the limitations put by the rigidity of the *Code*. One, illustrated above, is to turn to other nomenclatural rules, which do not restrict the number of potential ranks, or even ignore ranks. The other one is to use ‘informal’ nomenclatures with ‘*ad hoc* rules’ or no rules at all, e.g., in adding, between the ‘official’ ranks, some intermediate ranks not recognized by the *Code* and that therefore do not have to follow its basic rules, such as Priority or Coordination. Such systems have been and are used by some authors, sometimes only within a small subdiscipline of zoology, e.g., dealing with a given taxonomic group. Generalisation of such attitudes could lead rather quickly to a progressive chaos in zoological taxonomy and nomenclature.

Let us examine briefly an example of such a system. Deuve [66] recently proposed a detailed classification of the insect genus *Carabus* (Coleoptera). As understood by him, this genus includes 853 species, arranged in 90 subgenera. In order to express hypothesized relationships among these subgenera, he used nomina called ‘collective names’ and hierarchised in three additional ‘informal’ ranks between genus and subgenus. He wrote

expressly: “collective names have the characteristic of falling outside nomenclature, meaning that they do not form part of the ranks defined by the Code of Zoological Nomenclature.” [66 (p. 57)] Nevertheless, he credited these nomina with authors and dates and respected the Rule of Priority in case of synonymy. For these ‘informal’ taxa, he (after others) used nomina in the nominative plural, such as *Spinulati*, *Oreocaraboides* or *ArCIFera*. These nomina have their own authors and dates, and do not compete for priority with nomina of subgenera. Although some only of these nomina are based on the roots of the nomina of included subgenera (e.g., *Cathopliogenici* based on *Cathoplius*), such nomina are highly confusing, as they are in the nominative plural and are formed like nomina of the family-series or of the class-series in zoological nomenclature, although they apply to taxa undoubtedly of the genus-series, as being hierarchically below genus and above subgenus. If the *Code* did not limit the number of ranks acceptable in the genus-series, these taxa could be given, e.g., the ranks subgenus, infragenus and casta, and the subgenera of Deuve [66] could be given a rank still lower, e.g., subcasta, and bear genus-series nomina submitted to the Rules of Coordination and of Priority. Similarly, in the same work, Deuve [66] recognized two kinds of subspecies, called ‘strong subspecies’ and ‘weak subspecies’, the latter being subordinate to the former and their nomina following the Rules of Coordination and of Priority. Such a nomenclatural pattern is not acceptable under the rules of the *Code*, but it would be so if the *Code* accepted additional ranks, e.g., infraspecies, below the rank subspecies.

To avoid these problems, the *Code* should evolve to allow for the possibility, for those who may wish so, to use as many additional ranks as desired. This should apply both in the genus- and species-series of nomina. Multilevel taxonomic hierarchies below the rank species (using ranks such as variety, subvariety, form or subform, as recognized in botanical nomenclature) have long been rejected in zoology because of the largely arbitrary criteria used to recognize subspecies, and even more so for taxa at ranks below subspecies. But the recent multiplication of hypotheses of historical relationships between demographically isolated populations or groups of populations, based mostly on molecular analyses, strongly modifies this situation. Even if these remain hypotheses (as are all models), they are nevertheless more and more robust, and they are very useful as a help for building phylogeographic analyses and providing evolutionary scenarios for local populations currently classified as the same species or even subspecies. Perhaps more importantly, they provide ba-

sis for decisions in conservation biology, and this is a second reason for considering changes in the rules of the *Code*.

