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Michel Laurin

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MICHEL LAURIN

Centre de Recherche en Paléontologie – Paris (CR2P), UMR 7207, CNRS/MNHN/SU,
Muséum national d'Histoire naturelle, CP 38, 57 rue Cuvier, 75231 Paris cedex 05
(France)

Mél : michel.laurin@mnhn.fr

The PhyloCode : The logical outcome of millennia of evolution of biological
nomenclature?

Running title: The evolution of biological nomenclature

MICHEL LAURIN

Abstract

Biological nomenclature harks back to a remote prehistoric past, as shown by the universality of fairly sophisticated folk taxonomies and nomenclatures found on all inhabited continents. Ethnobiologists have suggested that these nomenclatures include cryptic “ethnotaxonomic ranks”, although the existence of these ranks has been increasingly questioned recently. The fact that no trace of such ranks has been evoked in Aristotle’s classification of animals but that they have been described in antique Roman ethnotaxonomies casts further doubts about these cryptic ranks. The advent of rank-based nomenclature (RN) in the mid-18th century has had a pervasive, but not only positive, influence on biological nomenclature. The use of a single type and of a subjective, artificial nomenclatural rank does not delimit taxa under RN. This is even a goal of RN, according to Principle 2 of the *Zoological Code*. This contrasts with the nomenclatures of other fields, some of which are designed to delimit entities fairly precisely (e.g., geopolitics, stratigraphy, chemistry), and in which ranks are either defined more objectively (e.g., geopolitics, chemistry), or used informally and relegated to a secondary role (e.g., biogeography, paleobiogeography), or vary in time (e.g., paleobiogeography) or space (e.g., stratigraphy). A trend towards more explicit and precise delimitation of entities over time is also discernible in some fields, especially geopolitics and stratigraphy. In this context, the development of phylogenetic nomenclature (PN) and the recent advent of the *PhyloCode* appear as the logical outcome of the development of evolutionary biology and phylogenetics.

EARLIEST BIOLOGICAL NOMENCLATURES

Our biological nomenclature (i.e., the set of rules for naming, and the names formed according to these rules) for taxa, which is routinely used by all systematists, is the result of a long evolution that took place over thousands of years, and which was shaped by a few revolutions, notably in taxonomy (the study of taxa, which are groups of biological organisms; today, taxonomy is tightly linked to phylogenetics to the extent that most systematists consider that supraspecific taxa should be clades). This brief essay reviews key stages of this history, with emphasis on the last three centuries, to show how the current revolution, embodied by phylogenetic nomenclature (PN) and the advent of the *PhyloCode*, embodies a paradigm shift that was allowed by scientific progress (in evolutionary theory and phylogenetics) and is paralleled by analogous developments in other fields, such as stratigraphy and geopolitics.

All indigenous peoples still living at least in part by hunting, fishing, and gathering food in highly biodiverse environments have very elaborate biological nomenclatures and taxonomies (Berlin, 2014). The similarities between these indigenous nomenclatures and taxonomies, which can be considered as “cultural synapomorphies”, suggest a distant origin, probably prehistoric and dating back to several millennia, before these peoples dispersed to all inhabited continents. Studies in the field of glottochronology, which aims at dating when various ancestral languages were last spoken, supports a great antiquity of folk taxonomies and nomenclatures. Glottochronology is vaguely reminiscent of molecular node dating in being based on “the assumption that lexical replacement of core vocabulary on the average occurs at a relatively constant rate over time” (Brown 2010: 77), which amounts to assuming a linguistic clock. Thus, Brown (2010) estimated that some folk taxon names used in Mesoamerica (maize, maguay, avocado, nopal and squash) are probably more than 7 000 years old, and the peak of the naming rate of botanical folk taxon names in Mesoamerica appears to be around 3500–3200 years ago, at the latest (Brown 2010; Hunn and Brown, 2011: 325). By 2400 BP, 95% of a sample of 41 names of culturally significant plants had been formed (Brown 2010: 90). In addition, folk taxonomies existed in the civilizations that have produced the earliest written records, such as the Sumerians (Peterson, 2007; Chalendar, 2020).

