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Phylogenetic hypotheses, taxa and nomina in zoology*

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Abstract

Taxonomic paradigms have changed several times during the history of taxonomy, yet a single nomenclatural system, so-called Linnaean, has remained in force all along. It is theory-free regarding taxonomy as it relies on ostensional allocation of nomina to taxa, rather than on intensional definitions of nomina (e.g., “phylogenetic definitions”). Nomina are not descriptions, definitions or theories but simple labels designating taxa. Both for theoretical and practical reasons, this system should be maintained for the allocation and validity of nomina under a cladistic taxonomic paradigm. Whereas taxa can be cladistically defined by *apognoses* or *cladognoses*, nomina should remain attached to taxa through onomatophores, combined in some cases with a Principle of Coordination. Under such a system, the allocation of nomina to taxa is automatic, unambiguous and universal, and nomenclature does not infringe upon taxonomic freedom. However, to avoid misunderstandings and to solve some current problems, the current *Code* of zoological nomenclature should be improved in several respects. The distinction should be made clear between *taxonomic categories*, which have biological definitions, and *nomenclatural ranks*, which do not, as they give only a position in a nomenclatural hierarchy: if used consistently under a cladistic paradigm, they simply allow to express hypotheses about successive branchings and sister-taxa relationships. Taxa referred to a given rank in different groups cannot therefore be considered equivalent by any biological criterion. The nomenclatural rules should cover the whole taxonomic hierarchy, which is currently not the case in zoology. The recent strong increase in the number of higher taxa which results from cladistic analyses may quickly lead to chaos and problems in communication if the nomina of these taxa continue to be based on personal tastes and opinions. There is an urgent need for the zoological *Code* to cover these nomina with automatic and stringent rules leaving no place to subjective interpretation. Just like for those currently covered by the *Code*, the status of these nomina should be established in their first publication (*nomenclatural founder effect*). The *Code* should be protected against alternative nomenclatural systems by rejecting as unavailable all nomina and nomenclatural acts published without respecting the basic Linnaean system of nomenclatural hierarchy of ranks.

Key words: Allocation of nomina to taxa, Apognoses, Cladistic hypotheses, Cladognoses, *Code*, Definitions of taxa, Diagnoses, Equivalence between taxa, Hypotheses, Linnaean nomenclatural hierarchy, Monosemy, Nomenclatural founder effect, Nomenclatural parsimony, Nomenclatural ranks, Nomenclature, Nomina, Onomatophores, Polysemy, Principle of Coordination, Redundancy, Taxa, Taxonomic categories, Taxonomy

Printing conventions

In the text and tables below, species-series and genus-series nomina are printed, as usual, in lower case *italics*, whereas nomina of higher-ranked taxa are printed in small capitals, with the following distinction: family-series nomina are in *ITALICS*, whereas class-series nomina are in **BOLD**. In this paper, “the *Code*” designates the edition currently in force of the *International Code of Zoological Nomenclature* (Anonymous 1999) and “ICZN” the International Commission on Zoological Nomenclature.

A preliminary statement

At the beginning of the “century of extinction” (Dubois 2003), the science of biology is facing a new paradigm, which results from the combination of two different facts: the taxonomic impediment and the biodiversity crisis. This statement is summarized in the following sentences: “In face of the biodiversity crisis, the need for urgency could be no greater. (...) The grand biological challenge of our age is to create a legacy of knowledge for a planet that is soon to be biologically decimated.” (Wheeler *et al.* 2004: 285). This well-known statement will not be discussed further here but these ideas will be kept in mind throughout the discussion below.

Taxonomy and nomenclature

Science is the study of reality, not reality itself. It provides methodologies, concepts, theories, models and hypotheses. Theories and hypotheses are accepted and used as valid as long as they have not been refuted. This does not mean that they are "true" or that they reflect exactly the reality.

Taxonomy is the *science* of classification of organisms. It recognizes classificatory units, the *taxa* (singular *taxon*). Within any given classification or *ergotaxonomy* (Dubois 2005c), taxa may be defined according to a taxonomic paradigm, i.e., a theory of biological classification.

Nomenclature is a *technique* allowing to name the taxa. It makes use of Latin or Latin-like "scientific names" or *nomina* (singular *nomen*) (see Dubois 2000b), that allow finding the taxonomic information they refer to. A nomen is just a label—not a description, a diagnosis, a definition, a coordinate, a model or a theory. A nomen may be either *defined* by *intension* (e.g., "all black animals") or *extension* (e.g., a list of black animals), or simply *attached* to a taxon by *ostension* (e.g., pointing to a particular black animal).

A nomen is not a taxon. A taxon may be defined without being named: for example, it may simply be described, diagnosed or defined, or it may be designated by a code or a number (numericlatures). A nomen may be created without designating a taxon (*nomen nudum*). Several distinct nomina may designate the same taxon (*synonymy*): this may result from objective or nomenclatural synonymy, or *isonymy* (Dubois 2000b), or from subjective or taxonomic synonymy, or *doxisonymy* (Dubois, 2000b). Two identical nomina may designate different taxa: as we will see, this may result (1) from *homonymy*, i.e., identity or similarity between *different* nomina, or (2) from *eponymy*, a situation resulting from the partially *polysemic* nature of the current nomenclatural systems relying on a *Principle of Coordination*, according to which the same nomen designates several coordinated taxa, e.g., a genus and one of its subgenera, or (3) from changes in the ergotaxonomies used by different authors and therefore in the intensions and extensions of taxa.

The aim of taxonomy is to provide a scientific classification of living organisms. Like all scientific disciplines, taxonomy relies on scientific theories or paradigms. Several "schools" of taxonomy or *taxonomic paradigms* have been in force during the long history of biology since the middle of the XVIIIth century. They differ mostly by their concepts of taxa. This is a well-known and long-discussed matter (e.g., Mayr 1982), that needs only to be very briefly reminded here.

Under an *essentialistic* or typological taxonomic paradigm, taxa were viewed as corresponding to an essence (Platonic *eidos*), fixed forever by their creator and unliable to change or evolve: the duty of taxonomists was then understood as to discover the "design" of God and to translate it into a classification. Under a *phenetic* taxonomic paradigm, the classification was based on overall similarity, and the role of taxonomists was seen mostly as developing reliable methods for measuring this similarity. Both these approaches, as well as others not mentioned here, are now largely obsolete, although the last one may have to be revived in the future, at least for the taxonomy of organisms in which lateral gene transfer is an important evolutionary phenomenon and concerns a large part of the genomes (Doolittle 1999). Two main taxonomic paradigms are currently in force in zoology and botany. Under a *cladistic* taxonomic paradigm, the classification is based on cladistic relationships, and the role of taxonomists is seen mostly as developing reliable methods for inferring these relationships and reconstructing the "tree of life": the only taxa recognized are groups considered *holophyletic* (Ashlock 1971) or "monophyletic" sensu Hennig (1950, 1966), i.e., including an ancestor and all its descendants. Finally, under an *evolutionary* or synthetic paradigm, classification is understood as aiming at reflecting the patterns of evolution, considered not only as a series of cladogenetic events, but also of anagenesis and adaptation: therefore two kinds of taxa can be recognized, either holophyletic or *paraphyletic* (Hennig 1950, 1966), both categories of taxa that are *homophyletic* (Dubois 1986, 1988b) or "monophyletic" sensu Haeckel (1866), i.e., non-polyphyletic. These current taxonomic paradigms cannot be considered as "the final word" in the history of taxonomy, the "ultimate taxonomic paradigm", especially as they do not account for phenomena like lateral gene transfer and reticulate evolution, and do not take into account the complex phenomena that are involved in the relationships between genetics and development (Evo-Devo), so that there is no *a priori* reason for rejecting the possibility that they might be replaced in the future by another paradigm or several (Dubois 2005c).

In contrast, nomenclature is not a science but a technique, a *tool* at the service of taxonomy. In order to play properly this role, to remain universal and to follow the changes occurring in taxonomic paradigms while keeping a high robustness in the nomina of taxa, nomenclature should not be linked to a scientific theory of classification, but should depend on a set of stringent, universal and stable rules, i.e., on a *Code*, that can be used under any taxonomic paradigm.

Nomenclatural rules should therefore be *theory-free* regarding taxonomy (Dubois 2007a). This tool should be as neutral as possible, in order to respect what the *Code* calls "the freedom of taxonomic thought and action". This is similar to grammatical rules relative to language or literature: they do not tell us what to say or write, but how to do it, and they are universal and stringent for proper communication. The rules should be devised in such a way that they can be used by all taxonomists whatever their opinions on taxonomy, and that they apply to nomina created within any given taxonomic paradigm, even after their transfer into another paradigm.

In some recent publications, the term "clade" has been used to designate some kinds of taxa, i.e., groups that are considered holophyletic under a cladistic hypothesis of relationships. In the scientific field of phylogenetic research, hypotheses can be built about relationships between organisms. Clades no doubt have existed and exist in the real world, but the "clades" resulting from cladistic analysis are not the "real clades" of the real world: they are theories, hypotheses, that can be refuted. Several terms have been proposed to designate such hypotheses (see Dubois 2006b: 826), among which the clearest one is that of "cladon" (Mayr 1995). Cladons are taxa of a particular kind, recognized under the tree of life (cladistic) paradigm. Cladons, just like any other kind of taxa, can be *defined*, but not *discovered*. Below, they will simply be designated as "taxa", not "clades", as I do not think that taxonomy deals with clades, but with hypotheses about clades.

Categories and ranks

Most scientific classifications of living organisms so far have used hierarchical nomenclatural systems with successive ranks from the highest to the lowest. Thus, in zoology, the partial nomenclatural hierarchy regulated by the *Code* recognizes at least 11 ranks: superfamily, family, subfamily, tribe, subtribe, genus, subgenus, species group, species, subspecies group and subspecies. Additional ranks between superfamily and subtribe can be used also if necessary, but not between subtribe and subspecies.

In zoology, the nomenclatural hierarchy has been arbitrarily divided into five *nominal-series* (Dubois 2000b). Each nominal-series includes several *ranks*. Several recent authors made a confusion between rank and nominal-series, so some clarifications may be useful.

Three nominal-series ("groups of names") are recognized by the *Code*, which regulates the use of their nomina. The *family-series* includes nomina of the ranks superfamily (ending in *–OIDEA*), family (ending in *–IDAE*), subfamily (ending in *–INAE*), tribe (ending in *–INI*), and subtribe (ending in *–INA*), and possible additional ranks without fixed endings. Bour & Dubois (1985, 1986) and Dubois (2006a) proposed standard endings for some of these ranks. The *genus-series* includes only two ranks allowed by the *Code*, genus and subgenus (see Dubois 2006b,d, 2007b). The *species-series* includes four ranks recognized by the *Code*, species-group (as "aggregate of species"), species, subspecies-group (as "aggregate of subspecies") and subspecies, no additional ranks being allowed by the *Code* (see Dubois 2006b).

Besides, two nominal-series are not recognized and regulated by the *Code*. The *class-series* (Dubois 2000b) includes all nomina of taxa of the highest ranks: order, class, phylum, reign, etc. These nomina are currently not regulated by the *Code*, but this would be very useful to avoid the progressive instauration of a chaos in higher nomenclature with the increase in the number of higher taxa that follow the multiplication of molecular phylogenies. Detailed rules have been proposed to incorporate these nomina into the *Code* (Dubois 2006a). The *variety-series* (Dubois 2005a,c) includes the nomina of all taxa of the lowest ranks, such as variety, natio, form, etc. Incorporating these nomina into the *Code* would also be useful, in order to allow naming entities at low levels of analysis, e.g. for phylogeographic studies or for conservation biology (Dubois 2006b).

Nominal-series play a crucial role in the functioning of zoological nomenclature, much more important than ranks by themselves. This is misunderstood by all those who qualify the nomenclatural system of the zoological *Code* as a "rank-based nomenclature". The two main characteristics of this nomenclatural system, which regulate the valid nomen of any taxon within the frame of any taxonomic arrangement, are the allocation of nomina to taxa through *ostension* using *onomatophores* (Simpson 1940; Dubois & Ohler 1997; Dubois 2005c), and the recognition of three distinct *nominal-series* among which a *Principle of Coordination* is in force (Dubois 2005c). Ranks by themselves play no role in the establishment of the valid nomen of a taxon. It would be more appropriate to call this system "onomatophore-based nomenclature" (Dubois 2005c), "ostensional nomenclature", or "ostensional eponymic nomenclature", but such terms would be pedant and cumbersome, so it seems better to keep the traditional term "Linnaean nomenclature", although this nomenclatural system is quite different from that used by Linnaeus himself (Moore 2003; Dubois 2005c, 2006c).

The basic function of nominal-series is to allow nomenclatural parsimony, as any nomen given to a taxon *within* a nominal-series is available also for other taxa in the same nominal-series. This is made possible in this system because all nomina in the same nominal-series interact concerning: (1) coordination and eponymy; (2) synonymy; (3) homonymy; (4) priority. Among all nomina that may potentially apply to any given taxon of a nominal-series in a given ergotaxonomy, the valid nomen is usually established by priority of publication.

On the other hand, nomina do not interfere *between* nominal-series for eponymy, synonymy, homonymy and priority. The only interactions between nomina of different nominal-series are: (1) through the use of some nomina in a lower series as onomatophores for nomina of an upper series: "type-species" for nominal genera or subgenera, and "type-genera" for nominal family-series taxa; (2) in a few very special cases (Art. 32, 33, 35, 39 and 40 of the *Code*) which concern only family-series nomina (Dubois 2008c).

