The splendid isolation of biological nomenclature

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Recent arguments against phylogenetic nomenclature (PN) rest on the assumption that, generally, consensus about the meaning of taxon names arises spontaneously. A brief historical review shows that this is not the case. Comparisons with other fields as diverse as physics, geology and geopolitics show that precision in the meaning of terms is essential to produce consensus, which is precisely the opposite as the avowed aims of rank-based nomenclature (RN). The difficulty in reaching consensus increases with the weight of tradition and decreases with the number of objective tests to falsify competing theories. In both respects, biological nomenclature is handicapped because the weight of tradition is extreme and rules of nomenclature cannot be discovered in nature. These facts may explain the difficulty in reaching consensus on the most appropriate system of nomenclature for the 21st century. Therefore, comparisons between RN and PN should focus on minimal taxonomic stability, rather than realized or maximal stability. A four-taxon example shows that in this respect, PN vastly outperforms RN. Opponents of PN often predict that implementation of PN will cause considerable confusion. A comparison with computer science shows that confusion is often associated with progress, and may be unavoidable for nomenclature to prosper in the new millennium.

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Introduction

A vigorous and passionate debate in current systematics centres on the controversy triggered by the introduction of phylogenetic nomenclature (PN) and recent progress towards the implementation of the PhyloCode (Cantino 2000; Bryant & Cantino 2002; Laurin *et al*. 2005, 2006; Pickett 2005; Polaszek & Wilson 2005). Recently, Lee & Skinner (2007) pointed out that many discussions of this topic are buried in lengthy or technical papers, and may thus not be fully accessible to many systematists. This may explain, to a certain extent, why recent exchanges on this topic have not resulted in much consensus. This may be a time to step back and put this debate into a broader perspective, to compare developments of biological nomenclature with those in other sciences and even fields as remote as geography and politics. Such comparisons may highlight in a vivid and accessible manner a few peculiarities of biological nomenclature and shed new light on this debate. This is all the more necessary because recent exchanges in the literature suggest that the two camps are talking past each other. Proponents of rank-based nomenclature (RN) have claimed that RN leads to greater taxonomic stability because of the flexibility in this system (Benton 2007), whereas proponents of PN claim that RN fails to delimit taxa objectively and precisely, and thus causes much taxonomic instability. The very same properties of RN and PN have been argued to have opposite effects by proponents of the two parties. Since nearly a decade of debate on this topic has failed to produce a consensus or even to convert significant numbers of members of either camp, a fresh, more global perspective might be useful.

The arguments of proponents of RN rest on two key assumptions. The first is that the systematic community can and will spontaneously settle on a consensus about the choice of taxon names and the delimitation of taxa. The second is that, in such an idyllic world, the vague definitions (here taken as statements which allow recognition of boundaries of entities, or membership in classes) of taxon names (based on a rank and a type) are not a limitation but an advantage because the systematic community can keep the contents of taxa maximally stable by spontaneously settling on the delimitation that minimizes changes. An argument often presented against PN is that the presence of two competing systems (RN and PN) will only create confusion.

The purpose of this paper is to demonstrate that these arguments are, for several reasons, not convincing. First, the history of biological nomenclature fails to support the claim

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that consensus can, does or will spontaneously arise in most cases. Second, using examples from other fields and from history, I show that consensus on various topics involving definitions of terms is rarely achieved spontaneously in most fields, and is usually imposed by regulation or recorded in authoritative compilations. History also shows that humans have tried to precisely delimit various kinds of entities for at least a few thousand years. Thus, the deliberate lack of delimitation of taxa in RN seems to run counter to most or all other fields, where we usually try to make the meaning of words, and especially technical terms, as precise as possible. In contrast, proponents of RN deliberately avoid this: 'Nomenclature does not determine the inclusiveness or exclusiveness of any taxon, nor the rank to be accorded to any assemblage of animals, but, rather, provides the name that is to be used for a taxon whatever taxonomic limits and rank are given to it.' (principle 2 of the Introduction of the fourth edition of the ICZN [International Commission on Zoological Nomenclature 1999]). Third, the logical conclusion of this line of argument is that the relative virtues of RN and PN should be assessed not by the maximal stability that they could provide if consensus were spontaneously achieved (as this is unlikely), but by the minimal stability that will result from the use of nomenclature if such a consensus fails to arise. This paper shows, through a very simple example with four terminal taxa (species) that in terms of minimal stability PN is far better than RN. Fourth, through an analogy with computer science, I show that the kind of confusion that can be generated by the presence of two nomenclatural systems is often associated with progress. This paper concludes with responses to claims about the usefulness of Linnean ranks, a discussion about the relationship between taxonomy (which deals with representation of relationships between organisms, i.e. identification of taxa) and nomenclature (which consists in naming taxa, that is, determining to which taxa names pertain), and a discussion of prospects for biological nomenclature.