According to some pioneers in ethnobiology such as Brent Berlin and Peter Raven (among others), these nomenclatures include cryptic ranks, which are never mentioned by the natives using these ethnotaxonomies (Berlin, 2014; Laurin, 2023). These are generally referred to as “ethnotaxonomic ranks”, although they are nomenclatural rather than taxonomic because they are based more on linguistic properties of taxon names than on similarities of the taxa themselves. Taxa of variety, species, genus and at least three higher ranks, are generally recognized (Berlin, 2014). This is vaguely reminiscent of Linnaean categories (Raven et al., 1971), but the rank allocations of taxa in these two types of nomenclature (Linnaean and ethnobiological) do not correspond (Laurin, 2023: table 1.1); thus, taxa considered folk generics may frequently be ranked as genera, families, or orders in rank-based nomenclature (abbreviated RN below). The existence of such ethnotaxonomic ranks has been postulated for the folk taxonomies and nomenclatures of many peoples, such as the Tzeltal Maya of southern Mexico and the Fore of Papua New Guinea. But do these ranks really exist, or are they the product of the imagination of ethnobiologists too inclined to draw inspiration from RN, which at the time was the sole embodiment of scientific biological nomenclature, for lack of alternatives (Laurin, 2023)?

Well after the origin of folk taxonomies, Aristotle founded western (scientific) zoology and proposed a taxonomy and nomenclature that deeply influenced zoologists until at least the 16th century. Unexpectedly, in some respects, Aristotle's taxonomy and zoological nomenclature were as least as good as those of Linnaeus! For example, his taxon *ichthyes* (which gave “ichthyan” and became *Pisces*, via Latin) included a primary dichotomy between *kalymmata* (teleosts) and *selache* (selachians), which shares similarities with current taxonomy, in which these two clades are still recognized, except that teleosts are more closely related to tetrapods (within the osteichthyans) than to selachians. Linnaeus (1758: 196) placed the selachians in the taxon *Nantes*, which also included two actinopterygians (the teleost *Lophius* and the sturgeon), among others, but excluded most teleosts, which Linnaeus placed in the taxon *Pisces*. *Nantes* belonged to his taxon *Amphibia*, which included reptiles. This position of selachians, close to some tetrapods in Linnaeus' taxonomy, was no improvement compared to Aristotle's taxonomy. Aristotle must have been a good naturalist, as he described fairly accurately many systematically-relevant characters in

various taxa. These data found in Aristotle's *History of Animals* can be used to score a data matrix, which has been subjected to phylogenetic parsimony analysis in two studies (Fürst von Lieven and Humar, 2008; Laurin & Humar, 2022). In these studies, the trees were rooted using the sea anemone, known to Aristotle as *akalēphē*. This obviates the need to polarize characters directly, though one might wonder if Aristotle's *Scala naturae* might be considered as a kind of pre-evolutionary polarizing principle (Laurin & Humar, 2022: 14). These parsimony analyses found many taxa that Aristotle recognized, some of which are still valid, such as *Selachii* (mentioned above), but also *Gnathostomata*, *Ruminantia*, *Diptera* and *Malacostraca*, among others, which were named differently by Aristotle. All this is quite surprising, as many authors think that Aristotle was not really trying to propose a new taxonomy (e.g., Pellegrin 1986), but that he needed to classify animals to describe their characters.

A recently noticed anomaly is that studies on Aristotle's zoology do not mention ethnotaxonomic ranks (Laurin 2023). This is strange since ethnobiologists believe that the nomenclature of the ancient Romans displayed such ranks (Guasparri, 2022). However, it is well known that the Romans were strongly influenced by Greek culture, and thus, by the zoology of Aristotle. Could the lack of discussion of ethnotaxonomic ranks in Aristotle's works simply reflect a difference in academic community? Indeed, Aristotle's zoology was studied by the community of philosophers, classics, and historians, who were perhaps less influenced by RN (with some possible exceptions, such as Pellegrin) than ethnotaxonomists. Thus, it seems that the early history of biological nomenclature is still poorly understood.