4.2. Nomenclatural ranks and conservation biology

Although we are now at the beginning of the century of extinctions, unfortunately today the relationships between conservation biology and taxonomy are difficult. One reason for this is the misunderstanding by many conservation biologists of the nature and amplitude of the taxonomic impediment [23]. Another one is the absence or inappropriateness in taxonomy of some tools that could be useful in conservation biology. This is the case of lower nomenclatural ranks. Conservation biology has long had a ‘black box’ concept of species taxa, tending to consider that all organisms bearing the same scientific Latin nomen are ‘the same’. Such a typological, pre-populational approach of species variability has given support to some questionable actions of ‘conservation biology’, e.g., introducing organisms from alien populations of ‘the same species’ into an endangered population in order to ‘reinforce’ it. When specimens of bears from Slovenia are introduced in the French Pyrenees to ‘reinforce’ the local populations, such a ‘genetic pollution’ [67] in fact results in destroying the genetic identity of the receiver population and prohibits or complicates the possible study and understanding of its features and of its past evolution by population biologists [68–70]. That such actions can be taken by biologists is largely made possible by the fact that the two populations are referred to the same species-series taxon, thus bearing the same nomen. A similar problem applies to many decisions regarding the listing of some taxa as ‘endangered’ or ‘threatened’ and the impact upon conservation policy of their presence in an area, e.g., for the recognition of protected areas or taxa, for commercial purposes or for other reference texts. ‘Official lists’, as used, e.g., by administrations, governments, juridical texts and international conventions, usually only recognize taxa bearing Latin nomina, but not local ‘unnamed’ populations. In this respect, the situation is largely different in zoology and in botany, as the botanical code recognizes several nomenclatural ranks below subspecies, and a variety, for example, is sometimes listed as protected in an area or a country, although the species or subspecies including this variety is not.

For the time being, a possible ‘solution’ to this problem is an artificial one: whenever zoologists wish to point to the need of considering special measures for the conservation of a population or group of population, they may recognize the latter as a taxon of rank species

or at least subspecies, even when by all other criteria this is not warranted. Such a practice cannot be helpful for the recognition of taxonomy as a ‘serious’ discipline: if taxa can be defined differently for practical, but not scientific, reasons, no respect for taxonomy from the part of other fields of biology can be expected, and this problem is an additional one among all those currently facing taxonomy as a scientific field [23].

Discussions are currently raging (as they have for decades already) concerning the taxonomic concept of species, and more recently about its implications in conservation biology (e.g., [12,71–81]). It is not enough to say that species are “the units of biodiversity” [73], as several kinds of units (from molecules to biomes) can be considered in biodiversity according to the level of analysis chosen. The complexity of the ‘species problem’ has several independent causes, among which three are particularly important: (1) the genuine diversity of biological situations, with a wide variety of modes of speciation, resulting both in ‘true species’ (i.e., bisexual organisms with ‘normal’ meiosis and free interbreeding among members) and in special cases with particular meioses and/or modes of fertilization, clonal or hemiclinal heredity [49]; (2) the incompleteness of the available information in many cases (e.g., in palaeontology); (3) the social requirements associated with the use of nomina in legislative texts and in conservation biology. Although the dominant mode of thinking in biology, i.e., reductionism, requires to have a single taxonomic concept of species for all organisms, and although each school of thought claims that its concept is the ‘best’ [82], the solution to the ‘species problem’ might well lie in an intermediate, pragmatic attitude. For the time being, a practical and temporary solution to this problem may be to use different taxonomic concepts in different zoological groups and in particular situations as appropriate [83]. In conservation biology, the use or special-purpose categories such as ‘evolutionary significant units’ or ‘management units’ [71,72,77] can have a practical utility and should not be discouraged simply because of a rigid taxonomic attitude.

But nomenclature is not taxonomy. Whether or not taxonomists and conservation biologists will find it useful, especially for biodiversity conservation purposes, to use more ranks than one below the rank species in zoological nomenclature is not a nomenclatural problem *per se*. This question is not yet satisfactorily solved and should be so through careful discussions among taxonomists and with other biologists. But the *Code* should not put a *technical* limitation on these discussions, by *a priori* prohibiting the use of additional ranks. Both taxonomy and conservation biology of animals would

probably benefit from the nomenclatural recognition of more infraspecific ranks than is currently possible under the *Code*. Although such a move would probably have been premature a few decades ago, when infrasub-specific taxa were proposed by some authors mostly on the basis of rare mutations or local short-term selection, recent progresses in low-level molecular analysis and phylogeography are modifying the situation, and this should be acknowledged by an evolution of the rules of the *Code*.