The present article should not be taken to imply that all systematists are unconditional supporters of PN or RN; many have not explicitly taken sides, and some have proposed a mixed approach. For instance, Kuntner & Agnarsson (2006) proposed to retain binomial names for species and to retain the main Linnean ranks (species, genus, family, order, class, phylum and kingdom, but not ranks created using prefixes such as superorder), but to use phylogenetic definitions for all clade names. A few of these proposals have been incorporated into PN to the extent that it was decided in the second meeting of the International Society for Phylogenetic Nomenclature to let the RN codes rule species names (Laurin & Cantino 2007). However, the suggestion that 'in practice, it may be simpler to adjust the existing codes by implementing in them the best elements of the PC [PhyloCode]' (Kuntner & Agnarsson 2006: 781) disregards the fact that all proposals in that direction submitted to the governing bodies of the RN codes have been either rejected or ignored. For instance, J. Gauthier suggested to two members of the ICZN to apply formal taxonomic names ruled by the zoological code only to clades (at least for supraspecific taxa) and to abandon Linnean ranks, but these two members promptly rejected these ideas (J. Gauthier, pers. comm. dated 2 November 2007). Similarly, the proposal to erect rankless suprageneric names (typified or not, and potentially delimited using PN) under the botanical code (Reveal 1998) was considered (proposal H for modification of Article 16 of the botanical code), along with many other proposed amendments (Greuter & Hawksworth 1999: 91), but was rejected by 68% of the nomenclatural section of the subsequent International Botanical Congress (Barrie & Greuter 1999: 779). Even less revolutionary suggestions to amend the International Code of Zoological Nomenclature to extend the principle of priority above the superfamily level (Dubois 2005a), to allow more ranks to be used in various nominal-series (called 'groups' under the RN codes, like the family group; Dubois 2006), or to use a single fixed diagnostic character to delimit taxa under the ICZN (Laurin 2005: 87) have not yet been commented or voted upon by the Commission, and many papers submitted in the last few years to the Bulletin of Zoological Nomenclature have been rejected, often without any reply from the Commission (Dubois 2005b: 423–424). Similarly, the suggestion that combined approaches in zoology and botany 'clearly circumvent the problem of nonmonophyly in a ranked system, while requiring minimal alterations of the existing codes' (Kuntner & Agnarsson 2006: 777) seems overly optimistic because the RN codes are based on ranks and it is not clear how they could be modified to deal with priority of phylogenetically defined names. Indeed, RN codes apply the principle of priority within ranks (botanical code) or within sets of coordinate ranks (zoological code), so it is not obvious how to deal with cases in which two names of different ranks refer to the same clade under the proposed mixed system, unless ranks, which are fundamental to the current RN codes, lose their role in these codes (in which case they would no longer be rank-based). Extensive rewriting and a fundamental shift in the basic approach of the RN codes (which deliberately avoid delimiting taxa; see above) would be required to achieve such a compromise. Thus, based on previous experience, the prospects of incorporating principles of PN in RN codes currently look rather bleak. Recent attempts at combining use of PN and RN codes simultaneously for clade names (Hillis & Wilcox 2005) highlight practical problems with this approach (Dubois 2007). These proposals to use hybrid systems will not be discussed further here because this is beyond the scope of this study and a thorough discussion of this topic would considerably lengthen this paper. To conclude, I suspect that PN and RN will coexist for some time and both will rule clade names (currently, there are no plans for a PN code for species names, so these will remain entirely in the realm of the RN codes, at least in the foreseeable future), until the scientific community is able to decide which of these two kinds of nomenclature is preferable.

Consensus about names, definitions and delimitation in RN: does it exist?

Consensus in the history of biological nomenclature

Benton (2007), Nixon *et al.* (2003) and others (Pickett 2005; Polaszek & Wilson 2005, etc.) argue that RN, as implemented in the ICZN (International Commission on Zoological Nomenclature 1999), yields maximal stability in taxon content because systematists spontaneously and consensually adjust this content whenever required by new discoveries (new phylogenies or new taxa). The very existence of codes of biological nomenclature suggests that this is not the case. In fact, if such consensus were spontaneously achieved, no code would be needed. The very first code of biological nomenclature, the Stricklandian code, was precisely proposed to try to reduce the taxonomic chaos which prevailed in the mid-19th century. This is clear in the introduction of that code (Strickland *et al.* 1842: 2), which states that the major problem in nomenclature was that 'when naturalists *are* agreed as to the characters and limits of an individual group or species, they still disagree in the appellations by which they distinguish it. A genus is often designated by three or four, and a species by twice that number of precisely equivalent synonyms; and in the absence of any rule on the subject, the naturalist is wholly at a loss what nomenclature to adopt' (emphasis in original).

More recent developments in biological nomenclature show that the same taxon name has been applied to several nested clades or partially overlapping paraphyletic taxa. These include, among many others, Mammalia (Rowe & Gauthier 1992), Anthracosauria (Laurin 1998) and Tetrapoda (Laurin 2002; Laurin & Anderson 2004). It could be argued that these names are above the family group rank and that, since the principle of priority does not apply to them, the ICZN cannot stabilize their usage. However, taxa of the rank of family, genus or species are not more stable. Examples of unstable taxonomy in cases in which the phylogeny is relatively stable abound and include, among others, haptodontine sphenacodontids (Currie 1979; Laurin 1993, 1994).

This sad situation should not surprise us because the ranks, on which the traditional (RN) codes are based, are purely artificial. As Ereshefsky (2002: 309) stated, 'they are ontologically empty designations'. Ranks were initially thought to be objective because, for Linnaeus, each rank reflected the plan of the Creator and could be recognized on the basis of different kinds of characters. For instance, the classes of angiosperms reflected the number and arrangement of stamens, whereas the orders generally reflected the number of pistils (Schmitz *et al.* 2007: 82). However, this practice did not persist long after Linnaeus; with acceptance that taxon characteristics are generated by evolution, Linnean categories are now devoid of the significance that their creator gave them, and no other justification replaced it.