THE LINNAEAN REVOLUTION

More recently, "barely" two and a half centuries ago, Linnaeus introduced binominal nomenclature, or at least systematized its use, which profoundly influenced his successors. Other more or less binominal forms of nomenclature had existed before, both among systematists (Wilkins 2018: 62; Laurin, 2023: 31) and in a broader sense, even among indigenous peoples (Berlin, 2014: 264-265). Following Linnaeus' work, binominal nomenclature became ubiquitous in systematics, because it provided a welcome simplification in names. Indeed, following the discoveries of the great explorers, the explosion of our knowledge of biodiversity had resulted in a progressive lengthening of species names, which described species enough to differentiate them

from other species assigned to the same genus. Tournefort (1694: 37-38) complained that some names were “so long that one loses breath reciting them”! However, this binominal nomenclature, which seduced many of our 18th century pre-evolutionary predecessors by its simplicity, is now problematic because binominal names include taxonomic information (the name of the genus), which must change with the reference phylogeny whenever this results in a different genus allocation of a given species. For example, the large anuran originally named *Rana marina* by Linnaeus, which for a long time was called *Bufo marinus*, is now known primarily as *Rhinella marina*, although some authors call this taxon *Chaunus marinus* (Frost et al., 2006: 364). To find all the relevant articles on this taxon, it is therefore necessary to search under these four names (and to know their existence); not convenient for literature searches!

Linnaeus created other problems, in the long term, by reinforcing the use of the famous “Linnaean categories”, an expression that is a bit ill-chosen because some of them existed long before Linnaeus’ work, while others were introduced long after. Thus, it is generally considered that Magnol (1689) introduced the use of the family rank in botany, whereas the phyla were introduced by Haeckel (1866), nearly two centuries later. In Linnaeus plant taxonomy, each category of angiosperms was defined by a given type of character. Classes were defined by the number and arrangement of stamens, while the number of pistils determined the orders (Schmitz et al., 2007). This provided a simple, objective criterion to rank taxa. In contrast, the absolute rank (in biological systematics, represented by the Linnaean category) of animal taxa never had such an objective basis, and many botanists contemporary with Linnaeus never accepted his ranking criteria, which were abandoned shortly after Linnaeus’ death. These absolute ranks are therefore now (even in embryophytes) artificial and subjective. However, the so-called “Linnaean” codes (better named “rank-based codes”) of nomenclature use types and Linnaean categories (absolute ranks) to define taxon names, and this does not provide delimitation. Some systematists might think that diagnoses could provide delimitation, but this is incorrect because diagnoses can be revised regularly (this is an established practice) and are therefore not part of the definition, unlike the types and ranks associated with taxon names, which are highly regulated and cannot be changed easily. In addition, the use of multiple characters in diagnoses (even

if these were restricted to apomorphies) prevents precise delimitation (Laurin 2023: 111).

RANK-BASED NOMENCLATURE AND ASSOCIATED PROBLEMS

Since Linnaean categories exist only as human constructs, assigning such a rank to a taxon is a subjective exercise, so this system does not delimit taxa (or rather, this delimitation may vary among studies of a given taxon). Surprisingly, this is the purpose of these codes, as stated in Principle 2 of the introduction to the *Zoological Code* (ICZN, 1999), which states: “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.”

The avowed aim is therefore not to delimit the taxa named and defined according to this nomenclature. And this goal was achieved! Indeed, despite the application of the rules of these codes by systematists, disputes over the limits of taxa continue, even for taxa whose phylogeny seems fairly well established. These debates are especially lively in paleontology, but even in relatively well known extant taxa, such as the bufonids, nomenclatural confusion is great (Dubois, 2007).

Delimitation under RN sometimes appears stable when only extant taxa are considered, but when the fossil record is taken into consideration, the limits appear fuzzy. The phenotypic gaps that so obviously separate many extant taxa from one another generally reflect the extinction of intermediate forms. Yet, about two centuries of paleontological work have partially filled many phenotypic gaps (at least among taxa with good fossilization potential), including those that separate birds and mammals from their closest known extant relatives, as well as the emergence of tetrapods within the sarcopterygians (Laurin 2010). Thus, various Mesozoic dinosaurs document the emergence of birds, the transformation of the forelimb into a wing (Wagner & Gauthier, 1999), and the development of increasingly complex feathers (Witmer, 2009). The origin of mammals and birds can be traced back to their last common ancestor in the Carboniferous (Carroll, 1988; Benton, 2014), about 330 Ma ago (Didier & Laurin, 2020). This rich fossil record of stem-mammals partly (but only partly) explains why the name *Mammalia* has been applied to many nested clades, which could be called, from smallest to largest (non-exhaustive list), *Theria*, *Mammalia*, *Mammaliaformes*,

Mammaliamorpha, *Cynodontia*, *Therapsida*, and even *Synapsida* (Rowe & Gauthier, 1992). Is this nomenclatural ambiguity, desired by the bodies responsible for at least some rank-based codes, beneficial for systematics?