Are nomenclatural ranks useful or harmful?

The usefulness of nomenclatural ranks has been challenged recently by some authors who support unranked nomenclatural systems recognizing only "taxa" (or sometimes "clades") which are not referred to ranks. In fact, few of these authors really follow a fully unranked nomenclatural system, which would require abandoning also the ranks species and genus. Most of them in fact adopt a "partially ranked" nomenclatural system, using Linnaean nomenclature for taxa at the ranks species and genera, and sometimes also families, superfamilies, subfamilies and tribes, but using the term "taxon" for all other taxa above, between or below the latter in their hierarchy. In particular, as will be discussed in more detail below, some authors use *pseudoranked* nomenclatural systems (Dubois 2007a), in which they refer some taxa to formal ranks (genus, subfamily, family) but without respecting the hierarchical arrangement of taxa in which sister-taxa are afforded the same rank.

Discussing the usefulness of ranks will require exploring two distinct questions: (1) the problem of arbitrariness of ranks and equivalence of taxa referred to the same rank; (2) the hierarchical organisation of taxonomic information.

The equivalence of taxa referred to the same taxonomic category

In the scientific literature dealing with biodiversity, in various fields including evolution, palaeogeography, biogeography, ecology, conservation biology, etc., there is a widespread use of ranks for taxonomic comparisons between taxa, faunae, periods, etc. Such works rely for example on numbers of genera, families, orders or classes to compare faunae in different regions or at different epochs. This would suggest that evolutionary patterns, taxonomic richness and diversity, etc., can be inferred from nomenclatural patterns, as such calculations rely on the nomenclatural ranks afforded to taxa. Are such comparisons warranted? They would be so only if taxa at the same rank in different groups were "equivalent", at least by some criteria.

In this context, equivalence requires common criteria (Schaefer 1976). Such criteria can be used either to *establish* taxa that are equivalent in some respect, or to *measure* the equivalence between taxa previously established using other criteria. Various criteria have been used for this purpose (Dubois 1988b), e.g., among others, quantitative metataxonomic criteria, phenetic criteria relying on characters, relational criteria or absolute age of taxa. Let us consider some of these approaches more closely.

The metataxonomic criterion of Van Valen (1973) relies on the number of taxa at different ranks in different taxonomies. Some taxonomies appear "well-balanced" (e.g., **CHONDRICHTHYES**), others "oversplit" (e.g., **AMPHIBIA**) and others "overlumped" (e.g., **AVES**), but these disparities can have various causes, from different taxonomic practices in different zoological groups to genuine differences in their evolutionary patterns. Therefore, this criterion can hardly be used to *standardize* the use of ranks in zoology, but it can provide interesting information when *comparing* classifications (Dubois 1988a-b).

Phenetic criteria relying on *characters* (obtained from morphological, molecular, karyological, ethological, bioacoustical or other data) allow estimates of various "distances" between taxa (Dubois 1988b) and provide measurements of variability and dispersion within various taxa. Such criteria can also be used to *compare* the taxonomies of these different groups, but hardly to *standardize* the use of ranks in zoology. Within a given group, it is possible to use some ecological or behavioural characters to homogenize the use of ranks: for example, in the **AMPHIBIA**, it has been suggested that holophyletic taxa with different reproductive modes be afforded the rank of genus, except when this contradicts the crossability criterion discussed below (Dubois 1988b, 2004b). However, such criteria cannot be generalized to the whole taxonomic hierarchy, as they can be used only for closely related taxa sharing homologous characters (Schaefer 1976).

Relational taxonomic criteria or *relacters* (Dubois 2004b), based on real interactions between organisms (not on comparisons of characters by scientists), such as the mixiological criterion at the species level (Mayr 1940, 1942, 1963; Dubois 2008d,f) or the crossability criterion at genus level (Dubois 1981, 1988b, 2004b) require certain precautions for proper use, but these are not always respected. For example, according to the "biological species concept"of Mayr (1940, 1942), the mixiological criterion at the species level states that whenever two entities freely exchange genes *in nature*, i.e., when an unbiased bidirectional introgressive gene flow exists between them in a contact zone, these two entities are part of the same species taxonomic unit. But the fact that, in captivity or in artificial conditions, individuals of two entities are able to give birth to living offspring, is not by itself sufficient to consider them conspecific, as suggested by some (e.g., Samadi & Barberousse 2006), as various factors, e.g. behavioural, can impede gene flow between them in nature: many cases are known of species fully separated in nature although they are genetically compatible. In contrast, at generic level, the crossability criterion simply states that whenever two species are liable, in natural *or artificial* conditions, to produce viable hybrids, these two species should be referred to the same generic taxonomic unit, but the reverse is not true: intersterile species may well be congeneric (for details, see Dubois 1988b). When used carefully and rigorously (i.e., respecting these precautions), relacters are very helpful for a standardization of taxonomy at and between the ranks species and genus in some zoological groups. However, such criteria cannot be generalized to the whole taxonomic hierarchy, as they cannot apply to ranks above genus and to organisms that are not bisexual or that have peculiar meioses (Dubois 2008d, 2008f), not to mention the fact that they cannot be applied to fossils.

The proposal to standardize the use of ranks over the whole zoology through the absolute age of taxa was first made by Hennig (1936, 1950, 1966), subsequently abandoned and recently revived by Avise & Johns (1999) and Avise & Mitchell (2007). Thanks to the recent improvement of molecular dating methods of of cladogeneses, this criterion is very promising and might be implemented in the future, but for the time being this is difficult, because of three different kinds of problems. First, this approach cannot be of generalized use today because of missing information for many groups of organisms. This problem will progressively be solved as data are accumulated. Second, this approach applies only to organisms living synchronically, e.g., nowadays, as otherwise all fossil taxa would have to be given higher ranks simply because they lived long ago! The datation of fossil groups for which no representatives exist in the current fauna is today more difficult, but progress in dating methods for these groups can be expected. As molecular and palaeontological data increase, it will be possible to estimate the absolute age of all major taxa *at any period* of the earth's history, and therefore to use this method for rank assignation of taxa, but these ranks will be valid only for comparisons of synchronic taxa (living at the same period). Thirdly, implementing such a change in the allocation of ranks to taxa would pose strong problems regarding "taxonomic tradition", as well illustrated by Avise & Johns (1999): in the cases of the cichlid fishes of lake Victoria, of anthropoid primates and of fruit flies of the genus *Drosophila*, any time-scale standardization in the ranks given to taxa would result in changing drastically the ranks traditionally given to taxa in at least two of these three groups. Therefore, such a drastic change would be impossible to carry out through the individual action of some zoologists, and could be so only through a collective action of the international community in one or several large international meetings (Dubois 2007a), the organization of which may take a few decades, if it ever occurs.

In conclusion, for the time being, there exists no method for a *general* standardization of the "meaning" of ranks over the whole of zoology and palaeontology. The "meaning" of the rank family or genus is by no way equivalent in flatworms, beetles and birds. Therefore, any comparison between faunas or taxonomies using the ranks of taxa as a criterion (e.g., quantitative comparisons based on numbers of taxa at some ranks) is unwarranted and misleading (Minelli 2000). This statement was one of the main reasons why several recent authors rejected the use of ranks in taxonomy. But is this reason valid? It would be so only if nomenclatural ranks were viewed as identical with taxonomic categories, an opinion that is shared by many but that is questionable. Dubois (2005c, 2007a) proposed to recognize a basic distinction between these two concepts, stating that one refers to taxonomy and the other one to nomenclature.

The criteria of equivalence between taxa briefly reviewed above are of two kinds: biological and chronological. Biological criteria are all of limited use for equivalence, as they can be used only at low taxonomic levels (species and genus), and are not relevant in various situations. Chronological criteria are potentially general but face three problems (missing data, applicability only for synchronic taxa and taxonomic tradition) that preclude their implementation over the whole of zoology for the time being. This is true, but, as discussed below, the use of such criteria in some situations can however be informative as it allows to obtain useful information regarding the patterns of evolution. Sets of taxa defined by such criteria can be designated as *taxonomic categories*. Taxonomic categories are categories of taxa that share some common features and are equivalent by some taxonomic criterion. They do not provide information on cladogenetic relationships, but this information can be provided by *nomenclatural ranks*. On the other hand, nomenclatural ranks are nomenclatural tools which only provide information on the detailed hierarchical structure of a taxonomic hierarchy, but no information on the evolutionary peculiarities of the taxa in this hierarchy. To make this unusual distinction fully clear, a few words must be said about taxonomic categories as here defined.

Taxonomic categories

The interest in taxonomic categories, particularly in "evolutionary categories", was high in the middle of the XXth century, at the time of the "evolutionary synthesis" (Mayr 1982). In contrast with the current situation, the focus of interest of evolutionary biologists then was not so much in the cladistic relationships, but mostly in "micro-evolutionary processes", such as speciation, hybridization, adaptation, etc. Evolutionary taxonomic categories were developed then because they were considered a useful tool for evolutionary biologists: referring a taxon to one of these categories (Rassenkreis, Artenkreis, superspecies, semispecies, subspecies, etc.) is a simple and brief way to provide some information, for example on the "stage" in the process of speciation reached by various allopatric entities in an archipelago. This is part of the special domain of taxonomy that deals with species and other low-level taxa, which has been designated as *microtaxonomy* (Mayr & Ashlock 1980) or *eidonomy* (Dubois 2008d). In strong contrast with nomenclatural ranks, such categories are indeed *defined* by biological and/or chronological (i.e., evolutionary) criteria, and all taxa referred to one of these categories are indeed equivalent by these criteria. Many such taxonomic categories, most of which are at the nomenclatural rank of species, just above or just below, have been proposed, mostly in the first half of the XXth century. Several good reviews and syntheses about these eidonomic categories, their definitions and usefulness, with examples of evolutionary situations referred to by these concepts and terms, are available (Bernardi 1956, 1957, 1980; Haffer 1986). More recently, other eidonomic categories (klepton, klonon, kyon, etc.) were established to accommodate bisexual, unisexual or asexual entities that have special reproductive modes, often with particular gametogeneses with special meioses, metameioses or ameioses (Dubois & Günther 1982; Dubois 1991, 2008d,f; Bogart *et al.* 2007).

Although most of these taxonomic categories are situated around the species level, this approach can be useful also at the genus level, as shown by the proposal to use data from interspecific hybridization as a relacter to delimit genera (Dubois 1988b). Combined with the requirement to recognize as taxa only groups that appear holophyletic with the data available, and with the use of other criteria such as the reproductive mode, this criterion allows to greatly enhance the objectivity, repeatability and equivalence of generic taxa, as illustrated in the **AMPHIBIA** (Dubois 1987, 2004b), where genera recognized on the basis of cladistic data alone (e.g., Frost *et al.* 2006) are in no respect equivalent or even comparable, and may be considered much less useful to many biologists.

This evolutionary or synthetic approach to taxonomy is certainly not "fashionable" today, where few taxonomists work at population level, consider adaptation as an important taxonomic criterion or work on hybrid zones or artificial hybridization to obtain information that they will use in their taxonomic work. However, the idea that cladistic relationships between organisms is the only information interesting for taxonomists is a very strange one indeed, and it seems reasonable to think that times will come when young taxonomists become again interested in these matters. When this occurs, they will certainly take advantage of the rich literature of the last century on these questions, and of the evolutionary taxonomic categories created by the authors of this period.

As explained above, these categories are based on biological or chronological criteria, but not on cladistic data. They can be used in some cases to make taxa in different groups "equivalent" in some respect, but this has no generality over the whole animal kingdom as these criteria are irrelevant and non-usable in many cases. Thus, the mixiological criterion as used at species level cannot be used in allopatry or allochrony, or between species that are intersterile, whereas in contrast, knowing that two entities prove interfertile in captivity or under artificial fertilization does not tell us whether gene flow occurs between their populations when they get in contact in the field: the only way to have the answer to this question is through field work and observation of the contact zone. Such categories are often more meaningful to field naturalists than to laboratory workers.

The confusion between taxonomic categories as here defined and nomenclatural ranks has long created difficulties in theoretical discussions among taxonomists and even among evolutionary biologists. They stem in many cases from the use of the same term to designate different concepts. This is particularly true of the term *species*, which has been used in many senses in biology, and even in two fully different senses in systematics, to designate either a taxonomic category or a nomenclatural rank.