Comparisons with other fields: definitions and consensus

Physics, chemistry and geology

Comparisons between the nomenclature of biology and those of other natural sciences are enlightening. In physics and chemistry, the elements are defined by the number of protons found in the nucleus of their atoms. This classification was proposed by Mendeleev in 1869, so it is hardly new, but it is based on a single, objective criterion which precisely delimits entities. For instance, lithium (Li) has three protons, sodium (Na) 11 and potassium (K) 19 (these elements belong to the same group, which possesses a single valence electron). The boundaries between each element are clearly defined and the meaning of these terms is unambiguous. Perhaps proponents of RN should try to convince chemists and physicists of the benefits of adopting a system of nomenclature in which Li sometimes refers to atoms with three protons, sometimes refers to atoms with 3 or 11 protons, and other times, refers to atoms with 3, 11 or 19 protons, and in which all these meanings are simultaneously and indefinitely valid. Consensus on the exact element denoted by the term would then need to emerge through spontaneous agreement. This would be analogous with the contents of taxa in terms of species under RN (see below). It could be objected that there are natural discontinuities between atom types, but incomplete knowledge of nature, extinction and selective fossilization have also created gaps which have been used to informally delimit taxa. A more important difference which must be recognized is that taxa, according to several authors, are individuals and historical entities, whereas atoms are classes or natural kinds and atemporal (Ereshefsky 2007). This distinction is important because natural kinds are defined by properties (typically intrinsic ones), whereas individuals do not necessarily have defining properties other than their relationships (which are extrinsic properties). However, not all authors share these points of view and some, instead, consider that taxa are natural kinds (Rieppel 2006), and many (perhaps most) proponents of RN who have criticized PN view taxa as natural kinds rather than individuals. Furthermore, from a practical perspective, the nature of taxa (individuals or natural kinds) does not matter much in PN, which is compatible with these two possible ontologies (Pleijel & Härlin 2004). Under PN, taxa can be considered individuals (which is the prevailing view among proponents of PN), or as classes defined by extrinsic properties (their relationships) composed of a single individual (de Queiroz 1992). However, Ereshefsky

(2007) has provided a strong case in favour of the individuality thesis, which is accepted here.

In geology, time units were initially defined on the basis of a type-section, which formed the etymological basis of the period name. For instance, the type-section of the Permian is near Perm, Russia, and that of the Devonian is in Devon, UK. In this respect, early geological nomenclature was similar to RN because time units were defined on the basis of a single type (section) and a rank (era, period, stage, etc.). However, the meaning of these ranks was not objectively defined (e.g. the amount of time ascribed to an 'era'). As a result, the relevant boundaries could not be objectively recognized, but relied on consensus. However, as in PN, this did not yield stability, as the Great Devonian Controversy attests (Rudwick 1985). Thus, it is no surprise that, more recently, geologists have moved from this type of nomenclature to one based on boundary stratotypes, which precisely delimit successive (rock and therefore) time units (Gradstein *et al*. 2004: 20–21). Thus, the limits between successive time units are objectively fixed on the basis of a real section, at a precise layer, rather than by an arbitrary rank (period, stage, etc.). This approach is more similar to PN than to RN, since boundaries are objectively and precisely fixed (which is deliberately avoided in RN; see above).

Geography and politics

Surprisingly, closer analogies with biological nomenclature can be drawn from geography and politics because countries, provinces and cities, like taxa, are often not clearly delimited by natural discontinuities, and like taxa, they evolve with time (Hilgemann & Kinder 1968). They are also spatiotemporally circumscribed, just like biological taxa. For instance, the borders of countries or empires change with time; they can divide (analogous with cladogenesis) or disappear by being absorbed by another geopolitical entity, peacefully or not (vaguely analogous to either extinction or hybridization, depending on the exact situation). Geopolitical entities (one of Linné's favourite comparisons, e.g. Linné 1766: 13) are also ranked; from the highest category to the lowest, we find (this list is not exclusive): empires, countries, provinces or states, districts, cities and neighbourhoods. It could even be argued that they have types: the capital city for provinces, countries and empires, and various governmental buildings for neighbourhoods. However, every analogy has its limits, and in the realm of geopolitics, the ranks of entities are more objective than Linnean categories. For instance, countries are independent entities with their own sets of laws; by contrast, entities of lower ranks, when they have their own laws, must ensure compatibility of these laws with the constitution and laws of the country to which they belong. There is no equivalent objective criterion to determine ranks in taxa, with the possible exception of the specific rank.

Historically, countries have often been delimited by natural boundaries when they exist and are located near borders between peoples. A few examples include the Rhine between France and Germany, the Amur river between Russia and China, the Rio Grande (called Rio Bravo del Norte by the Mexicans) between the US and Mexico, the Alps between Italy and countries which border it to the North (France, Switzerland, Austria and Slovenia), the Pyrenees between Spain and France, or the Himalayas between India and Tibet (now politically part of China). Many states are composed of an island or a series of islands which are thus naturally delimited from neighbouring states; a few examples include Japan, Madagascar and Sri Lanka.

Whenever such natural landmarks cannot be used, governments have gone to great lengths to clearly delimit the borders of their states and to defend them. For instance, between the western shore of Lake Superior and the Rocky Mountains, the border between Canada and the US extends along the 49th parallel (49° of latitude North) (Anonymous 1995: 178). In antique Mesopotamia, where natural borders were lacking, signalling posts were placed along the borders of neighbouring city-states, and the repeated move of such posts by members of a city-state to gain territory at the expense of another caused war between them, as shown by the Stele of the Vultures (2450 BCE), now in the Louvre (Bottéro 1994).