Above, I have italicized all taxon names (not just those in the genus and species series). This is consistent with the recommendations of most nomenclature codes (botanical, those for prokaryotes and for viruses, as well as the *PhyloCode*), with the only exceptions of the *Zoological Code* (ICZN, 1999) and the code for cultivated plants (Brickell et al., 2016). In the latter case, this difference in typographic recommendations reflects the fact that this code manages names of groups of organisms (mostly sub-specific) that have been modified by humans and that should be distinguished from other naturally evolved life forms.

HOW TO RANK TAXA?

Let us now return to the deliberate lack of delimitation in RN. It results partly from the subjective nature of Linnaean categories, since the definitions of taxon names consist of type and absolute rank, and this does not match any plausible taxon concept (contrary to taxon name definitions in PN, which designate clades). Criteria have been sought for objectively allocating taxa to such categories, but none are satisfactory. Thus, Dubois (1982) had proposed to delimit genera by retaining within each one the smallest clade composed of all the species that can give viable, true hybrids (diploids with a haploid contribution from each parent), a proposal that he still supports (Dubois et al. 2021: 24). Only positive results are used; for instance in a clade in which species A–J are recognized, if species A and B, B and C, and C and E can hybridize (as described above), but D cannot hybridize with any other and species, and F–J can only hybridize with each other, if the reference phylogeny suggests that D is part of the smallest clade that includes A–C and E, and if this clade excludes species F–J, then species A–E would form a genus, and species F–J would form another genus, if they form a clade that excludes A–E. This suggestion has not met with much success, partly because of the difficulty of application (crosses must be attempted), but perhaps more so because of the drastic changes in genus delimitation that would result. For example, among birds, Gonzalez et al. (2009: 315) reported that 22 types of hybrids (out of 479 recorded) in *Anatidae* involve parental species then classified in different subfamilies!

Among more general solutions (not limited to a single Linnaean category), Hennig (1966) did suggest using the age of origin of taxa as shown by the fossil record and the geological time scale (this was before the era of molecular dating) to fix their ranks (from genus to class). However, he abandoned this idea three years later (Hennig, 1969), in a pioneering book that has not met the success it deserves, even though it was translated into English a good decade later. The English translation of the preface to the German version (of 1969) states (Hennig, 1981: xviii): “I have refrained from giving any categorical rank (‘order’, ‘suborder’, etc.) to groups of higher rank. I have done this because I have found that the fundamental questions of phylogenetic systematics so often become bound up with the subsidiary question of the rank of each group, and I wanted to avoid this kind of unfruitful debate.”

Strangely, authors who have recently suggested using the geological age of origin of taxa to objectively determine their ranks seem to ignore this very early reversal of Hennig's opinion! For example, Avise & Johns (1999), who revived this idea, credited Hennig (1966) with its authorship, but seem to have ignored that Hennig (1969) had subsequently rejected it. Avise & Liu (2011) presented the same incomplete history of this idea in Hennig's work. This bibliographic gap is not unique to these authors; the same problem is found in Zhao et al. (2016). Even Lücking (2019), in his discussion of this idea, attributes its authorship to Hennig and even cites Hennig (1969), but glosses over Hennig's reversal of opinion, which is relevant at least from a historical perspective. So far, the search for an objective basis of the Linnaean supra-specific categories has proven futile (Minelli, 2000, 2003; Laurin, 2023), and this is not disputed by some of the most enthusiastic proponents of RN. This can be illustrated by this very clear quote from Dubois et al. (2021: 5): “we stress the fact that nomenclatural ranks do not have biological definitions or meanings and that they should never be used in an ‘absolute’ way (e.g., to express degrees of genetic or phenetic divergence between taxa or hypothesised ages of cladogeneses) but in a ‘relative’ way: two taxa which are considered phylogenetically as sister-taxa should always be attributed to the same nomenclatural rank (Hennig, 1965: 115), but taxa bearing the same rank in different ‘clades’ are by no means ‘equivalent’, as the number of ranks depends largely on the number of terminal taxa (species) and on the degree of phylogenetic resolution of the tree”.