The many "species concepts" that are repeatedly discussed by theoreticians of systematics apply to the *taxon* species: they are taxonomic concepts. In contrast, the use of the *rank* species to designate a taxon is a matter of nomenclature. In order to avoid the confusion between the two distinct uses of the term "species", it appears useful, either to create two new terms, or to restrict the use of this term to one of these two situations. Being more parsimonious, the second solution was retained by Dubois (2007a, 2008d,f) who proposed to restrict the use of the term "species" to the nomenclatural rank. As a matter of fact, whatever the taxonomic paradigm they use, or even if they use none (which is often the case!), all biologists designate the organisms they study under a binominal Latin nomen, their species nomen, like *Drosophila melanogaster* or *Homo sapiens*. Such nomina, which carry by themselves no information on the criteria used to build the classification, are those which are found not only in all scientific publications, but also in all official texts and lists in force in commerce, customs, laws, conservation biology, etc. It seems therefore better to restrict the use of the term "species" to this nomenclatural acceptation of the term. For the taxonomic concept designating a unit in a classification, Dubois (2007a) suggested to use a similar term but ending in *–on*, just like the term "taxon": *specion*. As there are several distinct concepts of specion, they can be given different designations, such as *mayron* for the "biological species concept", *simpson* for the "evolutionary species concept", *klepton* for a taxon accommodating entities reproducing by "hybridogenesis" or gynogenesis, or *klonon* for those reproducing by parthenogenesis (for more details, see Dubois 2008d,f). These terms, and many others that could be coined in a similar way, designate different kinds of specions, i.e., taxonomic categories defined according to different criteria. They are therefore *alternative* categories, which have no hierarchical relationships between them. Nomenclaturally, all these taxonomic categories include taxa which are referred to the same nomenclatural rank, that of *species*.

The same distinction can be made for taxa referred to nomenclatural ranks above the species, e.g., *genion* for a taxonomic category that can be recognized on the basis of biological criteria like crossability for taxa referred to the rank genus (Dubois 2007a, 2008d). However, this process soon reaches its limits when one moves upwards in the nomenclatural hierarchy, because, for reasons discussed above, there are no common biological criteria allowing to define a taxonomic category like family, order, class or reign. The chronological criterion of the absolute age of taxa could allow defining such categories, but the time is not yet ripe for this, as we have seen.

Nomenclatural hierarchy: the Principle of Coordination

A hierarchical presentation of biological classifications has been used long ago, even before the works of Linnaeus, which however are striking as showing a very consistent use of such a system (Dubois 2007c). A hierarchical presentation is indeed much more informative than a non-hierarchical one (Knox 1998), just like a database or even a simple index where all items are listed alphabetically are less useful for finding an information than hierarchical ones (Dubois 2007a). This practical aspect of taxonomic hierarchies, as a device for storing, tracking and retrieving information is an important one, that should not be ignored or despised (Cracraft 1974; Mayr 1982; Ashlock 1984; Benton 2000). Besides and quite independently, although initially they were viewed as expressing the *scala naturae*, i.e., a scale of value and importance of organisms credited to God, it so happens that hierarchical taxonomies are particularly efficient for presenting cladistic information. Under the "tree of life" paradigm, diversification of organisms can be reduced to a succession of cladogenetic events. This is a simplified vision of evolution, which ignores the importance of anagenetic change within lineages as well as all phenomena of reticulate evolution, speciation through hybridization and lateral gene transfer, but this simplification provides an efficient tool for building taxonomies. Under this paradigm, each cladogenetic event in the "tree" can be expressed by a new hierarchical level in a classification. A hypothesis of cladistic relationships can be expressed in different ways, such as a tree, a list with successive indentations from the margin, or a hierarchical arrangement of taxa successively included in each other. In this case, inclusion of a taxon G in another one F (such as a genus in a family) expresses the fact that the cladogenesis which gave birth to G was posterior to that which produced F. In terms of logic, successive inclusion of taxa is strictly equivalent to a tree with successive branchings. This is for example the case of figures 2 and 3 in Dubois (2006a).

This taxonomic hierarchical representation of phylogeny can be expressed nomenclaturally, and this is the role of ranks. Although ranks were not used for this purpose in the early days of taxonomy, it turned out that they can play this role very well. However, to use the nomenclatural hierarchy as a reflection of the structure of a cladogram or a phylogenetic tree requires a few assumptions. It seems that misunderstanding these assumptions played a role in the recent rejection of ranks by some taxonomists.

The first important assumption is that sister taxa must always be referred to the same nomenclatural rank (Raikow 1985; Sibley & Ahlquist 1990): they are therefore *parordinate* (Dubois 2006b: 827). Second, any taxon is *subordinate* to a *single* upper taxon, which must be referred to the *just upper rank*. It may be *superordinate* to two or more taxa of *just lower rank*. In such a system, the relations between all taxa that are connected by superordination, parordination or subordination are *relations of coordination*. In the absence of such relations between them, two taxa may be described as being in a relation of *alienordination* (from the Latin *alienus*, "foreign", and *ordo*, "order")[1]. Thus, in the recent **AMPHIBIA**, according to the cladistic relationships currently agreed upon by most authors (e.g., Frost *et al*. 2006), and according to the higher nomenclature of Dubois (2004a, 2005d), the taxon **BATRACHIA** is the sister-taxon of the **GYMNOPHIONA**: they are parordinate taxa that must be given the same rank, in this case that of superorder. Both are subordinate to the subclass **NEOBATRACHI**, and the superorder **BATRACHIA** is superordinate to the orders **ANURA** and **URODELA**. The latter are alienordinate to any other taxon that is not directly related to them by coordination, e.g., the **GYMNOPHIONA**.

Under the *Code*, to be nomenclaturally available, any nomen must be published following a set of stringent rules (Dubois 2005c, 2008e). This includes the need to refer this nomen to one of the three nominal-series recognized by the *Code*: family-, genus- or species-series. As ranks and nominal-series have no biological meaning by themselves, this assignation is arbitrary, mostly guided by tradition and consensus. This poses (or should pose) no problem to taxonomists, who know (or should know) that ranks are meaningless, and it should be their duty to explain this to laymen in order to avoid them to believe the contrary (Dubois 2006c).

The *Principle of Coordination* is a major rule of the *Code*, which states that, within a nominal-series, among all the parordinate taxa that are subordinate to the same superordinate taxon, one, called in the *Code* the "nominotypical taxon", must bear the same nomen (with the same nomenclatural author and date) as this superordinate taxon. The nomen of the subordinate taxon is identical in spelling to that of the superordinate taxon in the species-series (subspecies *temporaria* of the species *Rana temporaria*) and in the genus-series (subgenus *Rana* of the genus *Rana*), but must be emended to indicate the rank in the family-series (subfamily *RANINAE* of the family *RANIDAE*). These different terms are not different *nomina*, as they keep the same author, date and onomatophore, but are different "avatars", or *morphonyms* (Dubois 2000b), of the same nomen. The terminology provided by the *Code* is not precise enough as it does not allow to point to the status of all these morphonyms of the same nomen created by the Principle of Coordination, so Dubois (2006b) proposed to call *epinym* the morphonym designating the superordinate taxon, and *hyponym* the morphonym designating the subordinate taxon. Epinym and hyponym are two *eponyms* of a single nomen, and the relation between

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[1] This term is here substituted to the term *xenordination* (Dubois 2006b: 827) which was ill-formed, being a combination of Greek and Latin roots.

eponyms can also be called *relation of eponymy*. Among the nomina available for all the subordinate taxa of a taxon, the hyponym is established by the Principle of Priority. As for the nomen of the parordinate taxon, it may be called the *getonym* of the latter (from the Greek *geiton*, “neighbour”, and *onoma*, “name”), and the relation between getonyms a *relation of getonymy.* The relation of coordination, which involves not only eponyms but also getonyms at all ranks, is more comprehensive than the relations of eponymy and getonymy, i.e., it is a combination of both. Nomina that are in a relation of alienordination are *telonyms* (from the Greek *tele*, “far away”, and *onoma*, “name”).

Because the zoological nomenclatural hierarchy is divided into five successive “slices”, the nominal-series, the relation of coordination does not cover the whole nomenclatural hierarchy but is limited to subsets of the latter. Thus, in a given ergotaxonomy, one such subset may be composed of a superfamily, its subordinate families, their subordinate subfamilies, tribes and subtribes, but it stops upwards when one reaches the lowest rank of the class-series (e.g., suborder) and downwards when one reaches the rank genus. The set of nomina which are involved in the relation of coordination in this case, from superfamily to subtribe, may be called a *coordinate nomenclatural set*. It corresponds to a set of nomina which, in a given ergotaxonomy, designate taxa that are either superordinate, parordinate or subordinate to each other, but it excludes all those which are alienordinate.

Monosemic and polysemic nomenclatural systems

The existence of the Principle of Coordination in the *Code* results in this nomenclatural system being partly polysemic. In grammar and linguistics, *monosemy* applies to a situation where one word has only one meaning, whereas in *polysemy* one word has several meanings.

Polysemy is very widespread in all “natural languages”. The same word may have several meanings, but the proper meaning is usually easy to identify because of the context. However, in science, in order to make communication more precise and to avoid possible confusions, most “technical” words have only one meaning. This is not the case in zoological nomenclature, because of the Principle of Coordination: several coordinate taxa bear the same eponym. Is this justified? This feature of the *Code* has recently been criticized, so what are the pros and cons of eponymy in nomenclature?

The major argument against eponymy in nomenclature is that it may be a source of ambiguity, particularly for non-taxonomists. Thus, Hillis (2006) suggested that “Google users” may be confused, when they search for a nomen, e.g., *Rana*, to receive replies that concern both the genus *Rana* and its hyponymous subgenus *Rana*, as they do not understand that the same nomen can designate two distinct taxa. This is certainly true. The question is whether a scientific discipline must be directed by laymen, be they “Google users” or governmental or other “experts”, or by the scientists involved in the discipline itself. Until now, science has been mostly directed by scientists, and, to take just one example, the systems of designation of atoms and of molecules have been decided by chemists: no “user” will challenge their decision to designate the atom of copper by Cu and the carbon dioxide molecule by CO_2.

Until now, the partially polysemic nature of zoological nomenclature does not seem to have been criticized by zoologists themselves, as they have apparently been able to distinguish easily between “genus *Rana*” and “subgenus *Rana*”. However, specialists should not remain deaf to the comments from non-specialists. Times are no doubt changing regarding access to scientific information, which is now much wider through the web than it has ever been, and this request for removing the possible ambiguity of some nomina should not be ignored, but discussed.

The main argument in favour of partial eponymy in nomenclature is *nomenclatural parsimony* (Dubois 2006b), i.e., the need of fewer nomina for the same number of taxa. For example, in the case of a superfamily A that contains families, subfamilies, tribes and subtribes, the same nomen A may designate 5 taxa, several other nomina 4 taxa, others 3 and 2 taxa. Altogether, over the whole of zoological taxonomy, this allows to spare the creation of a large proportion of nomina (a proportion which would be interesting to estimate from real ergotaxonomies).

Sparing the creation of nomina allows to make nomenclatural databases simpler and "lighter". It is furthermore fully justified in view of the fact that taxonomies are constantly changing and improving, as more data are obtained and as taxonomic methods and concepts evolve, so that many nomina once created disappear as synonyms. When this occurs to an eponym (a nomen that is used as valid at different ranks in a taxonomy), only one nomen is concerned by this synonymisation, whereas, if each taxon had been given a different nomen, several nomina would have been created uselessly and would have to be stored in synonymies. Thanks to the existence of eponymy, it is often possible to establish a new taxon without having to create a nomen, as nomina once considered synonyms can be resurrected from synonymy. In contrast, the suppression of eponymy in zoological nomenclature might possibly be another inducement for some zoologists to create nomina, just to "attach their names" to them, a real problem in biological nomenclature (Dubois 2008b; Evenhuis 2008).

Despite these advantages of polysemy, the question raised by Hillis (2006) needs consideration. It is clear that, in the coming decades, more and more non-specialists will have access to taxonomic databases and data, and that some of them will be confused by polysemy. Would it then be a good idea to remove eponymy from zoological nomenclature? Contrary to what is stated by some, who consider that eponymy is inherent to Linnaean nomenclature, this would be fully possible, by changing only one rule of the *Code*, i.e., by replacing the Principle of Coordination by another system, as will be discussed below. Before discussing this however, we need to come back to the distinction between *definitions of taxa* and *definitions of nomina*. This distinction is not made by some supporters of "phylogenetic nomenclature", and this confusion is basic for many endless discussions between the latter and partisans of keeping the Linnaean nomenclatural system.

A few final words of caution must be added here regarding the meaning of the term *eponymy*. The situation it describes can be, and has been, confused with two other situations regarding biological nomenclature. *Eponymy* is the situation where the *same nomen* (same author, date and onomatophore) is used *in the same ergotaxonomy* as the *valid nomen* for *several distinct, coordinate taxa*. In contrast, *homonymy* is the situation where *different nomina* (generally with different authors, dates and onomatophores, with a few exceptions, when the same author used the same nomen for naming two different nominal taxa) are *nomenclaturally available*—which results in one of them, usually the junior one, being rejected as *invalid*. Finally, a third situation results from the fact that zoological nomina under the *Code* are not *defined* by closed intension or extension, but *attached* to taxa by ostension (Stuessy 2000, 2001; Keller *et al.* 2003). This results in the same nomen being liable to designate quite different taxa in different ergotaxonomies, the only requirement being that these taxa must include the onomatophore of this nomen. The reasons why this is highly preferable to a system of closed intension or extension were explained in detail elsewhere (Dubois 2005a, 2006c, 2007a): if a nomen corresponded to a strict, unchangeable definition and/or content of the taxon, a new nomen would have to be coined every time a subordinate taxon or even a specimen is added to the taxon or removed from it, so that there would be no continuity in the use of nomina and no simple way to understand the taxonomic history of a group, as is now possible through "synonymies" or more exactly *logonymies* (see Dubois 2000b). The situation here described, where the *same nomen* applies to *different taxa*, but *in different ergotaxonomies*, is neither homonymy nor eponymy, and its clear distinction from the latter two requires a special designation. For this situation, I propose the term *astatonymy* (from the Greek *astatos*, "unstable", and *onoma*, "name"). This situation is extremely common in zoology, by far more than the situation where the nomen has always designated exactly the same taxon since its creation, which may be called *menonymy* (from the Greek *meno*, "I stay, I am stable", and *onoma*, "name").