The equivalent of using RN in geography would be to define geographical entities by their rank and capital city (or some governmental building in the case of neighbourhoods), and not to try to set precise borders. For instance, Germany could be defined as the geographical entity of the rank 'country' with Berlin as its capital ('type'). I am aware of no government which would be satisfied with such a system. Synonymy of countries in this system would involve proposing — as the Nazis did in 1939 — that the boundaries of the country 'Germany' (as defined above) need to be reinterpreted and expanded to include areas currently recognized as entities of the same rank (i.e. other countries). In RN, synonymy or erection of new taxa within previously recognized taxa is routinely performed even when no new data are available. By contrast, synonymy of countries usually requires war because few countries willingly let themselves be absorbed into another. Similarly, declaring a new country usually requires or leads to violence, as the numerous separatists groups attest (ETA in Spain, IRA in Northern Ireland, PLO/Fatah and Hamas in Palestine, etc.), and in many instances, such moves aim at restoring the integrity of an earlier state. Fortunately, geographers and politicians have done a much better job at delimiting countries than systematists at delimiting taxa (at least until the advent of PN).

Objective criteria and consensus

History suggests that the difficulty in reaching consensus increases with the weight of tradition and decreases with the number of objective tests to falsify competing theories. This point is illustrated by the violence with which members of various religious factions fight each other. In Iraq, most of the violence is between Muslims (Sunnites and Shiites), rather than being directed at the foreign armed forces which have destabilized the country. Similarly, in Northern Ireland, Catholic and Protestant Christians have fought each other, and India separated into two countries (India for Hindus and Pakistan for Muslims) when gaining its independence (Hilgemann & Kinder 1968). Needless to say, the debates between these religious groups tend to rest not on rational arguments and facts, but on faith, tradition, and ultimately, personal preferences (to the extent that we choose the religion to which we belong, if any). On the contrary, the choices that these same people make in terms of the medicines or energy sources they use seldom gives rise to conflicts of a comparable intensity; yet, their practical and economic impact on the population of these countries can be far greater. This is because such choices are more heavily influenced by scientific evidence and less by belief and tradition.

Like other social phenomena, science is subject to this paradox, and topics on which few objective arguments apply are the most hotly debated. Fortunately, scientists rarely resort to physical violence, but similarly, the most acrimonious debates concern matters about which there is the least amount of data and the fewest objective criteria to decide between competing theories or methods. Biological nomenclature is a language for communicating about biodiversity, and consequently, facts do not fully prescribe rules of nomenclature, which cannot be discovered in nature. (However, the nested pattern of taxa created by evolution implies that some rules are more appropriate than others.) Furthermore, even within a system of nomenclature, the choice of names for taxa and initial taxon delimitation are arbitrary (although taxon delimitation is no longer arbitrary once its name has been defined, under PN). Even when a name is etymologically based on an apomorphy, such as Mammalia (mammary glands), Tetrapoda (four feet) and Anura (without tail), incomplete information about character evolution leaves ambiguity about the clade to which a given name should be applied if etymology were used as a criterion (no code requires this, in PN or RN). Furthermore, the choice of the apomorphy is subjective; for instance, Salientia (jump) can be used to designate the same clade as Anura, and both names can be treated as synonyms (Dubois 2005c). Alternatively, in PN (de Queiroz & Gauthier 1992; Cannatella & Hillis 1993; Laurin 1998; Pough *et al.* 2004: 65), and occasionally in RN (Duellman & Trueb 1986: 514), as well as outside both (Frost *et al.* 2006), Salientia has been used for a more inclusive clade than Anura and both have been given precise definitions, so the choice of names is no longer subjective, once they have been defined. Many taxon names are etymologically based on plesiomorphies; needless to say, in such cases, etymology does not help in determining to which clade they apply. A few examples include Caudata (tailed), Reptilia (crawling), Amphibia (with a double life, both in water, as larva, and on land, as adult; this is also an apomorphy, but one of part of Stegocephali, which persists today only in Amphibia), Anapsida (without arch, i.e. without a temporal fenestra) and many others. Thus, biological nomenclature is among the fields of science in which the fewest objective criteria can be used to settle differences of opinion, and as a consequence it is also one of the scientific fields which has produced the most passionate debates. It has also been 'slower in adopting novelties than other fields of biology', apparently 'due to tradition rather than sound scientific reasoning' (Kuntner & Agnarsson 2006: 776). This is exemplified by the preface of a recent edition of the botanical code (ICBN; the Saint Louis Code), which states that: 'We have, however, been saddened by the context in which these decisions took place. Passion in nomenclatural discussions is fine and (which is perhaps surprising with as dry a subject) has a solid tradition of long standing; but hatred has not. The Jacobine frenzy with which the Section was induced to eradicate all traces of registration from the Tokyo Code is we believe unprecedented. The refusal to listen to others, to let contradictory arguments be exposed and explained, has worried us deeply. With such a large and largely novel audience, nomenclature had a unique chance to prove itself a rational discipline. In this it has failed.' (Greuter *et al.* 2000: xvii–xviii). Given that such passionate discussions took place between practitioners of RN and concerned rather minor changes to the code compared to the introduction of PN, it is perhaps not surprising that the PhyloCode initiative has been qualified as 'pure folly' (Carpenter 2003) and 'a criminal operation against the study of biodiversity' (Dubois 2006: 825); these wordings are more reminiscent of passionate religious zeal than of constructive, objective scientific discourse. The statement that 'the PhyloCode operation might still be judged dispassionately if it had the decency to leave the current system of nomenclature alone' (Greuter 2004) corroborates this impression, since it amounts to admitting that at least some opponents of PN (and not the least prominent ones) do not judge the PhyloCode dispassionately. Fortunately, proponents of PN have never used such language, to my knowledge. I am not aware of similarly heated debates in physics or mathematics, or in similar fields where matters can be solved by using objective criteria.