One might think that objectively determining the specific rank (which is at the core of most rank-based codes) is easier, since many systematists see the species as the fundamental unit of biodiversity. Unfortunately, here again, reality is much more complex than the established dogma suggests. This taxonomic and nomenclatural level seems almost as arbitrary as the others, for two main reasons. First, there are many definitions of species, and second, even if one were to agree on the very popular “biological species concept” (BSC below), it would be very difficult to use this concept to objectively delineate species.

Let’s take these problems one by one. How many species concepts are there in biology? Lherminier & Solignac (2005: 111-123) listed 146 definitions of species. Of course, not all of them correspond to a different concept, but these definitions nevertheless express many species concepts. According to Wilkins (2011), there are 27 species concepts, but he grouped them into seven types of concepts, including the classic biological species concept (BSC), defined as a breeding community. Seven species concepts is far fewer than 146, but still too many to claim that there is consensus on the definition of “species”! According to some authors, there is a single species concept, but several operational criteria to delimit them (de Queiroz, 2007); however, this view has been disputed (Cellinese et al., 2012).

Let us now address the second problem: if we could get a consensus in the scientific community to adopt the BSC, which may well be the species concept supported by the greatest number of systematists (Minelli, 2022), how would we apply it? In most sexual, extant organisms, identifying reproductive communities is in principle feasible, even though very few species have actually been delimited that way (Minelli, 2022). In paleontology, this is impossible, because fossils rarely mate! The best that can be done is to infer reproductive communities from phenotype (and, to a lesser extent, geographical and stratigraphic distribution). Using the BSC is not easier for bacteriologists and virologists, because sexual reproduction is not universal (and does not occur in bacteria and archaea); it seems to have appeared near the base of eukaryotes (Malik et al., 2008; Schurko et al., 2009: 211). Moreover, some eukaryotic taxa have reverted to asexual reproduction (this includes, among our closest relatives, parthenogenetic squamates). Even if one restricts the question to extant sexual forms, the application of BSC is difficult because interfertility decreases gradually with

evolutionary distance; one does not find in nature only distinct groups of organisms forming reproductive communities completely isolated from other communities; rather, gene flow decreases gradually with evolutionary distance. This phenomenon was noticed by botanists decades ago (e.g., Carson, 1975) and was most explicitly stated by Mishler (1999). Perhaps our own reproductive isolation leads us to think (falsely) that this is a general phenomenon in metazoans. Even in the human lineage, this isolation is a recent phenomenon, relative to the origin of this lineage between 6 and 7 Ma ago (Besenbacher et al., 2019). Indeed, studies incorporating data from ancient DNA and various present-day human populations concluded that Neanderthals and Denisovans hybridized about 90,000 years ago (Slon et al., 2018; Rogers et al., 2020) and contributed to the genomes of many present-day human populations subsequently; the last of these exchanges took place only a few tens of thousands of years ago, after *Homo sapiens* left Africa (Prüfer et al. 2014: fig. 8). In short, all of these problems combined (the multiplicity of species concepts and to a lesser extent, problems in applying the BSC, and the gradual decrease in gene flow with evolutionary distance) imply that the specific level is no more objective, no more real, than the supra-specific ranks, as Ereshefsky (2002) had already concluded.

RANKS, TAXA, PHYLOGENY AND NOMENCLATURE

Since there are no absolute ranks in nature, what natural objects do systematists study? There are evolutionary lineages, made up of reproductive communities that follow one another in time, that are linked by a relationship of ancestor to descendant, and that can either become extinct or split into two or more lineages (this is cladogenesis). There are also clades, consisting of one or more lineages. Evolutionary lineages could be considered species, as one of the many concepts of species (or possibly the only one, according to de Queiroz, 2007) is precisely the evolutionary lineage, especially considered between two cladogeneses or a cladogenesis and an extinction (e.g., Hennig 1965; de Queiroz, 2007; Didier et al., 2017: 967). But it is impossible to objectively assign rank to clades; above lineages, there are only clades nested within each other (Laurin, 2023). This biological reality seems difficult to reconcile with the rank-based codes, which are designed neither for evolutionary lineages nor for clades (the words “clade” and “monophyly” are not even mentioned in the *Zoological Code*).