Definitions of taxa

Definitions of taxa are a matter of taxonomy, not of nomenclature. Different taxonomic "schools" use different kinds of definitions of taxa. Nowadays, no taxonomic school claims to be "Linnaean", i.e., to use "Linnaean" definitions of taxa. There exist no such things as "ICZN-taxa" (Joyce *et al.* 2004) because the *Code* does not provide any guideline for defining taxa, being theory-free regarding taxonomy. In current taxonomy, only two kinds of definitions of taxa are widely used: phenetic definitions or *diagnoses*; and cladistic or "phylogenetic" definitions, or *cladognoses* (Dubois 2007a: 43).

Diagnoses are definitions of taxa which are not associated with a cladistic hypothesis. They are based on "character states" or *signifers* (Ashlock 1985) that are considered to be shared by all members of the taxon and absent in all non-members.

Cladognoses are definitions of taxa that are associated with a cladistic hypothesis. They may be based either on characters or on relations.

Cladognoses may be based on signifers (1) that are considered to be shared by all members of the taxon and absent in all non-members, and (2) that are regarded, on the basis of a cladistic analysis and hypothesis, to be autapomorphic for the taxon. Such cladognoses have received the long and cumbersome designation of "apomorphy-based definitions" (de Queiroz & Gauthier 1990), but may be called more shortly *apognoses* (Dubois 1997). Alternatively, cladognoses may be based directly on the hypothesized cladistic relationships between taxa. Such cladognoses, which received no general designation by de Queiroz & Gauthier (1990) and their followers, can be called *coinognoses* (from the Greek *koinos*, "common, kindred", and *gignosko*, "I know"). They are of two kinds: "node-based definitions" (de Queiroz & Gauthier 1990) or more briefly *rhizognoses* (from the Greek *rhiza*, "root", and *gignosko*, "I know"), and "branch-based definitions" (de Queiroz & Gauthier 1990) or more shortly *caulognoses* (from the Greek *kaulos*, "stalk", and *gignosko*, "I know"). Although de Queiroz & Gauthier (1990) stated that these definitions apply to *nomina*, they in fact apply to *taxa*, as they are based on statements about the organisms and are a matter of taxonomy (Dubois 2005c).

Allocation of nomina to taxa

Three systems have been used in zoological nomenclature to allocate nomina to taxa: extensional definition, intensional definition and ostensional allocation. They were described in some detail elsewhere (Dubois 2006c, 2007a) and only a summary will be presented below.

(1) *Extensional definitions of nomina* provide a statement about the extension or circumscription of the taxon designated by the nomen. This may be a list of the members of the taxon (inclusive extension) or of its non-members (exclusive extension). This system is theory-free regarding taxonomy. There are two distinct ways of defining nomina by this system.

(a) *Closed extension*, which allows no modification of the extension of the taxon (addition or removal of members), is always monosemic. This system is favoured by some computer specialists. It would be appropriate for a taxonomy including a very low number of units or taxa, all already known or close to it (such as the planets of the solar system or anthropoid primates). As this is not the case in zoology, where millions of species await discovery, description and naming, this system is much too rigid to be appropriate in zoological nomenclature.

(b) *Open extension* is more flexible, as it allows changes in the content of the taxon without having to change its nomen. The situation is complex if *removal* of members is allowed, as this often results in a modification of the original intension of the taxon and can lead in some cases to a significant drift from the original taxon, which in fact amounts to a change in the intension of the nomen and therefore to the creation of a new nomen (a junior homonym of the original one): this system is inappropriate in zoological taxonomy. But if only *addition* of members to the taxon is allowed, the original intension may be kept, which allows to avoid such a drift. This latter system does not provide a strict definition of the taxon to which the nomen may apply, as no limits are assigned to the taxon. Pushed to its extreme, this system is equivalent to that of ostension presented below.

(2) *Intensional definitions of nomina* provide a statement of some of the *characters*, *properties* or *relations* (e.g., as inferred from cladistic analysis) considered to be shared by all members of the taxon. Such a system is always monosemic and tied to a taxonomic paradigm. Three major kinds of such definitions have been in use in zoological taxonomy, the last two being still in use by different authors nowadays. In the case of *essentialistic* intension, the nomen was supposed to express the Platonic *essence* of the taxon. In *phenetic* intension, the nomen is bound to a *diagnosis* of the taxon (a list of its differential characters). In *cladistic* intension (used e.g. in "phylogenetic nomenclatures"), the nomen is bound to a *cladognosis* of the taxon, which can be either a list of its autapomorphic characters (*apognosis*) or a statement of its hypothesized cladistic relationships (*coinognosis*). Intensional definitions of nomina are inappropriate in zoological taxonomy for not being universal, being linked to a theory of taxonomy. Furthermore, in some of the proposals of "phylogenetic nomenclatures" published in the recent years, this system is partly subjective and circular within language, for relying only on verbal definitions of taxa without the compulsory use of reference specimens.

(3) In *ostensional allocation of nomina to taxa*, nomina are not *defined* but *pointed to* by an *onomatophore* (nomen-bearing device), that may be either a *specimen* or a *nomen* (which itself in the end refers to a specimen through a species-series nomen). This system provides neither characters, properties or relations for the taxon, nor a list of its members or non-members, nor its limits: all this is left to taxonomy and is not part of the nomenclatural process. This system is *objective* as based on specimens. It can be either monosemic or polysemic.

Interestingly, this system of ostension is not proper to biological nomenclature. A similar system is rather frequently used in geography. Many administrative divisions in many countries are named by reference to the name of their major city or of a river that flows, at least in part, within the province or district. Just like in biological nomenclature, naming a province "Padova" only tells us that the city of Padova is included in the province, but not the limits of the latter. Just like in biological nomenclature also, in some countries, several progressively comprehensive administrative units included in one another (district, province, etc.) may bear the same name, that of their main city. Just like in biological nomenclature also, the extension of administrative divisions and their boundaries are liable to change without entailing a change in their name. This may even cause problems to zoologists when trying to locate an ancient collection locality for specimens: this is the case of the frog species *Rana maritima* Risso, 1827, which had been stated to have been collected at Napoléon's time near the sea in the French département of the "Alpes Maritimes", an administrative division that straddled the current French département of the "Alpes-Maritimes" and the Italian regione of Liguria (Dubois & Ohler 1995). Countries usually keep their names although their extension and boundaries may change: just compare the successive maps of "France" during the last five centuries… In the case of geography however, the reference to an onomatophore is not always strict and stable, as even the capital of a country may shift from a city to another, and there existed for several centuries a "Roman Empire" that did not include the city of Roma! However, in many cases, the nomination of administrative divisions relies on a system close to that of onomatophores in biological nomenclature.

Five different systems of ostensional allocation of nomina to taxa have been described in details by Dubois (2006b), which are only summarized here.

(a) The system of *onomatophores with a Principle of Coordination* is in force in the three nominal-series recognized by the *Code*. This partially polysemic system uses inclusive ostension with eponymy. The valid nomen of any ergotaxon is the oldest among all the nomina created for protaxa whose onomatophores are included in the ergotaxon.

(b) A system of *onomatophores with absolute ranks* would tie each nomen to a rank, thus suppressing the nominal-series. In such a fully monosemic system, the valid nomen of each ergotaxon would be the oldest one for a taxon of this rank including an onomatophore referred to this taxon. This system is the only one that would deserve the designation of "rank-based nomenclature" which is used improperly by some to designate Linnaean nomenclature. It is not to be recommended, as it would put inappropriate emphasis on ranking and appear to support the idea that ranks have a meaning by themselves, other than expressing sister-taxa relationships and hierarchical relationships between taxa. Furthermore, it would result in many nomina having to be often abandoned, during the frequent process of modification of taxonomic hierarchies with upgrading or downgrading of taxa without modification of their intension, extension and nomen.

(c) A system of *progressive additivity of onomatophores* can be thought of in order to allow nomenclature to be monosemic without having to tie nomina to ranks. Within a nominal-series, the onomatophores of two lower taxa could be added to make the onomatophore of an upper, more inclusive, taxon. This system could be appropriate if all the nomenclature of organisms was created at once, simultaneously, but it is not so within a nomenclatural system that has been incremented progressively over decades, for reasons explained in details elsewhere (Dubois 2006c: 21–24).

(d) The system of *indissoluble set of onomatophores with inclusive ostension* is a monosemic system without eponymy relying on special onomatophores composed of one or several specimens or taxa indissolubly linked together. Unlike in the *Code* for genus-series and species-series nomina, such onomatophores cannot be modified by restriction to one specimen or taxon among several originally included. In this system, a nomen applies to the *least inclusive* taxon including entirely its onomatophore, and the valid nomen of any taxon is the oldest one meeting this requirement. This system is one possible solution for obtaining a monosemic nomenclatural system, i.e., for getting rid of eponymy, but it allows mostly to name the least inclusive taxa in a taxonomy. When additional taxa are discovered that should be included in the taxon according to its original intension, the original nomen cannot be kept for the more inclusive taxon including them (Dubois 2006c: 25). To solve this problem, a last system of allocation of nomina to taxa has to be considered.

(e) The system of *indissoluble set of onomatophores and onomatostases with bidirectional ostension*, first proposed by Dubois (2004a, 2005b, 2005e, 2006a) for class-series nomenclature, is a monosemic system without eponymy relying on indissoluble onomatophores and *onomatostases*. The latter are specimens or taxa originally and expressly excluded from the taxon for which the nomen was coined. In this system, a nomen applies, within an ergotaxonomy, to the most inclusive taxon including all its onomatophore and excluding all its onomatostase, and the valid nomen of any taxon is the oldest one meeting this requirement.

When proposing rules for class-series nomenclature in zoology, Dubois (2004a, 2005b,e, 2006a) suggested to use a combination of the two latter nomenclatural systems for the establishment of the valid nomen of a taxon in the nominal-series. This suggestion was based on the idea that, as higher zoological nomenclature has never been regulated by the *Code* until now, implementing such rules nowadays should be done carefully, without disrupting the existing nomina for higher zoological taxa. Another proposal of rules for these nomina (Alonso-Zarazaga 2005) fails to solve this problem, as it would result in considerable changes in higher zoological nomenclature. This latter proposal was based on the idea that the Principle of Coordination should be extended to this nomenclature. As this rule has never been in force in the class-series and as it results in a partly polysemic nomenclatural system which poses problems of ambiguity, it would be a bad idea to follow this suggestion. The rules proposed by Dubois allow to keep the long-established nomina for higher taxa and to respect monosemy for the nomina of such taxa, and should be preferred on that account (Dubois 2006c).

The question is now: should this example be followed further by shifting the whole of zoological nomenclature to a monosemic system?

Should zoological nomenclature shift to a fully monosemic system?

We now have the elements to discuss the possible shift of zoological nomenclature from a partly polysemic system to a fully monosemic one. As we have seen, this would require only to change a single rule of the *Code*, i.e., to replace the Principle of Coordination by one of the monosemic nomenclatural systems discussed above. The two most appropriate ones for this change are *indissoluble onomatophore with inclusive ostension* and *indissoluble onomatophore and onomatostase with bidirectional ostension*. This shift would pose no theoretical problem, but several practical ones.

It would require the creation of thousands or probably hundreds of thousands of nomina, to replace the epinyms and hyponyms made invalid by this change of rule. For example, if a genus *Rana* contains several subgenera, in the current system one of them has to bear also the nomen *Rana*, which should then be replaced by another nomen, in order for all subgenera to have nomina distinct from that of the genus, as in the nomenclature of Hillis & Wilcox (2005), which is invalid under the *Code* (Dubois 2006b,d, 2007b).

Let us consider a superfamily including taxa of four family-series ranks from family to subtribe as evoked above. In the case of an unbalanced taxonomy with 9 taxa, where each family-series taxon contains only two subordinate taxa, one of which does not contain subordinate family-series taxa, the *Code* requires 5 nomina to name these 9 taxa, but removing eponymy would require the creation of 4 nomina (tables 1–2), therefore 80 % additional nomina . With the same hierarchy but a balanced, completely resolved, taxonomy (without polytomies), 16 nomina instead of 31 are needed under the *Code* for 31 taxa (tables 3–4), so that transfer to a monosemic nomenclature would require 94 % additional nomina. The number of additional nomina needed increases with the resolution of the tree, and then with the number of ranks. In all cases however, the nomenclature of all the taxa of a *coordinate nomenclatural set* in any given nominal-series requires far less nomina in a partially polysemic nomenclatural system. In the case of a fully resolved tree and of recognition of a new taxon at each dichotomy, transfer from a polysemic nomenclature with n nomina to a monosemic one requires (n–1) additional nomina, or, to put the same thing differently, the complete nomenclature of n taxa under the Principle of Coordination requires (n+1)/2 nomina, against n nomina under any monosemic system.