Conclusions about consensus, definitions and delimitation

The previous discussion shows that our predecessors have tried since the greatest antiquity to define terms as precisely as possible, especially technical or legal terms, except in biological nomenclature (until the advent of PN). Thus, the rank-based codes appear to be in splendid isolation since they exhibit a stark contrast compared to most other scholarly enterprises. Indeed, it could be argued that taxon names are not really defined in RN because the definition of 'define' is 'mark out limits of' (Sykes 1982). This is precisely the opposite of the stated purpose of the ICZN, according to which '[n]omenclature does not determine the inclusiveness or exclusiveness of any taxon' (ICZN, Introduction, principle 2). The only explanation I can find for this is historical burden; RN has been around for so long that we are used to it, and many taxonomists want to keep it simply because it is familiar. However, the subjective component of RN may be partly responsible for the poor reputation and support that taxonomy enjoys in science, a situation which has worsened in the last decades, despite initiatives such as Partnerships for Enhancing Expertise in Taxonomy (PEET), which was designed by NSF to reduce the 'taxonomic impediment' (Agnarsson & Kuntner 2007).

Minimal taxonomic stability in RN and LN: an example

I call 'minimal taxonomic stability' the stability that will be automatically provided by a nomenclatural system, whether or not taxonomists spontaneously agree on choices of names of taxa or on their delimitation. This concept has not often been discussed because many previous discussions on this topic have not distinguished between the maximal stability (which could be achieved if all taxonomists agreed on matters not automatically enforced by the codes), which has seldom been reached (Currie 1979; Rowe & Gauthier 1992; Laurin 1998; Laurin & Anderson 2004), realized stability (or lack thereof), which has been achieved using RN and LN in the past, and minimal stability, which is automatically provided by the codes, as long as taxonomists abide by them.

Minimal taxonomic stability can be assessed using a simple example. Let us consider a phylogeny with four Operational Taxonomic Units (OTUs), often referred to as species, but sometimes, and more objectively, as LITUs, also known as Least Inclusive Taxonomic Units (Pleijel & Rouse 2003). A similar example with more taxa (six LITUs) was presented by Pleijel & Rouse (2003), but not all possible alternative taxonomies allowed by RN given the phylogeny were examined. Here, I explore all possible alternative taxonomies allowed by the two systems (RN and PN) given the same initial phylogeny, an initial taxonomy and nomenclature presented in the context of both systems, and the principle that only clades are named (which is inherent in PN but not in RN, although it is today widespread among users of RN as well). The minimal taxonomic stability is examined in two situations: one in which the phylogeny is stable (Fig. 1), and another in which it is not (Fig. 2).

Under RN, three higher taxa — two genera and a single family — are recognized by the taxonomist (Fig. 1A). Under PN (Fig. 1E), three node-based taxa with equivalent content are erected: O, P and Oidae, two of which have two specifiers (Oidae is defined on the basis of all four specifiers, although this is one of many options).

Let us first consider the case in which the phylogeny remains stable. Under RN, through subjective synonymy, one of the original genera (e.g. P) can be synonymized (Fig. 1B). By erecting new genera, three more taxonomies can be created (Fig. 1C). By recognizing new families (Fig. 1D), eight more taxonomies can be generated (here, a taxonomy designates a unique combination of taxa recognized on a given phylogeny). Note that between any two of these 13 classifications, the contents of at least one taxon differs, so this amounts to having 13 possible meanings (collectively) of the three or more supraspecific taxa. These 13 taxonomies do not exhaust all the possibilities — many more taxonomies could be generated by using additional ranks — for example, by raising Oidae in Fig. 1A to an Order (and changing the suffix). All of these taxonomies are simultaneously valid and can be used indefinitely in this system; no amount of research can possibly falsify any of them.

Under PN, there is no alternative, so the meaning of all supraspecific taxa is unambiguous (Fig. 1E,F). Species names will not be governed by the PhyloCode, at least initially (Cantino & de Queiroz 2007; Laurin & Cantino 2007); therefore, this example does not discuss problems in delimiting species, which are far more complex but affect both systems equally.

We can now turn to the impact of changes in the reference phylogeny, which several opponents of PN have argued create major problems in PN. In this case, we will switch the positions of species n and k. As we will see, even in that case, PN vastly outperforms RN in terms of minimal taxonomic stability.

Under RN, 14 solutions are allowed by the codes to deal with this situation, if we want taxa to be monophyletic, and continue to only use the ranks of family and genus (neither is required by these codes, so in fact, far more possibilities are allowed). Five possibilities enable us to keep the genera monophyletic (Fig. 2B), for example, by expanding genus O to include all four species in genus O, or by retaining both genera and reassigning species n to genus O and species k to genus P. Nine more are allowed by the erection of new families (Fig. 2C). Again, all these alternative taxonomies are simultaneously valid and are not falsifiable, so they can be used indefinitely.