5. Proposals

5.1. Allowing for an indeterminate number of ranks

In order to suppress all restrictions to the number of ranks potentially usable in zoological nomenclature, I propose the following new wordings for Articles 35.1, 42.1 and 45.1 of the *Code*:

Article 35.1. “The family group encompasses all nominal taxa at the ranks of superfamily, family, subfamily, tribe, subtribe, and any other rank below the class group and above the genus group in the nomenclatural hierarchy that may be desired (see also Article 10.3 for collective groups and ichnotaxa).”

Article 42.1. “The genus group encompasses all nominal taxa at the ranks of genus and subgenus, and any other rank below the family group and above the species group in the nomenclatural hierarchy that may be desired (see also Articles 10.3 and 10.4).”

Article 45.1. “The species group encompasses all nominal taxa at the ranks of species, subspecies, aggregate of species and aggregate of subspecies, and any other rank below the genus group in the nomenclatural hierarchy that may be desired (see also Article 10.2).”

In the proposed new wordings above, the formula ‘nomenclatural hierarchy’ is preferred to the formula ‘hierarchy of classification’ that appears in the current wording of Art. 42.1, because of the distinction advocated here between ‘nomenclatural ranks’ and ‘taxonomic categories’ [2].

These changes would be simple to decide upon and to implement by a vote of the International Commission on Zoological Nomenclature, without having to wait for a new version of the *Code* to be prepared and adopted. They would certainly be appreciated by many users of zoological nomina, especially among taxonomists working on the tree of life (at all levels) and by conservation biologists. On the contrary, delaying or rejecting their adoption might contribute to provoke adhesion of some of these biologists to alternative nomenclatural systems such as the *Phylocode*, and nothing

could be more harmful to taxonomy, at the beginning of the century of extinctions, than the chaos that would result from having two widely used nomenclatural systems in parallel for the whole of zoology [2,4,19].

I am presenting below a few additional suggestions, the discussion of which however is less urgent than that of the three articles above. These are meant at proposing a standardization and homogenisation of the use of ranks in zoological nomenclature, at all level of the nomenclatural hierarchy. Agreement with these suggestions, however, is not necessary for adhesion to the more basic proposals made above.

5.2. Standardizing the hierarchy of ranks in zoological nomenclature

For the time being, the *Code* regulates only a few ranks in the whole nomenclatural hierarchy used in zoological taxonomic works: five in the family-series, two in the genus-series and four in the species-series. In the family-series, the *Code* allows us to use additional ranks below superfamily and above genus, but in the other two nominal-series no such possibility exists. In the past, in the family- and species-series, various authors have used additional ranks, but there has never been any uniformity in this respect over the whole of zoology [46]. In particular, different traditions exist in the literature dealing with different zoological groups. Standardisation of rank number and designations for the whole zoology and over the complete nomenclatural hierarchy, from imperium to forma, would allow better and clearer communication among taxonomists and between them and other users of nomina. Hence the recent proposal [46] to distinguish two kinds of ranks in the hierarchy: *key ranks* designated by special terms (ordo, familia, genus, etc.), and *subsidiary ranks* derived from the former through the use of prefixes or *modifiers* (super-, sub-, infra-, etc.). The new detailed hierarchical system [46] is nothing but an extension of the traditional system as implemented in the *Code*, and for more clarity can be called *expanded nomenclatural system*.

Except for the use of a few terms rarely found in publications of the past, the new system is not very different from the traditional one in the class- and family-series of nomina, but it is more so in the genus- and species-series. In the genus-series, it is proposed to recognize two key ranks instead of one: *genus* and *casta* (below genus). Ten subsidiary ranks can be added to each of them, which provide a total of 22 potential ranks in the genus-series: here also this is probably much more than will ever be necessary, even in highly diversified groups of insects for example. The fact that these 22

ranks belong in the same nominal-series means that they are submitted to the Rule of Coordination, i.e., that any nomen created at any of these ranks is thereby made simultaneously available for any taxon at another rank in this hierarchy (as is the case under the *Code* for family-series nomina). In the example above, the two key ranks of the genus-series, genus and casta, but only three subsidiary ranks of the descending hierarchy, were used, which provides a hierarchy of six ranks in the genus-series. This is only a small part of the total number of 22 ranks allowed by the new proposed expanded system in the genus-series.