The total number of eponyms used in the current zoological nomenclature is unknown, but certainly high, especially in the family-series, as subgenera and subspecies, which are frequently used in some zoological groups, especially the best studied ones, are almost ignored in other groups, mostly for reasons of tradition. Therefore, although removing polysemy from the *Code* would be theoretically possible, it would be a very heavy, time- and money-consuming endeavour. Furthermore, this would be a very specialized work, which should be carried out by well-trained, professional taxonomists. Would this be a good choice during the century of extinctions, when taxonomists are not numerous enough and lack professional positions, student grants, funding for field and laboratory work, and for collection management? Asking the question provides the answer: although in an ideal world it might be considered desirable to shift from a partially polysemic nomenclatural system to a fully monosemic one, this is not an urgent matter today and this should be postponed until we have highly improved our knowledge of the living species of the planet (see the introductory preliminary statement above). Besides, transferring millions of data from a system to another would be bound to entail loss of information, and likely to introduce errors. This would be inappropriate at all times. The implementation of such a shift would appear to be justified once we have a much more exhaustive inventory of the living organisms of the planet, a complete database with all necessary information on all zoological taxa and nomina, and a fully automatic method for the replacement of invalid epinyms and hyponyms by existing nomina or by new nomina created especially for this purpose. Until this is the case, it is necessary to keep the current nomenclatural system in zoology, within the frame of which millions of nomina and nomenclatural acts have already been stored.

TABLE 1. The family-series nomenclature of a hypothetical unbalanced zoological taxonomy, according to the *Code*'s nomenclatural system based on the Principle of Coordination. Nomina of taxa are symbolized by letters and numbers: those in **bold** indicate eponyms, i.e., nomina that are used as valid for several taxa at different ranks. In this system, 5 nomina are sufficient to designate the 9 taxa recognized.

- Superfamilia **A01**
  - Familia **A01**
    - Subfamilia **A01**
    - Subfamilia A03
      - Tribus **A01**
      - Tribus A04
        - Subtribus **A01**
        - Subtribus A05
  - Familia A02

TABLE 2. The family-series nomenclature of the same hypothetical unbalanced zoological taxonomy as in table 1, according to a hypothetical nomenclatural system based on bidirectional ostension (see Dubois 2007a). Nomina of taxa are symbolized by letters and numbers. This system does not recognize eponyms. The four nomina in *italics* are nomina the creation of which is required by the suppression of eponymy. All other taxa keep the same nomina as in Table 1. In this system, 9 nomina are required to designate the 9 taxa recognized.

- Superfamilia A01
  - Familia *B01*
    - Subfamilia *B02*
    - Subfamilia A03
      - Tribus *B03*
      - Tribus A04
        - Subtribus *B04*
        - Subtribus A05
  - Familia A02

TABLE 3. The family-series nomenclature of a hypothetical fully balanced zoological taxonomy, according to the *Code*'s nomenclatural system based on the Principle of Coordination. Nomina of taxa are symbolized by letters and numbers: those in **bold** indicate eponyms, i.e., nomina that are used as valid for several taxa at different ranks. In this system, 16 nomina are sufficient to designate the 31 taxa recognized.

- Superfamilia **A01**
  - Familia **A01**
    - Subfamilia **A01**
      - Tribus **A01**
        - Subtribus **A01**
        - Subtribus A09
      - Tribus **A05**
        - Subtribus **A05**
        - Subtribus A10
    - Subfamilia **A03**
      - Tribus **A03**
        - Subtribus **A03**
        - Subtribus A11
      - Tribus **A06**
        - Subtribus **A06**
        - Subtribus A12
  - Familia **A02**

- Subfamilia **A02**
  - Tribus **A02**
    - Subtribus **A02**
    - Subtribus A13
  - Tribus **A07**
    - Subtribus **A07**
    - Subtribus A14
- Subfamilia **A04**
  - Tribus **A04**
    - Subtribus **A04**
    - Subtribus A15
  - Tribus **A08**
    - Subtribus **A08**
    - Subtribus A16

TABLE 4. The family-series nomenclature of a hypothetical fully balanced zoological taxonomy, according to a hypothetical nomenclatural system based on bidirectional ostension (see Dubois 2007a). Nomina of taxa are symbolized by letters and numbers. This system does not recognize eponyms. The fifteen nomina in *italics* are nomina the creation of which is required by the suppression of eponymy. In this system, 31 nomina are required to designate the 31 taxa recognized.

- Superfamilia A01
  - Familia *B01*
    - Subfamilia *B02*
      - Tribus *B04*
        - Subtribus *B08*
        - Subtribus A09
      - Tribus A05
        - Subtribus *B09*
        - Subtribus A10
    - Subfamilia A03
      - Tribus *B05*
        - Subtribus *B10*
        - Subtribus A11
      - Tribus A06
        - Subtribus *B11*
        - Subtribus A12
  - Familia A02
    - Subfamilia *B03*
      - Tribus *B06*
        - Subtribus *B12*
        - Subtribus A13
      - Tribus A07
        - Subtribus *B13*
        - Subtribus A14
    - Subfamilia A04
      - Tribus *B07*
        - Subtribus *B14*
        - Subtribus A15
      - Tribus A08
        - Subtribus *B15*
        - Subtribus A16

The problem of redundancy

Another criticism that has been raised against the use of ranks in zoological nomenclature is the problem of redundancy of taxa. In order to express nomenclaturally a taxonomy based on a cladistic hypothesis, two kinds of taxa require to be named (Dubois 2007a: 48–49): (1) all taxa including subordinate taxa referred to the same coordinate nomenclatural set; (2) all taxa which are parordinate to the latter, even if they do not include subordinate taxa of the same coordinate nomenclatural set. If the latter are not named, because this would be "redundant" for example with the nomen of the taxon of the next lower nominal-series, this results in having sister-taxa with different ranks, a nomenclature which does not convey any information about the hierarchical structure of taxonomy and therefore on cladistic relationships. Such *pseudoranked* nomenclatures (Dubois 2007a: 34) exist, and will be discussed below.

Following a long tradition in zootaxonomy, Dubois (2006a: 217, 2007a: 50) and Kuntner & Agnarsson (2006) further suggested that, in all ergotaxonomies, a third kind of taxa should always be recognized and named, namely taxa belonging to the seven primary key ranks regnum, phylum, classis, ordo, familia, genus and species. The purpose of this proposal is that, once they have been studied, at least superficially, all organisms of the earth should be referred, sometimes provisionally, to a taxon of these seven ranks. Unlike in the two preceding cases, this is not meant at always expressing cladistic relationships (although in most cases it also plays this role). For example, a taxon T may be referred to the rank classis to express its parordination to another classis including many subordinate taxa at various ranks, but the class T may include only one species: in this case, naming also an order, a family and a genus for this species is indeed redundant, as it does not carry additional cladistic information. However, naming these taxa is important to comply with an important function of biological classifications, besides its "explanatory" one about evolution: that of providing a universal system of storage and retrieval of information (Cracraft 1974; Mayr 1982, 1997; Ashlock 1984; Benton 2000; Dubois 2005c). The existence of these seven "compulsory" ranks for all organisms would greatly facilitate the building of taxonomic and nomenclatural databases and the search for this information in the latter. In a database like the *Zoological Record*, a single hierarchy using only, but always, these seven ranks can be used for all organisms of the earth. In all cases of redundancy of nomina within a nominal-series (e.g., a single order in a class), Dubois (2004a, 2006a: 203) proposed to implement a modified Principle of Coordination, using the same eponym for both taxa, although in this case the hyponym has no getonym: this avoids the useless creation of a new nomen for the redundant subordinate taxon.

Dubois (2006a) provided a review of all ranks that have been used by zoologists in their taxonomic hierarchies in the past, and proposed a standardisation of this system for the whole of zoology, with 209 ranks including 9 primary key ranks (e.g., family), 10 secondary key ranks (e.g., phalanx) and 10 subsidiary ranks (e.g., subfamily) for all key ranks. This system should be largely sufficient to cover all the needs for future taxonomies. As a matter of fact, no real ergotaxonomy recognizes taxonomically all the nodes of a tree, as this would result in much too cumbersome and useless classifications. Despite this high number of potential ranks, which are sometimes quite useful as illustrated below in table 10, most ergotaxonomies only use about 10 to 20 ranks (see e.g. Minelli 1991). Among these, the 7 primary key ranks listed above should always be present. In order not to upset the tradition, the best known nomina, such as **AMPHIBIA** or **AVES**, should as far as possible be allocated to primary, not secondary or subsidiary ranks (Dubois 2006a: 224, 2007a: 50). This can usually be realized easily, provided some attention and care are given to this question, as ranks are fully arbitrary and can be fixed by arbitrary decision.

Pseudoranked nomenclatures

Although they have until now been considered by most taxonomists as far less informative than the Linnaean nomenclatural system (as clearly shown by the fact that the overwhelming majority of ergotaxonomies published nowadays follow the latter), unranked nomenclatural systems are theoretically justified and follow an internal logic. This is not the case however of nomenclatures that may be known as *pseudoranked* (Dubois 2007a: 34). Such nomenclatures have been used in recent years without any theoretical justifications by a few authors who remain, so to speak, half-way between Linnaean and unranked nomenclatures: they claim that ranks are useless or harmful, and they use unranked nomina (just designated as "taxa") for the most comprehensive taxa of their taxonomies, but they still use nomina referred to formal ranks for families, genera and species, and also sometimes for superfamilies, subfamilies and tribes. It is difficult to understand this intermediate attitude, except as a way to avoid seing "their" taxa named validly under the *Code* by others, as has happened already in a few amusing cases (e.g., Pleijel 1999, Muona 2006). Having two strings to their bows will allow such authors to see "their" new nomina survive at any rate in the future, whatever nomenclatural system ultimately wins the "war of nomenclature".

However, for such nomina to be available and valid under the *Code*, they should follow strictly the rules of the latter, which is not always the case. Several examples of similar situations are available in recent publications dealing with the **AMPHIBIA**. The cases of the nomenclatures of the salamander genus *Eurycea* by Hillis *et al.* (2001) and of the frog genus *Rana* by Hillis & Wilcox (2005) were discussed in detail elsewhere (Dubois 2006b,d, 2007b) and need not be so again here. Let us consider here three other recent works, those of Vieites *et al.* (2007), Frost *et al.* (2006) and Grant *et al.* (2007), which are good illustrations of this problem.

The nomenclature of the salamander family *PLETHODONTIDAE* recently proposed by Vieites *et al.* (2007: Online Supporting Information), shown here in table 5, is not acceptable under the *Code*, for two distinct reasons. First, it includes a rank (supergenus) which is not recognized by these rules. This rank, which would belong in the genus-series, would indeed be useful in zoological nomenclature (Dubois 2006b), but until the *Code* is modified to allow for the recognition of more than two ranks in this nominal-series, this rank should not be used, at least in a formal nomenclature following the *Code*. This nomenclature is also invalid under the *Code* for not respecting the Principle of Coordination. It is not possible to recognize a tribe *SPELERPINI* in the subfamily *HEMIDACTYLIINAE* without also recognizing at least one other tribe, the *HEMIDACTYLIINI*. A third, related, problem with this nomenclature, although this does not by itself make it invalid under the current *Code*, is that it is based on a partially resolved tree with polytomies where parordinate taxa are given different ranks. Let us just consider the four taxa immediately subordinate to the subfamily *HEMIDACTYLIINAE*. The nomenclature proposed fails to convey any cladistic information, as it is impossible to know, from the nomina of these taxa alone (i.e., without seeing a tree or a complete taxonomy of this family), that the genera *Batrachoseps* and *Hemidactylium*, the "supergenus" *Bolitoglossa* and the tribe *SPELERPINI* are the four members of an unresolved polytomy.

TABLE 5. The supraspecific nomenclature of the family *PLETHODONTIDAE* proposed by Vieites *et al.* (2007: Online Supporting Information). This nomenclature is not valid under the *Code*, which does not recognize a rank "supergenus", and which requires to follow the Principle of Coordination: if a tribe *SPELERPINI* is recognized in the *HEMIDACTYLIINAE*, the *Code* requires to recognize at least one other tribe, the *HEMIDACTYLIINI*. The use of ranks in this nomenclature is non-informative, as parordinate taxa are not afforded the same rank. In the table below, within each rank, taxa are presented in alphabetical order of their nomina, unlike in Vieites *et al.* (2007), who apparently followed a "phylogenetic" order (although these hypothesized cladistic relationships are not expressed in their nomenclature).

- Familia *PLETHODONTIDAE*
  - Subfamilia *HEMIDACTYLIINAE*
    - Genus *Batrachoseps*
    - Supergenus *Bolitoglossa*
      - Genus *Bolitoglossa*
      - Genus *Bradytriton*

    - Genus *Chiropterotriton*
    - Genus *Cryptotriton*
    - Genus *Dendrotriton*
    - Genus *Ixalotriton*
    - Genus *Lineatriton*
    - Genus *Nototriton*
    - Genus *Oedipina*
    - Genus *Parvimolge*
    - Genus *Pseudoeurycea*
    - Genus *Thorius*
  - Genus *Hemidactylium*
  - Tribus *SPELERPINI*
    - Genus *Eurycea*
    - Genus *Gyrinophilus*
    - Genus *Pseudotriton*
    - Genus *Stereochilus*
- Subfamilia *PLETHODONTINAE*
  - Genus *Aneides*
  - Supergenus *Desmognathus*
    - Genus *Desmognathus*
    - Genus *Phaeognathus*
  - Genus *Ensatina*
  - Supergenus *Hydromantes*
    - Genus *Atylodes*
    - Genus *Hydromantes*
    - Genus *Speleomantes*
  - Genus *Karsenia*
  - Genus *Plethodon*

TABLE 6. A possible supraspecific nomenclature of the family *PLETHODONTIDAE* following the taxonomy proposed by Vieites *et al.* (2007: Online Supporting Information) but respecting the *Code* and affording the same rank to parordinate taxa. Within each rank, taxa are presented in alphabetical order of their nomina. Nomina are followed by the date of their nomenclatural creation but not their authors, for reasons explained by Dubois (2008b). Tribal nomina between quotation marks are informal nomina without availability in zoological nomenclature. They are mentioned here just to show what the nomenclature of this family could be if the erection of these tribes was judged useful by specialists of this group. If it were the case, these nomina should be formally published with a diagnosis and a statement of intention of creating a new nomen, as, for the time being, no available nomina exist to name these tribes.