Under PN, O, P and Oidea have the same content, and since Oidea has priority (whenever publication date is the same, the registration number determines priority), O and P are junior synonyms under this phylogeny. New taxa (Q and R) can be erected for smaller clades (j, n; m, k). The only flexibility in the system at this point is the possibility to erect Q and R (which is not an obligation), the choice of the name and definition (specifiers, definition type [node-, stem- or

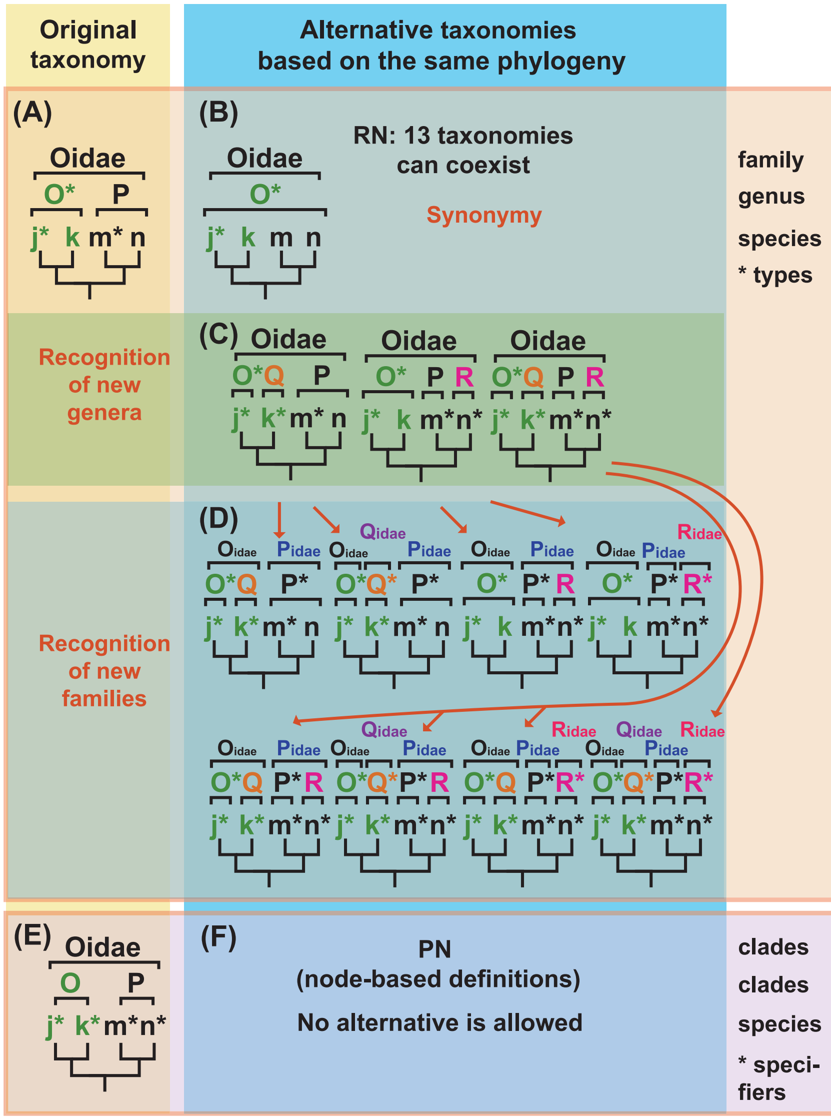

Fig. 1 A–F. Minimal taxonomic stability under RN and PN when the phylogeny is stable. Under the original phylogeny and taxonomy in RN (A), four species are recognized (j, k, m, n), two of which (j, m) are types of genera. Two genera are recognized (O, P), one of which is the type of the family Oidae. All types are identified by an asterisk (*; holotypes of species not shown). Under PN (E), four species j, k, m, n and three higher taxa (O, P, Oidae) are recognized, two of which (O, P) include two species each, and one of which (Oidae) includes all four species, in the context of this phylogeny. Specifiers are identified by asterisks (*). Under PN, all specifiers are specimens, species or characters. In this example, all definitions are node-based. Oidae is the smallest clade which includes j, k, m, n; O is the smallest clade which includes j and k; P is the smallest clade which includes m and n. Note that under RN 13 taxonomies (the original one, and 12 other alternatives) can coexist simultaneously in the literature (all are valid according to the codes of RN) because additional genera (C) and families (D) can be erected. This number would farther increase if para- or polyphyletic taxa were erected. Under PN, no alternative taxonomy is allowed (F), except the trivial case in which redundant taxa are erected (for instance, a taxon Q defined as the largest clade which includes j but not m), which would not change the composition of any of the other taxa (O, P and Oidae), and which could also be done under RN and increase further the number of taxonomies. Under both systems, O and the species which it initially included are in green, P and the species which it initially included are in black, and supraspecific taxa which may be erected under RN are in other colours.

apomorphy-based]). The definitions were deliberately chosen to create as many problems as possible in PN to show a worst-case scenario. If O and P had been defined using branch-based definitions (e.g. O is the largest clade which includes j but not m; P is the largest clade which includes m but not j), all taxa would remain valid (no synonymy results from the new phylogeny), the composition of Oidae is unchanged, and half the content of O and P changes (which is unavoidable under any system of nomenclature if only monophyletic taxa are recognized).

This comparison was deliberately performed on an extremely simple example with only four terminal taxa (species) to explore it thoroughly. It should be noted that in more complex examples with many more species, the number of alternative taxonomies which are simultaneously valid under RN increases very rapidly (and is always greater than the number of considered species), whereas under PN, a single taxonomy is valid no matter how many species are considered (disregarding the trivial cases of redundant taxa based on different kinds of definitions, or ambiguity in taxon delimitation under apomorphy-based definitions caused by incomplete knowledge about character distribution).