Each taxon at any rank is better designated by a combination of its rank and nomen, which avoids confusion between eponymous taxa: e.g., in nomenclature N3 of Table 2, ‘subcasta *Sierrana*’ is not the same taxon as ‘infragenus *Sierrana*’. In lower taxonomy, it is also possible to include the nomina of subordinate taxa below genus as ‘interpolated nomina’ presented between parentheses between the generic and the specific nomina. In order to show the hierarchy of taxa below genus, the sign ‘/’ could be used to separate nomina at different subsidiary ranks of the same key rank, and the double sign ‘//’ to separate nomina referring to different key ranks, i.e., in this case, between infragenus and casta. This system results in compound nomina of the form: *Lithobates* (subgenus *Lithobates* / infragenus *Sierrana* // casta *Pantherana* / subcasta *Pantherana* / infracasta *Pantherana*) *pipiens* Schreber, 1782, or more briefly *Lithobates* (*Lithobates* / *Sierrana* // *Pantherana* / *Pantherana* / *Pantherana*) *pipiens* Schreber, 1782. Although fully clear, such a notation is very cumbersome and unpalatable. It is unlikely to be used often in scientific publications, but it may be quoted only once in each, on the occasion of the first mention of a species, to provide condensed information on its taxonomic relationships. Such a detailed writing may also be useful in taxonomic or faunistic checklists or catalogues. In all other cases, it would be sufficient to write the binomen *Lithobates pipiens* without all these details.

It was also proposed [46] to recognize three additional key ranks below the rank species: *natio*, *varietas*, and *forma*. Altogether, with the subsidiary ranks this would provide 44 potential ranks below the genus-series, i.e., much more than will probably ever be needed in detailed cladistic analysis, phylogeography and conservation biology. The detailed nomina of taxa could be written, when exceptionally necessary, following the same system as shown above for genus-series nomina. If this system was adopted, a question would remain open to discussion: should the nomina of the three new key ranks be all referred to the species-

series, or to another, additional, lower nominal-series, the ‘variety-series’ [2]? The difference is not trivial. In the former case, the Rule of Coordination would apply to all nomina in the 44 ranks, i.e., a nomen created at anyone of these ranks would be available with its author and date for all other ranks, whereas, in the latter case, nomina created in the variety-series would be available with their own authors and dates, which may be very different and could entail changes in the valid nomina of some taxa because of the Rule of Priority. This would cause problems regarding the ‘real authors’ and dates of some nomina, as pointed out quite convincingly by Deuve [66 (pp. 63–66)], which would speak for inclusion of the new ranks in the species-series. However, when introducing a new rule in the *Code*, it is important to pay attention to the fact that it should not introduce a disruption in a nomenclatural usage established for long under the previous rules: stability of rules is more important than stability of the nomina themselves, which are bound to change when taxonomy evolves [2 (p. 378)]. To avoid disrupting the nomenclature of species-series taxa, it would seem better to create a new nominal-series, the nomina of which would not interact with those of the species-series for coordination, priority, synonymy and homonymy.

Recognizing all these potential additional ranks would expand very much the availability of ranks at lower nomenclatural levels. The so-called ‘aggregates of species and of subspecies’ currently recognized by the *Code* would only be a few among many ranks such as supraspecies, epispecies or hyperspecies that could be recognized (Tables 3–4), and thus mention of these ‘aggregates’ should then disappear from the *Code*. Anyway, as, according to the hierarchy proposed in Table 4, no rank would be possible between the key rank and the first level of the descending hierarchy of subsidiary ranks, designated by *sub-*, no ‘aggregates of subspecies’ could be recognized: it would then be necessary to afford the rank subspecies to the former ‘aggregates of subspecies’ that may have been recognized in the past, and to downgrade the former subspecies to the rank infraspecies. This would raise no theoretical problem, as ranks have by themselves no biological meaning of any kind, but are just a way to provide organizational models of hierarchical relationships between taxa.