- Familia *PLETHODONTIDAE* 1850
  - Subfamilia *HEMIDACTYLIINAE* 1856
    - Tribus "*BATRACHOSEPINI*"
      - Genus *Batrachoseps* 1841
    - Tribus *BOLITOGLOSSINI* 1856
      - Genus *Bolitoglossa* 1854
      - Genus *Bradytriton* 1983
      - Genus *Chiropterotriton* 1944
      - Genus *Cryptotriton* 2000
      - Genus *Dendrotriton* 1983
      - Genus *Ixalotriton* 1989
      - Genus *Lineatriton* 1950
      - Genus *Nototriton* 1983
      - Genus *Oedipina* 1868
      - Genus *Parvimolge* 1944

Genus *Pseudoeurycea* 1944
Genus *Thorius* 1869
Tribus *HEMIDACTYLIINI* 1856
Genus *Hemidactylium* 1838
Tribus *SPELERPINI* 1859
Genus *Eurycea* 1822
Genus *Gyrinophilus* 1869
Genus *Pseudotriton* 1838
Genus *Stereochilus* 1869
Subfamilia *PLETHODONTINAE* 1850
Tribus "*ANEIDINI*"
Genus *Aneides* 1849
Tribus *DESMOGNATHINI* 1850
Genus *Desmognathus* 1850
Genus *Phaeognathus* 1961
Tribus *ENSATININI* 1850
Genus *Ensatina* 1850
Tribus "*HYDROMANTINI*"
Genus *Atylodes* 1868
Genus *Hydromantes* 1848
Genus *Speleomantes* 1984
Tribus "*KARSENIINI*"
Genus *Karsenia* 2005
Tribus *PLETHODONTINI* 1850
Genus *Plethodon* 1838

TABLE 7. A possible supraspecific nomenclature of the family *PLETHODONTIDAE* following the taxonomy proposed by Vieites *et al.* (2007: Online Supporting Information) but respecting the *Code* and affording the same rank to parordinate taxa. Within each rank, taxa are presented in alphabetical order of their nomina. Nomina are followed by the date of their nomenclatural creation but not their authors, for reasons explained by Dubois (2008b). In this taxonomy, no tribes are recognized in the subfamily *PLETHODONTINAE*, which results in recognizing subgenera in the genera *Desmognathus* and *Hydromantes*.

Familia *PLETHODONTIDAE* 1850
Subfamilia *HEMIDACTYLIINAE* 1856
Tribus "*BATRACHOSEPINI*"
Genus *Batrachoseps* 1841
Tribus *BOLITOGLOSSINI* 1856
Genus *Bolitoglossa* 1854
Genus *Bradytriton* 1983
Genus *Chiropterotriton* 1944
Genus *Cryptotriton* 2000
Genus *Dendrotriton* 1983
Genus *Ixalotriton* 1989
Genus *Lineatriton* 1950
Genus *Nototriton* 1983
Genus *Oedipina* 1868
Genus *Parvimolge* 1944
Genus *Pseudoeurycea* 1944
Genus *Thorius* 1869
Tribus *HEMIDACTYLIINI* 1856
Genus *Hemidactylium* 1838
Tribus *SPELERPINI* 1859

- Genus *Eurycea* 1822
- Genus *Gyrinophilus* 1869
- Genus *Pseudotriton* 1838
- Genus *Stereochilus* 1869

Subfamilia *PLETHODONTINAE* 1850
- Genus *Aneides* 1849
- Genus *Desmognathus* 1850
  - Subgenus *Desmognathus* 1850
  - Subgenus *Phaeognathus* 1961
- Genus *Ensatina* 1850
- Genus *Hydromantes* 1848
  - Subgenus *Atylodes* 1868
  - Subgenus *Hydromantes* 1848
  - Subgenus *Speleomantes* 1984
- Genus *Karsenia* 2005
- Genus *Plethodon* 1838

TABLE 8. A possible supraspecific nomenclature of the family *PLETHODONTIDAE* following the tree of figure 1 of Vieites *et al.* (2007: Online Supporting Information). This nomenclature respects the *Code* and affords the same rank to parordinate taxa. Within each rank, taxa are presented in alphabetical order of their nomina. Nomina are followed by the date of their nomenclatural creation but not their authors, for reasons explained by Dubois (2008b). Family-series nomina between quotation marks are informal nomina without availability in zoological nomenclature. They are mentioned here just to show what the nomenclature of this family could be if the erection of these taxa was judged useful by specialists of this group. If it were the case, these nomina should be formally published with a diagnosis and a statement of intention of creating a new nomen, as, for the time being, no available nomina exist to name these taxa. For the subtribus "*PSEUDOTRINONINA*", the nomen *MYCETOGLOSSINA* Bonaparte, 1850 would have been available, if it had not been "suppressed" (invalidated) by ICZN (Anonymous 1997). The family-series ranks below subtribe and their endings follow the proposals of Dubois (2006a). If the genera *Atylodes* and *Speleomantes* were to be downgraded to the rank of subgenera of a single genus, the latter ought to bear the nomen *Speleomantes* for the reasons given by Crochet (2007).

Familia *PLETHODONTIDAE* 1850
- Subfamilia *HEMIDACTYLIINAE* 1856
  - Tribus *HEMIDACTYLIINI* 1856
    - Subtribus *BOLITOGLOSSINA* 1856
      - Infratribus "*BATRACHOSEPITA*"
        - Genus *Batrachoseps* 1841
      - Infratribus *BOLITOGLOSSITA* 1856
        - Genus *Bolitoglossa* 1854
        - Genus *Bradytriton* 1983
        - Genus *Chiropterotriton* 1944
        - Genus *Cryptotriton* 2000
        - Genus *Dendrotriton* 1983
        - Genus *Ixalotriton* 1989
        - Genus *Lineatriton* 1950
        - Genus *Nototriton* 1983
        - Genus *Oedipina* 1868
        - Genus *Parvimolge* 1944
        - Genus *Pseudoerycea* 1944
        - Genus *Thorius* 1869
    - Subtribus *HEMIDACTYLIINA* 1856
      - Genus *Hemidactylium* 1838
  - Tribus *SPELERPINI* 1859
    - Subtribus "*PSEUDOTRINONINA*"

- Infratribus “*GYRINOPHILITA*”
  - Genus *Gyrinophilus* 1869
- Infratribus “*PSEUDOTRITONITA*”
  - Genus *Pseudotriton* 1838
  - Genus *Stereochilus* 1869
- Subtribus *SPELERPINA* 1859
  - Genus *Eurycea* 1822
- Subfamilia *PLETHODONTINAE* 1850
  - Tribus “*HYDROMANTINI*”
    - Subtribus “*HYDROMANTINA*”
      - Genus *Hydromantes* 1848
      - Genus *Speleomantes* 1984
        - Subgenus *Atylodes* 1868
        - Subgenus *Speleomantes* 1984
    - Subtribus “*KARSENIINA*”
      - Genus *Karsenia* 2005
  - Tribus *PLETHODONTINI* 1850
    - Subtribus *DESMOGNATHINA* 1850
      - Infratribus *DESMOGNATHITA* 1850
        - Clanus “*ANEIDITOI*”
          - Genus *Aneides* 1849
        - Clanus *DESMOGNATHITOI* 1850
          - Genus *Desmognathus* 1850
          - Genus *Phaeognathus* 1961
      - Infratribus *ENSATINITA* 1850
        - Genus *Ensatina* 1850
    - Subtribus *PLETHODONTINA* 1850
      - Genus *Plethodon* 1838

There would be not one, but several ways to reconcile the ergotaxonomy adopted by Vieites *et al.* (2007) with a nomenclature respecting the *Code* and providing cladistic information through the use of ranks. This uncertainty is not problematic, as it is due to the fact that ranks are just arbitrary tools that carry by themselves no information on the taxa, their characters, their divergence or other non-cladistic data, but only information on the hierarchical structure of the ergotaxonomy and hence on the cladistic hypothesis adopted. Tables 6 and 7 present two possible nomenclatures for this family following the ergotaxonomy of Vieites *et al.* (2007). In the nomenclature of table 6, all genera afforded the rank genus by these authors are maintained at this rank, but then this compels to recognize several additional tribes to respect the taxonomic structure adopted and the rank equivalence between parordinates. Table 7 presents the same taxonomy with a different nomenclature, where the first rank subordinate to subfamily in the *PLETHODONTINAE* is genus, which obliges to downgrade five “genera” to the rank subgenus. Both taxonomies of tables 6 and 7 are *Code*-compliant and carry exactly the same cladistic information.

Interestingly, in their presentation of their taxonomy of the subfamily *HEMIDACTYLIINAE*, Vieites *et al.* (2007) did not follow the alphabetical order of the nomina of the taxa. They presented the taxa under the following succession: *Hemidactylium*, *Batrachoseps*, *Bolitoglossa* and *SPELERPINI*. Although they did not explain their reason for doing so, this is probably because they meant to express cladistic relationships through this succession. This is actually a common way of listing taxa in zoological monographs, revisions, etc. As a matter of fact, in the tree of their figure 1, their *SPELERPINI* appear as the sister-group of a group including the other three taxa, and, among the latter, their genus *Hemidactylium* appears as the sister-group of the group composed of their genus *Batrachoseps* and their supergenus *Bolitoglossa*. However, this expression of hypothesized cladistic relationships through the order of presentation of taxa in a list or table is highly confusing and ambiguous (it is not even quite clear if this was indeed the intention of the authors!). The only way to express clearly a cladistic hypothesis into a taxonomy using formal nomenclatural ranks like genus, tribe or subfamily is through the use of different ranks for superordinate and subordinate taxa, and the same rank for parordinate taxa.

Any taxonomist who uses a tree as a working hypothesis for building a taxonomy has two possibilities. The first one is to accept the whole tree as valid and to express all nodes through recognizing a new taxon for each of them, following a hierarchy of nomenclatural ranks for successive branchings. The other possibility is to recognize taxonomically and nomenclaturally only some nodes, leaving some unresolved polytomies. This may be due to doubts on the validity of the tree (e.g., because of medium or low values of Bayesian, bootstrap or other indices), or to a decision to use only a few ranks in order to have a simpler and "lighter" taxonomy and nomenclature. This choice is entirely in the hands of the author, and does not depend in any way on nomenclatural rules. However, once a choice has been made between these possibilities, the resulting taxonomy and nomenclature should not be ambiguous.

In their taxonomy of the *PLETHODONTIDAE*, Vieites *et al.* (2007) decided not to recognize taxonomically all the nodes of their tree, which is their full right. But, then, this taxonomy leaves some polytomies unresolved and this should be reflected in the nomenclature, as is the case e.g. in the figures 6 and 7 here. Another possibility would have been to recognize more taxa and ranks, in order to follow more closely the cladistic hypothesis of their figure 1. One possible way of doing so is shown here in figure 8. This is not meant to support this ergotaxonomy here, but to show that it is always possible to build a meaningful taxonomy and nomenclature on the basis of a given cladistic hypothesis. Many more unknown species of *PLETHODONTIDAE* remain to be discovered, and much more information remains to be obtained from the salamanders of this group, so that the taxonomy of the latter we have in 2008 is certainly not the "final word" on this question and further changes may be expected in the future: this is the normal way in which taxonomy evolves and there is nothing worrying about this. But, at any time during the taxonomic history of a group, taxonomists should care about producing well built and clear ergotaxonomies, with rigorous nomenclatures, providing unambiguous information on the cladistic hypotheses they accept as valid at this given stage of research.

A last interesting comment regarding this nomenclature is that, although it does not follow a strictly ranked taxonomy, it uses ranks, and in a way that suggests that ranks are credited with a "value" and a "meaning" by themselves—although the fact that this belief is unwarranted is precisely the main reason given by most authors for not using ranks! Some genera appear as parordinate to clusters of genera, so that, in this nomenclature, the rank genus does not convey any cladistic message. But then, different nomenclatural ranks are afforded to the two parordinate clusters of genera recognized in the subfamily *HEMIDACTYLIINAE*: "supergenus" and tribe. No explanation for this discrepancy is provided. As in both cases there is only one rank between subfamily and genus, one would expect to see these two generic clusters afforded the same rank, either "supergenus" or tribe. Why isn't it the case? One possible explanation could be that reinstating the nomen *Atylodes* as a valid generic nomen may have been used as a transitional step in order to provide this nomen with some "usage", making it possible later to synonymize the nomen *Speleomantes* with it and to nullify the nomenclatural correction of Crochet (2007) to the invalid nomenclature of Wake *et al.* (2005). If this is not the case, then the only possible reason that can be thought of to explain this unbalanced nomenclature is that the *SPELERPINI* were considered as "more divergent" from the other genera of the subfamily than the "supergenus *Hydromantes*". This would suggest that ranks, which were not used to convey cladistic information, can convey phenetic information on "the importance of divergence" between taxa, therefore reinstating a belief in ranks having a "meaning" *by themselves*, distinct from that of providing information on the hierarchical structure of the taxonomy and therefore of the tree used as a basis for the latter. Therefore, this pseudoranked nomenclature falls fully into the main criticism raised by several recent authors against the use of ranks: considering the latter somewhat "equivalent" from one group to an other.