Confusion and progress

Comparison with computer science

One of the most frequent argument against the PhyloCode is that it will cause chaos (Nixon *et al.* 2003: 112; Dubois 2006: 835). It is likely that some confusion will arise when the

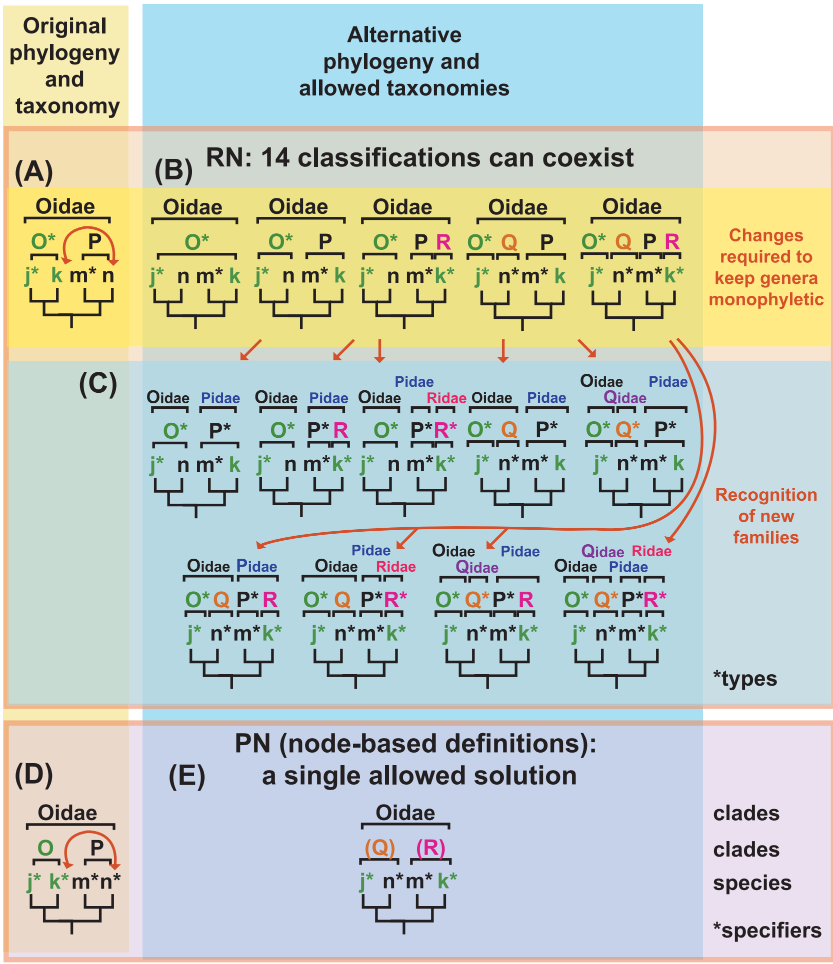

Fig. 2 A–E. Minimal taxonomic stability under RN and PN when the phylogeny changes. Under both systems, we assume that taxa have been erected in the same publication, and under PN, the registration numbers (which determine priority in that case) increase in the order Oidae, O, P. Given the original phylogeny and nomenclature in RN (A), and the change in phylogeny indicated by the arrows, 14 taxonomies can coexist (all are allowed by the codes to coexist indefinitely) if we require taxa to be monophyletic (this is not required by the codes of RN, and more possibilities exist if we allow paraphyletic and polyphyletic taxa). Five solutions allow to keep genera monophyletic (B) and nine other solutions reflect flexibility to erect new families (C). Under PN (D, E), O, P and Oidae now have identical contents because they include all four species; Oidae has priority. New names (Q and/or R) may or may not be erected (the parentheses indicate that this is optional) in addition. Under both systems, O and the species which it initially included are in green, P and the species which it initially included are in black, and supraspecific taxa which may be erected after the phylogeny changes are in other colours.

PhyloCode takes effect because this is a side-effect of the advent of any new theory or method, but it should be much less dramatic than often suggested, and the benefits may be much greater than suggested by opponents of PN. A comparison with developments in computer science in the last two decades can illustrate this point. Microsoft Disk Operating System (MS-DOS), invented in 1981, dominated the microcomputer Operating System (OS) market until the mid-1990s. This OS was command-driven, and learning to use software required memorizing dozens of commands. In retrospect, using DOS was not very easy. In 1984, Apple introduced its first Macintosh computers, which used a new operating system (later called Mac OS) with a Graphical User Interface (GUI). IBM and Microsoft also introduced new OSs with GUIs, named OS/2 (Operating System/2) and Windows, respectively. OS/2, introduced in 1987, was intended by IBM to replace DOS. Windows was introduced by Microsoft in the same year (but only fully replaced DOS, as opposed to providing a GUI on top of it, with the introduction of Windows XP in 2001). The introduction of these three OSs brought chaos and confusions to millions of computer users worldwide because the familiar command line was no longer there in the GUIs, and even worse, software created under one OS had to be rewritten or recompiled to run under another OS, and data files created by a software under one OS was often not compatible with software running under another OS. A single computer could even be equipped with several OSs (still today, some PC users have both Windows and Linux, a version of UNIX, on their computer, while some Macintosh users have also installed Windows on the new Mac Intel computers). Confusing. The fate of these three OSs with GUIs was variable. IBM discontinued support for OS/2 on December 21, 2006. The Mac OS is still alive and being actively developed, although it represents a small portion (on the order of 4%) of the market share of microcomputers. Windows now has about 90% of the client OS market share (servers predominantly use various versions of UNIX, including Linux). This GUI revolution in computer science brought far more confusion to a far greater

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number of people than the PhyloCode could ever possibly achieve, and it involved far more money than any revolution in biological nomenclature could ever attract, but it also brought about considerable progress. Should we have refrained from implementing these OSs, simply because some users did not wish to, or were unable to, face the challenge of dealing with a new operating system? A little confusion is the price to pay for progress, and this may apply also in biological nomenclature.