The proposed new system of nomenclatural hierarchy probably provides more ranks than will ever be needed in real taxonomies, as not all nodes of the cladogram have to be recognized nomenclaturally if taxonomy is to remain a useful tool [2 (p. 393)]. However, the aim of this proposal is not to introduce a new potential restriction to the freedom of taxonomic thought or

Table 3
Hierarchy of **primary** (P) and secondary (S) key ranks proposed for zoological nomenclature [46]

Code of key rank	Class-series (C)	Family-series (F)	Genus-series (G)	Species-series (S)	Variety-series (V)
CS01	imperium				
CP02	regnum				
CS03	provincia				
CP04	phylum				
CS05	circulus				
CP06	classis				
CS07	legio				
CP08	ordo				
CS09	phalanx				
FP10		familia			
FS11		stirps			
FP12		tribus			
FS13		clanus			
GP14			genus		
GS15			casta		
SP16				species	
VS17					natio
VP18					varietas
VS19					forma

Reasons for the choice of the names of these ranks are detailed in [46]. For this standardised hierarchy, it is suggested to use Latin terms to designate the ranks, and to avoid rank designations that have been used at widely different ranks during the history of zoological taxonomy. Thus for example, the term *cohors* (or ‘cohort’, ‘cohorte’, etc.) has been used in zoology to designate a rank situated either between class and order, or between order and family, or between genus and species, and in botany it has been used for a rank between kingdom and class: so it would be better not to use this ambiguous term at all. The same applies to terms like *divisio*, *sectio* or *series* or their equivalents in other languages.

Table 4
Hierarchy of subsidiary ranks proposed for each key rank of zoological nomenclature [46]

Letter of subsidiary rank	Ascending hierarchy of subsidiary ranks	Key rank	Descending hierarchy of subsidiary ranks
E	<i>suprem-</i>		
D	<i>ano-</i>		
C	<i>hyper-</i>		
B	<i>epi-</i>		
A	<i>super-</i> (<i>supra-</i> in the species-series)		
		See Table 3	
a			<i>sub-</i>
b			<i>infra-</i>
c			<i>hypo-</i>
d			<i>cato-</i>
e			<i>infim-</i>

Reasons for the choice of these prefixes are detailed in [46]. The prefixes retained all indicate hierarchy or “nobleness” [84], not dimension or size (e.g., *gig-*, *magn-*, *micr-*, *nan-* or *parv-*) or anteriority or priority (e.g., *pre-* and *post-*). In the species-series, the prefix *super-* is replaced by *supra-*, to avoid confusion with *superspecies*, an evolutionary taxonomy category but not a nomenclatural rank (see text for this distinction). Combination of the 19 key ranks of Table 3 with the 10 subsidiary ranks of this table provides a total potential number of ranks of $11 \times 19 = 209$.

actions, so this system should remain open: in the possible new wordings of the *Code* that would implement it, it should be stated that additional ranks can be added by any authors who think this is useful, but these new ranks should only be used after all 209 possible ranks provided by this system [46] have been used. Whether or not recognition of as many ranks will be needed is a matter of taxonomy, not of nomenclature, and therefore outside the scope of the present paper: I am not advo-

cating here the *use* of so many ranks (especially below the rank species), but the mere *possibility* of this use.

6. Conclusion: comparison of the two nomenclatural systems

The data of Table 2 allow comparing some aspects of the proposed expanded nomenclatural system and of the *Phylocode*.