In fact, the same tendency can be observed in several other recent pseudoranked nomenclatures. Another good example is provided by the nomenclature used by Frost *et al.* (2006) in their ergotaxonomy of the **AMPHIBIA**. As discussed elsewhere already (Dubois 2007a: 34), this nomenclature is pseudoranked because, in many occasions, different ranks are afforded to parordinate taxa. It is difficult to understand the rationale for allocating ranks to taxa in this nomenclature. At first look, one could think that it a simple matter of progressive incrementation of levels above genus. Taxa could simply be given successive ranks when going upwards in the hierarchy: subfamily, family, superfamily, then various levels of unranked "taxa". This is not the case, however, because the hierarchy of ranks used above genus in this nomenclature is different from one group to another. Although all genera in this ergotaxonomy are referred to families, the ranks subfamily and superfamily are not used consistently: in some cases, genera are directly referred to a family and the latter to a "taxon", whereas in other cases the ranks subfamily or superfamily, or both, are interpolated. Here again, the only possible explanation seems to be that subfamilies are viewed as "less divergent" than families, and superfamilies "more divergent" than families, hence giving credit to the idea that ranks are meaningful by themselves and somewhat "equivalent" by some mysterious criteria.

Such problems are present throughout the ergotaxonomy of Frost *et al.* (2006). To save space, it will be enough to illustrate them with an extract of this classification, dealing with their "taxon **HYLOIDES**" (table 9). The purpose here, as in the case studied above, is not to challenge or even discuss their taxonomy, but to examine the nomenclature used to express this taxonomy. Table 9 shows clearly that in many cases parordinate taxa are given different ranks, and are often even referred to different nominal-series. In some cases, this nomenclature also does not eliminate completely the so-called "redundant taxa": the families *HEMIPHRACTIDAE* and *THOROPIDAE* and the subfamilies *PELODRYADINAE*, *TELMATOBIINAE* and *ALLOPHRYNINAE* are redundant with their unique genera (other similar cases exist in other parts of their ergotaxonomy that are not examined here). Therefore this argument is not valid to explain why they did not follow a Linnaean ranked taxonomy, at least for all taxa below the class-series. This nomenclature is as poorly informative as that of the preceding example. Here also, there would be many ways of expressing nomenclaturally the cladistic relationships on which the ergotaxonomy is based, and table 10 provides only one of them. In this table, the choice was made, following the example of the ergotaxonomy of **AMPHIBIA** of Dubois (2005d), to use only family-series nomina above the rank genus. This does not mean that, in the end, class-series nomina will not have to be used for the higher nomenclature of **AMPHIBIA**, but time is clearly not ripe for this. Frost *et al.* (2006) ignored some existing class-series nomina and therefore proposed new nomina for taxa that had already nomina (see e.g. Dubois & Ohler 2008). They did not follow rigorous or even clear rules for the allocation of nomina to higher taxa (using sometimes original extension or intension, sometimes "tradition", sometimes opinions and tastes) and therefore had a lax concept of synonymy for class-series nomina, etc. Consequently, several of their nomina would have to be changed if their taxa had to be named in the nominal class-series. Developing this here would be beyond the scope of the present work, and, for more simplicity, only family-series nomina are used in the suprageneric nomenclature of table 10. This nomenclature is fully informative by itself about the cladistic hypothesis retained by Frost *et al.* (2006) to build their taxonomy. It makes use of 12 distinct ranks in the family-series, and even more could be used if needed. Because of the Principle of Coordination, many of these nomina are eponyms and are used under different morphonyms at different ranks. These different spellings allow to distinguish between them and to identify immediately the getonyms by their endings. Such a nomenclature is much more informative about the status of nomina and taxa than that of the pseudoranked nomenclature used by Frost *et al.* (2006).

TABLE 9. The suprageneric nomenclature of the “taxon **HYLOIDES**” proposed by Frost *et al.* (2006). Note that, according to the nomenclatural rules proposed by Dubois (2004a, 2005b,e, 2006a,c), the nomen used for the latter taxon is invalid, being a junior homonym of several other class-series nomina (see Kuhn 1967); the same is true of the nomen of their “taxon **RANOIDES**”. In the table below, within each rank, taxa are presented in alphabetical order of their nomina, unlike in Frost *et al.* (2006), who apparently followed a “phylogenetic” order (not expressed in their nomenclature). Nomina are followed by the date of their nomenclatural creation but not their authors, for reasons explained by Dubois (2008b). Shortly after publication of this nomenclature, several parts of it were modified by Grant *et al.* (2006).

- Taxon **HYLOIDES** 2006
  - Taxon **NOTOGEANURA** 2006
    - Taxon **AUSTRALOBATRACHIA** 2006
      - Familia *BATRACHOPHRYNIDAE* 1875
        - 3 genera
      - Superfamilia *MYOBATRACHOIDEA* 1850
        - Familia *LIMNODYNASTIDAE* 1971
          - 8 genera
        - Familia *MYOBATRACHIDAE* 1850
          - 13 genera
    - Taxon **NOBLEOBATRACHIA** 2006
      - Familia *HEMIPHRACTIDAE* 1862
        - 1 genus
      - Taxon **MERIDIANURA** 2006
        - Familia *BRACHYCEPHALIDAE* 1858
          - 15 genera
        - Taxon **CLADOPHRYNIA** 2006
          - Familia *CRYPTOBRANCHIDAE* 2006
            - 2 genera
          - Taxon **TINCTANURA** 2006
            - Familia *AMPHIGNATHODONTIDAE* 1882
              - 2 genera
            - Taxon **ATHESPHATANURA** 2006
              - Familia *HYLIDAE* 1815
                - Subfamilia *HYLINAE* 1815
                  - 38 genera
                - Subfamilia *PELODRYADINAE* 1858
                  - 1 genus
                - Subfamilia *PHYLLOMEDUSINAE* 1858
                  - 7 genera
              - Taxon **LEPTODACTYLIFORMES** 2006
                - Taxon **CHTHONOBATRACHIA** 2006
                  - Familia *CERATOPHRYIDAE* 1838
                    - Subfamilia *CERATOPHRYINAE* 1838
                      - 6 genera
                    - Subfamilia *TELMATOBIINAE* 1843
                      - 1 genus
                  - Taxon **HESTICOBATRACHIA** 2006
                    - Taxon **AGASTOROPHRYNIA** 2006
                      - Familia *BUFONIDAE* 1825
                        - 48 genera
                      - Superfamilia *DENDROBATOIDEA* 1850
                        - Familia *DENDROBATIDAE* 1850
                          - 11 genera
                        - Familia *THOROPIDAE* 2006
                          - 1 genus

                    - Familia *CYCLORAMPHIDAE* 1850
                      - Subfamilia *CYCLORAMPHINAE* 1850
                        - 11 genera
                      - Subfamilia *HYLODINAE* 1858
                        - 3 genera
                - Taxon **DIPHYABATRACHIA** 2006
                  - Familia *CENTROLENIDAE* 1951
                    - Subfamilia *ALLOPHRYNINAE* 1978
                      - 1 genus
                    - Subfamilia *CENTROLENINAE* 1951
                      - 3 genera
                  - Familia *LEPTODACTYLIDAE* 1838
                    - 11 genera
  - Familia *SOOGLOSSIDAE* 1931
    - 2 genera

TABLE 10. A possible suprageneric nomenclature of the "taxon **HYLOIDES**" of Frost *et al.* (2006) using only family-series nomina and following the rules of the *Code*. In the table below, within each rank, taxa are presented in the same order as in table 9, to facilitate comparisons. Nomina are followed by the date of their nomenclatural creation but not their authors, for reasons explained by Dubois (2008b).

- Anofamilia *HYLAIDAI* 1815
  - Hyperfamilia *HYLAIDIA* 1815
    - Epifamilia *MYOBATRACHOIDIA* 1850
      - Superfamilia *BATRACHOPHRYNOIDEA* 1875
        - Familia *BATRACHOPHRYNIDAE* 1875
          - 3 genera
      - Superfamilia *MYOBATRACHOIDEA* 1850
        - Familia *LIMNODYNASTIDAE* 1971
          - 8 genera
        - Familia *MYOBATRACHIDAE* 1850
          - 13 genera
    - Epifamilia *HYLOIDIA* 1815
      - Superfamilia *HEMIPHRACTOIDEA* 1862
        - Familia *HEMIPHRACTIDAE* 1862
          - 1 genus
      - Superfamilia *HYLOIDIA* 1815
        - Familia *BRACHYCEPHALIDAE* 1858
          - 15 genera
        - Familia *HYLIDAE* 1815
          - Subfamilia *CRYPTOBRANCHINAE* 2006
            - 2 genera
          - Subfamilia *HYLINAE* 1815
            - Infrafamilia *AMPHIGNATHODONTINEI* 1882
              - 2 genera
            - Infrafamilia *HYLINEI* 1815
              - Tribus *HYLINI* 1815
                - Subtribus *HYLINA* 1815
                  - 38 genera
                - Subtribus *PELODRYADINA* 1858
                  - 1 genus
                - Subtribus *PHYLLOMEDUSINA* 1858
                  - 7 genera

- Tribus *BUFONINI* 1825
  - Subtribus *BUFONINA* 1825
    - Infratribus *CERATOPHRYITA* 1838
      - Clanus *CERATOPHRYITOI* 1838
        - 6 genera
      - Clanus *TELMATOBIITOI* 1843
        - 1 genus
    - Infratribus *BUFONITA* 1825
      - Clanus *BUFONITOI* 1825
        - Subclanus *BUFONILOI* 1825
          - 48 genera
        - Subclanus *DENDROBATILOI* 1850
          - Infraclanus *DENDROBATISOI* 1850
            - 11 genera
          - Infraclanus *THOROPISOI* 2006
            - 1 genus
      - Clanus *CYCLORAMPHITOI* 1850
        - Subclanus *CYCLORAMPHILOI* 1850
          - 11 genera
        - Subclanus *HYLODILOI* 1858
          - 3 genera
  - Subtribus *LEPTODACTYLINA* 1838
    - Infratribus *CENTROLENITA* 1951
      - Clanus *ALLOPHRYNITOI* 1978
        - 1 genus
      - Clanus *CENTROLENITOI* 1951
        - 3 genera
    - Infratribus *LEPTODACTYLITA* 1838
      - 11 genera
- Hyperfamilia *SOOGLOSSAIDIA* 1931
  - Familia *SOOGLOSSIDAE* 1931
    - 2 genera

Interestingly, only five months after publication of the work by Frost *et al.* (2006), the same research team published another work (Grant *et al.* 2006) which modified significantly the cladistic hypothesis and taxonomy of the "taxon **ATHESPHATANURA**" defined in the first work and presented here in table 9. As a result, a class-series nomen published on 15 March 2006 (**DIPHYABATRACHIA**) was invalidated on 15 August 2006 by the same authors, and several new class-series nomina were created. No doubt further changes can be expected in this ergotaxonomy in the coming years, as more species and genes, from well-identified vouchers, are analysed, as more morphological and other characters are taken into account, etc. (see e.g. Wiens 2007). This strongly supports the statement above that naming all these class-series taxa in these works was largely premature. Using only family-series nomina, like in table 10 here and in Dubois (2005d), provides a temporary, but non-ambiguous, nomenclature, during a period of intense research on the cladistic relationships among **AMPHIBIA**. Family-series nomina follow the Principle of Coordination, so they need far fewer nomina than class-series nomina to express the same relationships: whereas the suprageneric nomenclature of table 9 uses 34 nomina, that of table 10 uses only 21 distinct nomina, including 7 eponyms, for exactly the same taxonomy, hence sparing 38 % of the nomina. In the future, whenever this ergotaxonomy is changed, epinyms and hyponyms can easily be abandoned, without having to store these morphonyms in synonymies and online nomenclatural databases. In contrast, all the nomina created by Frost *et al.* (2006), some of which were considered valid by their own authors only for five months, will have to be stored permanently in such databases. When the present period of intense research is over, and when cladistic relationships among **AMPHIBIA** are more consensual and stable, it will be time to provide a class-series nomenclature for these animals.