The story of the GUI revolution in computer science shows another important point: if the PhyloCode proves unsuccessful, and if it is flawed as some authors suggest, it will cause very little confusion. This is shown by the negligible impact that OS/2 has had on computer users. But if the PhyloCode proves successful, as OSs with GUIs have generally been in the computer world, the benefits could be substantial. Thus, there is much to gain, and little to lose, in implementing the PhyloCode.

Are Linnean ranks useful?

Some advocates of RN argue that ranks are useful in comparative studies (Benton 2007), but ranks also convey much disinformation. I have already shown this (Laurin 2005), as have others (Bertrand *et al*. 2006), but it is worth emphasizing here that Benton's (2000) own taxonomies include several nested inversions of the Linnean hierarchy, with the infraphylum Gnathostomata in an unnamed subclass, the superorder Tetrapoda in the infraclass Rhipidistia, the class Reptilia nested in the subclass Reptiliomorpha and the class Aves nested in the division Maniraptora, itself part of the infraorder Tetanurae (four nested inversions in just a few taxa). This contradicts suggestions that ranks convey useful information about nesting. Some orders, such as Heterostraci, originated in the Ordovician (about 500 Mya), whereas others (most orders of placental mammals) originated in the early Palaeogene or latest Cretaceous (between 80 and 60 Mya). The number of species included in these orders is equally variable; the order Panderichthyida includes one to three species, whereas the order Anura includes 5471 species (Anonymous 2000). Therefore, it is obvious that taxa of a given Linnean rank, even in Benton's (2000) taxonomy, are not comparable in any meaningful way. Absolute ranks (Linnean categories) have been misused in studies on conservation, speciation and extinction rates, and should be discarded (Hennig 1981: xviii; Bertrand *et al*. 2006). Measures of biodiversity that use phylogenies instead of classifications exist (e.g. Faith 1992) and are used in conservation biology (Nehring & Puppe 2004).

Taxonomy and nomenclature: how closely linked must they be?

Some practitioners of RN have argued that nomenclature and taxonomy are distinct activities, which is correct, and that the PhyloCode conflates the two (Dubois 2007: 7), which is incorrect (de Queiroz 2006). Practitioners of PN simply believe that, given a nomenclature and a phylogeny, attribution of names to taxa should be as automatic and objective as possible. RN yields names which are almost devoid of meaning and which can be placed in several locations on a given phylogeny, whereas PN provides objective, unambiguous means of assigning names to clades, once these names have been selected and defined (the initial choice of name and definition is subjective in both PN and RN). Given that in other fields, scientists, linguists, philosophers and historians try to describe the meanings of words as precisely as possible (this is the whole purpose of dictionaries, for instance), the latter seems preferable.

Biological nomenclature today and in the future

Ereshefsky (2002: 309) has convincingly argued that nomenclatural ranks are 'ontologically empty designators'. As such, they are ill-suited to define taxon names. Ranks do not exist in nature. Thus, taxon name definitions under RN are also nearly ontologically empty designators; they are not entirely devoid of meaning because they necessarily include types, which are real specimens. However, the remaining content is not prescribed at all. Unlike ranks, clades exist in nature and can be discovered empirically, so taxon names under PN are more clearly defined and refer to entities which can be objectively delimited (through phylogenetic analysis), whereas taxon boundaries under RN are not determinable using empirical evidence and hence lie beyond the realm of science. Of course, under both systems, the choice of which clades are named is subjective.

Adepts of RN often claim that introduction of the PhyloCode will be disastrous for biological nomenclature. For example, Benton (2007: 654) has stated that '[t]he net will extend through systematics and evolutionary biology and the distress could be immense if the Phylocode is ever accepted [...] Working systematists [...] should devote their efforts to discovering nature [...] and not to semantic issues that are liable to suck too many people dry with anger and unhappiness.' Others stated that 'nothing could be more harmful to taxonomy [...] than the chaos that would result from having two widely used nomenclatural systems [the second one being PN] in parallel for the whole of zoology.' (Dubois 2006: 835). Some have stated that the PhyloCode is 'a poorly reasoned, logically inconsistent, and fatally flawed new code that will only bring chaos' (Nixon *et al*. 2003: 112) and that 'The consequence [of adoption of the PhyloCode] for biological classification would obviously be disastrous, but as a language for scientific discourse the prospect is even more damning.' (Carpenter 2003: 91). Such apocalyptic statements are unfounded. As others (Niels Bohr [1885–1962], Robert Strom Petersen [1882–1949] and perhaps even Mark Twain [1835–1910]) have remarked, 'Prediction is very difficult, especially about the future'. No valid evidence was ever presented to justify these bold claims. The past is no guide to the future here because although PN has been in use for over 15 years, the PhyloCode has not taken effect yet. Thus, the principle of priority has not been enforced yet, and consequently, the achievements of PN cannot be compared with those of RN, which has been regulated by codes for nearly a century.

In conclusion, a passage of the Strickland code, which remains highly relevant today, may be cited: 'The undivided attention of chemists, of astronomers, of anatomists, of mineralogists, has been of late years devoted to fixing their respective languages on a sound basis. Why, then, do zoologists hesitate in performing the same duty?' (Strickland *et al*. 1842: 2).

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