(1) Both systems are fully unambiguous to designate a taxon *under a given cladistic or taxonomic hypothesis*. In both cases however, any change in the latter would entail changes in the *contents* of taxa and therefore in the nomina born by some organisms, whatever kinds of definitions ('phylogenetic' or not) are used to qualify nomina [2].

(2) Because of the Rule of Coordination, the expanded system is clearly more *parsimonious* concerning the number of nomina needed to express a given taxonomic scheme, without any risk of ambiguity or confusion, than any system devoid of a Rule of Coordination (such as the *Phylocode*). Any genus-series taxon with two or more subordinate taxa must include one hyponymous taxon. For the 24 taxa below genus and above species recognized in the taxonomy of Table 1, the *Phylocode* requires 18 nomina (as four monospecific taxa do not need to be named under this system), whereas the expanded system, which requires to name all 24 taxa, can do so with only 13 distinct nomina. Although this has been underestimated by most authors who have compared both systems until now, the existence of nominal-series and of a Rule of Coordination acting within each of them is one of the major differences between the *Code* and the *Phylocode*, much more important than 'ranks' by themselves: if ranks were not associated with nominal-series, a given nomen would also apply to a single taxon, in the *Code* just like in the *Phylocode*, and no difference in nomenclatural parsimony would exist between both systems.

(3) As reminded above, the ranks afforded to taxa have by themselves no special meaning. The important matter here is that when a taxon is designated as 'infracasta *Pantherana*', this provides the information that it has a twin taxon of same rank infracasta and that both are included in the same subcasta, which in its turn is a member of a casta, etc. This information is readily available simply by looking at the nomen, without having to refer to a cladogram or a complete taxonomy. No such information is available when reading a *Phylocode* nomen such as <PANTHERANA>: without an attached cladogram or taxonomy, this nomen by itself provides no information on the place of this taxon in the taxonomy, on its relative inclusiveness and on its relationships with other taxa. Nomina are not meant at being useful only to taxonomists and phylogeneticists, but also to all other biologists and non-biologist users of taxonomy. It is fully unrealistic to think that, every time one of the latter users will encounter, or use, a nomen in a text, he/she will refer to, or provide, a cladogram or a detailed taxonomy. Nomina should be informative by themselves,

"self-speaking", and this is the case of a nomen like 'infracasta *Pantherana*', but not like <PANTHERANA>.

A last word can be added regarding the use of a large array of ranks in expanded nomenclature. Rather than 'stability', an important feature of any good nomenclatural system is that it displays a rather high *robustness*, i.e. that it does not change *easily* but that it *can* change whenever needed by the progress of knowledge [2]. However, there is no need of robustness in the *ranks of taxa* such as there is for the *nomina of taxa*. Many new cladistic analyses result in the addition or suppression of nodes in cladograms, and by way of consequence of ranks in the hierarchy of ranks, at least for nodes which taxonomists consider important enough to be denoted by a distinct taxon [2]. But in many cases this does not result in major changes in the contents and definitions of most taxa. Changes in the ranks of taxa resulting from such changes in cladistic hypotheses are trivial, as these ranks do not carry any biological information on taxa, but only practical information on the hierarchical relationships between these taxa. 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 [46]. This is indeed what Hillis and Wilcox [64 (p. 304)] suggested, when they wrote: "We recommend that *Rana* still be the primary clade name used with species epithets to promote nomenclatural stability; the other clade names, in turn, are useful for discussing historical groups of species within *Rana*." Given the present poor state of knowledge regarding relationships within *Rana* at worldwide scale, this is 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. Under the *Code*, such a move will not raise any problem, as new or redefined taxa will automatically be renamed using the existing nomina, as exemplified by the taxonomy of this group proposed in [13]. As shown by this example, the expanded system is highly flexible and likely to be easily adapted to any new finding or hypothesis regarding cladistic relationships between taxa. It can be used easily to express even very detailed infraspecific cladistic relationships, as it can be useful both for phylogeographic studies and for conservation biology.

In parallel with the present paper, these proposals have been formally submitted to the International Commission on Zoological Nomenclature for consideration and possible inclusion in the *Code* [48].

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