A nomenclature like that shown in table 10 is complex, as it uses many ranks and similar nomina with different endings. Such a nomenclature is not meant to be used daily by taxonomists, and is of little interest to non-taxonomists. When dealing with a species, in most cases the latter only need to know its generic and specific nomen, and sometimes its familial allocation. In this respect, the nomenclature of table 10 is highly informative, as it places many taxa, previously referred to several families, into a single family *HYLIDAE*. The latter is by no way equivalent to the traditional family *HYLIDAE* in the batrachological literature, but is a very large group that encompasses several of the former families of anurans. For examples, the two families *HYLIDAE* and *BUFONIDAE* had been recognized as taxa of the same rank in all amphibian classifications since Gray (1825), which suggests that they had been considered more or less "equivalent" in phenetic terms, but, according to Frost *et al.*'s (2006) taxonomy, these two taxa now appear in table 10 as just two subsets at different ranks (tribe *HYLINI* and subclan *BUFONILOI*) of a much larger unit, along with various other groups. Keeping the same rank family for both, as done by Frost *et al.* (2006) themselves (table 9), obscures this message. Of course, the rank family in the nomenclature of table 10 is fully arbitrary, and this rank could well be moved upwards or downwards in the scale, but then all other ranks would have to follow and the relations of subordination and parordination between taxa would remain the same. At any rate, if the cladistic relationships and the taxonomy presented by Frost *et al.* (2006) are accepted as valid, keeping the traditional *HYLIDAE* and the *BUFONIDAE* as two families is as misleading and illogical as keeping the **REPTILIA** and the **AVES** as two classes: in any taxonomy supposed to reflect cladistic relationships, these latter two taxa can be retained, but at different ranks, e.g., classis for the former and phalanx for the latter (Dubois 2006a: 193).

Discussion: from phylogenetic taxonomy to hierarchical nomenclature

Reasons have been given above and elsewhere (Knox 1998; Dubois 2005c, 2007a) for preferring a hierarchical taxonomic and nomenclatural system to a non-hierarchical one. Nominal-series and ranks provide an efficient way to express nomenclaturally the hierarchical organisation of the taxonomy. In Linnaean nomenclature, the way nomenclature is used to express the taxonomy is regulated by precise and stringent rules, which leave no space for "interpretations", "opinions" or "tastes". These rules require to follow three steps, the three "storeys of the nomenclatural house" (Dubois 2005a–c,e), to establish the valid nomen of a taxon under a given ergotaxonomy. *Availability* of nomina under the *Code* requires following some simple but stringent rules. *Allocation* of a nomen to a taxon is made by (1) its *onomatophore* in all cases and (2) the *Principle of Coordination* in all cases where the ergotaxonomy uses more than one rank in the *coordinate nomenclatural set* considered. Finally, the *validity* of a nomen to designate a given taxon is usually established automatically by the Principle of Priority, and only in a few cases by recourse to "usage" or by a vote of ICZN.

Once again, nomenclature is not taxonomy. Whereas taxonomy defines taxa, nomenclature does not: it only allocates and validates nomina for the designation of a given taxon in a given ergotaxonomy. The same nomen can have different meanings in different taxonomies (*astatonymy*) or at different ranks in the same taxonomy (*eponymy*). To understand a cladistic hypothesis from a taxonomy, much more important than the nomina themselves are the relations between nomina as shown by the ranks: the relations of eponymy and getonymy are highly informative regarding phylogeny.

An ergotaxonomy without a nomenclature cannot be communicated easily, and a nomenclature makes sense only by reference to an ergotaxonomy. As different taxonomic paradigms are used by different authors, the relation between an ergotaxonomy and a nomenclature has to rely on objective criteria (the onomatophores) and on criteria that rely on the internal structure of the nomenclatural hierarchy (relations of eponymy, getonymy and telonymy).

The combination of a taxonomic paradigm with the partly polysemic ostensional system of the *Code* provides a hierarchical nomenclature that reflects through its ranks the structure of the tree accepted as taxonomic hypothesis for the group, at a given stage of research. Within a given coordinate nomenclatural set, three kinds of taxa require to be named, the first two in order to express nomenclaturally the cladistic hypothesis used to build the ergotaxonomy, and the third one in order to have a fully efficient nomenclature for the storage and retrieval of taxonomic data: (1) all taxa including subordinate taxa referred to the same coordinate nomenclatural set; (2) all taxa which are parordinate to the latter, even if they do not include subordinate taxa of the same coordinate nomenclatural set; (3) if they were not named already for the first two reasons, all taxa that correspond to one or several of the seven primary key ranks regnum, phylum, classis, ordo, familia, genus and species. These three different reasons for naming taxa in a nomenclature devised in order to reflect a cladistic hypothesis are illustrated in figure 1 in Dubois (2007a: 49).

The taxonomic information and concepts on which an ergotaxonomy is based can be made clear by definitions that are given of the *taxa*, not of the *nomina*. Under a *phenetic* taxonomic paradigm, a taxon may be defined by a *diagnosis*, whereas a nomen is allocated to this taxon using its onomatophore and the Principle of Coordination. Under a *cladistic* paradigm, a taxon may be defined by a *cladognosis* (i.e., either an *apognosis* or a *caulognosis*, or both), but there is no difference in the way a nomen is allocated to this taxon: this is still through its onomatophore and the Principle of Coordination. The same applies to an ergotaxonomy following an *evolutionary* paradigm, i.e. recognizing homophyletic but not necessarily holophyletic taxa: a taxon may be defined by a combination of cladognosis and diagnosis, but its nomen remains attached to its taxon through onomatophore and coordination. Dubois (2007a: 60–68) provided the example of an ergotaxonomy in which taxa are defined both by cladognoses and diagnoses, whereas nomina are attached to taxa through the rules of the *Code*.

As we have seen, the hierarchical organisation of taxonomic information through nomenclatural ranks is very informative and useful. It is therefore strange that, unlike in botany, nomenclatural rules in zoology only apply to a portion of the nomenclatural hierarchy, from superfamily to subspecies. There exists in fact no theoretical or practical reason for the *Code* to limit the number of potential ranks, either outside the three nominal-series it recognizes, or also within these series (Dubois 2006b). This prevents universal, non-ambiguous and automatic nomenclature for all taxa that may be recognized by a taxonomist, and these limitations put the *Code* in a situation of inferiority relative to alternative nomenclatural proposals such as those, entitled “phylogenetic nomenclatures”, that have been published in the last two decades.

This problem exists at three levels in the nomenclatural hierarchy: (1) above the rank superfamily, nomenclatural rules for the class-series should be integrated into the *Code*; if these rules are well devised, this would be possible without threatening the tradition of use for well-known nomina of higher taxa (Dubois 2004a, 2005b,e, 2006a,c); (2) for lower nomenclature below the rank subspecies, nomenclatural rules for the variety-series should also be integrated into the *Code*, especially for use in phylogeographic analysis and for conservation biology purposes (Dubois 2006b); (3) within the three nominal-series recognized by the *Code*, no limitation should exist in the number of potential ranks that can be used by taxonomists, as is the case currently (above superfamily and below subtribe in the family-series, and above, between and below the two and four ranks recognized by the *Code*, respectively in the genus- and species-series); this would be useful for example to name taxa at several infrageneric and supraspecific ranks (Dubois 2006b,d, 2007b). Additionally, it would be useful to implement in the *Code* a few rules or, at least, recommendations, regarding the different kinds of ranks (primary and secondary key ranks, subsidiary ranks), and also the endings of the nomina at all ranks in the family-series. Detailed suggestions in these respects have been offered (Dubois 2006a).

If ICZN decides to incorporate these new nominal-series and ranks into the *Code*, it will be important to care for implementing rules that respect a basic feature of the current rules of the *Code*: the *nomenclatural founder effect* (Dubois 2005e). This means that the nomenclatural status of a nomen is fixed once and for all in the original publication where this nomen is created. This applies to its author, date, nominal-series of allocation, spelling and, above all, onomatophore. As the latter is the tool that allows objective, automatic, stable and universal allocation of the nomen to a taxon or several taxa (in polysemic nomenclatural systems), it is crucial that it cannot be changed in subsequent publications—even by its original author!

Nomenclatural rules in all nominal-series should be strict in not allowing any change in the onomatophore (or onomatophore and onomatostase in bidirectional ostensional systems) of a nomen, because if this were allowed it would open the Pandora's box of "emendations" and "redefinitions" of nomina, which may be a virtually endless process, as illustrated in the recent literature (e.g., Laurin & Anderson 2004 and references therein; Frost *et al.* 2006; Vidal & Hedges 2005; Martin & Benton 2008). In our special historical period, the century of extinctions, taxonomists have certainly more urgent matters to deal with than permanently "redefining" nomina that have been published one or two centuries ago! Allocation of nomina to taxa should be automatic and not liable to open discussions. Nomina should remain permanently attached to their original onomatophore (and onomatostase if relevant). If a nomen, given the rules of allocation of nomina to taxa, can be used for a taxon recognized in a recent ergotaxonomy, it must be kept. If it does not, a new nomen must be coined for the taxon, but an existing nomen should not be "redefined"!

Two exceptions only should be accepted to the nomenclatural founder effect: (1) whenever the original publication left some ambiguity regarding the onomatophore (e.g., for a species nomen, several "syntypes" belonging to different biological species, or, for a genus nomen, several "originally included species", now referred to different genera, without designation among them of a "type-species"), this ambiguity should be clarified by a *first-reviser action*—which then plays the role of nomenclatural founder effect; (2) whenever, because of the original onomatophore, strict application of the rules results in threatening a *sozonym* (Dubois 2005b–c), i.e., a *genuinely very well-known* nomen, used in many publications *outside the specialized field of systematics*, then ICZN should be entitled to use its Plenary Power to replace the original onomatophore by another one in order to solve this problem. In all other cases, no change in onomatophore should be allowed because otherwise nomenclatural chaos will soon be in order, as is currently the case in higher zoological nomenclature (Dubois 2005c, 2006a).

A final, but important, suggestion, may be offered here regarding the necessary changes that should be brought to the *Code* to avoid this almost bicentennial set of rules to be threatened by alternative nomenclatural systems (Dubois 2008a,e). One of the first step that was taken by the founders of this nomenclatural system (Strickland *et al.* 1843) was to draw a line of delimitation between authors following these rules, and those not following them. This step was the rejection outside the nomenclatural system of all publications that did not follow the Linnaean system of binominal nomenclature for species. This rule is still in vigour today, and allows rejecting as unavailable all nomina proposed under other rules (e.g. Muona 2006). The same could, and should in my opinion, be done today regarding publications that do not follow the Linnaean principle of a hierarchy of ranks. This would require some modifications in the *Code*. First of all, the *Code* should give clear *definitions of nomenclatural ranks*, contrasting them with taxonomic categories, and it should provide guidelines for their use in zoological nomenclature (Dubois 2007a: 54). It should make compulsory: (1) that in any nomenclature following the *Code*, two parordinate taxa be always given the same nomenclatural rank (a genus cannot be parordinate to a family), even if they do not include the same number of lower-ranked taxa; and (2) that a subordinate taxon cannot share the same rank as a taxon subordinate to it, or vice versa (a species cannot be included in a species, a genus in a genus, a family in a family). Such statements should be presented as *stringent rules*, not mere "recommendations".

I even suggest that the *Code* should go still one step further, by stating that any new nomen or nomenclatural act provided in a publication where this basic Linnaean use of nomenclatural hierarchy is not followed should be rejected as unavailable in zoological nomenclature—just like works that do not follow a binominal species nomenclature are rejected as unavailable under the *Code*. Such an act of *self-protection* of the *Code* against alternative nomenclatural systems and, what is perhaps worse, about half-way systems that try to be compatible with several non-miscible nomenclatural systems, would greatly clarify the matter by requiring from all taxonomists to choose which system they decide to follow. Nobody is obliged to adhere to the *Code*, but it should be clear to all readers of a taxonomic work whether its author adheres to it or not, and hence if its nomina or nomenclatural acts should be taken into account by taxonomists adhering to the *Code*. Such a clarification would certainly be very beneficial to the universality and efficiency of zoological nomenclature, at a time when zoologists need to concentrate their efforts on describing the vanishing biodiversity of our planet, not on producing new nomenclatural systems every two weeks.

Conclusion

Nomenclatural rules must be completely disconnected from taxonomic paradigms, i.e., they must be theory-free regarding taxonomy. A given nomenclature makes sense only within the frame of a given ergotaxonomic scheme. The request for "nomenclatural stability" sometimes presented to taxonomists amounts in fact to an anti-scientific plea for "taxonomic stability", i.e., for ignorance (Gaffney 1979; Dominguez & Wheeler 1997; Benton 2000). As long as taxonomy remains a living scientific discipline, taxonomic schemes will be permanently changing. At least, because of the taxonomic impediment, this will be so for many decades yet, and the request for "taxonomic stability" is a weapon against the discipline of taxonomy that should not be accepted by taxonomists or by other biologists (Dubois 1998, 2000a).

The current nomenclatural rules of the *Code* allow taxonomists to do their work well, and particularly to express cladistic hypotheses clearly and unambiguously under the form of hierarchical nomenclatures using onomatophores, nominal-series, ranks and eponymy. These rules should not be drastically modified, but they can and should greatly be improved, especially in order to draw a clear line between users of these rules and non-users.

Working taxonomists are a small and "endangered" group of scientists, and they bear on their shoulders the historical responsibility to try their best to discover as many as possible of the living species of our planet before they get extinct just before our eyes, in the indifference of most of our contemporaries. The main urgency for taxonomy is not to implement brand new nomenclatural rules, but to improve the existing ones in order to facilitate this work of inventory. The use of a clear methodology, with clear concepts expressed under a clear, precise, unambiguous terminology, for taxonomy and nomenclature, are liable to help them in this difficult task.

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