This is why systematists developed PN a few decades ago. Important theoretical works that subsequently allowed the development of PN were published by Darwin (1859) in the 19th century (mostly, the tree of life metaphor) and in the 20th century by Hennig who, as we have seen, recommended abandoning the Linnaean categories as early as 1969. Moreover, Hennig (1969) clearly distinguished the concepts of crown group and total group. A crown group is a clade for which both branches of the primary divergence are represented by extant taxa. For example, the taxon *Amniota* is a crown group if it is defined as the smallest clade that includes the mammals and reptiles (birds included). Similarly, the taxon *Mammalia* is a crown group when it is defined as the smallest clade that includes monotremes and therians, a clade that includes the extant taxa *Marsupialia* and *Placentalia* (Fig. 1). A total group includes a crown group, plus all extinct taxa closer to that crown group than to other crown groups. This can be illustrated by the taxon *Synapsida*, in its modern (monophyletic) sense, which includes mammals and all amniotes that are more closely related to mammals than to extant reptiles. *Synapsida* thus forms a total group. The part of the total group that is not part of the crown group is called the stem group (Fig. 1). Thus, the synapsids taken in their traditional (paraphyletic) sense, i.e., without the mammals, form the mammalian stem group.

Crown and total groups are special cases of taxa defined by nodes and branches, respectively, which have recently been renamed minimal and maximal clades, respectively (Cantino & de Queiroz, 2020). Explicit phylogenetic definitions were initially used in a thesis defended in 1984 and published two years later (Gauthier, 1986). They were formalized soon after (de Queiroz & Gauthier, 1990, 1992, 1994; Sereno, 1998). Node-based (minimal) definitions take the form “the smallest clade including A and B” (Fig. 2). Branch-based (maximal) definitions take the form “the largest clade containing A (or B) but not Z”. In these definitions, A, B and Z are species, or their type specimens. Finally, the definition by apomorphy takes the form “the clade diagnosed by the occurrence of apomorphy M synapomorphic with A (or B)” (Fig. 2). In the hypothetical case where only the taxa that A, B, and Z are known, all three definitions delimit clades with identical content (A and B). Two of the three taxa so defined are redundant in having the same content, but these names are not synonymous, because in PN synonyms must be of the same kind of definition. If the

taxa C and D are subsequently discovered, the three clades defined above are different; there is no longer redundancy, even though the definitions have not changed. And unlike what happens in RN, determining the membership of the newly discovered taxa (C and D) in the more inclusive taxa defined in this way does not require any arbitrary decision. Application of the definitions indicates unambiguously that C belongs to the taxon defined by a branch, but not to the other two, whereas D belongs to both the taxon defined by a branch and the one defined by an apomorphy. Note that in PN, the equivalent of types in RN, called “specifiers”, can be either a specimen, a species, or an apomorphy (but its use is necessarily accompanied by at least one specifier that is either a species or a specimen). In addition, some specifiers are excluded from the taxon, which has no equivalent under the rank-based codes, but this principle exists in an alternative system of RN that aims to assign names to taxa more objectively than under the established rank-based codes (Dubois, 2016).

Use of PN spread among systematists (initially, mostly in North America and especially among vertebrate specialists, and a bit later, among botanists) in the 1990s (e.g., Laurin, 1991; Wolsan, 1993; Bryant, 1996; Holtz, 1996; Cantino et al., 1997; Baum et al., 1998). The International Society for Phylogenetic Nomenclature (ISPN) was inaugurated in 2004 at the Muséum national d'Histoire naturelle in Paris (Laurin & Cantino, 2004); it has since been overseeing the development of the *PhyloCode* (the code that regulates PN for all taxa), which took effect in 2020 (Cantino & de Queiroz, 2020), simultaneously with the publication of *Phylonyms*, the monograph that includes the first set of names established under this code (de Queiroz et al., 2020).

PHYLOGENETIC NOMENCLATURE TODAY

Phylonyms includes 285 chapters (and 1324 pages) by hundreds of authors, because some chapters were written by several authors (sometimes, more than ten). This suggests that acceptance of PN among systematists has progressed substantially over the last two decades. Each chapter is devoted to the definition of a single taxon name, and is structured into a few sections that provide the definition and relevant background information, such as a historical review of the taxon showing how ideas about its composition evolved over time, and how this justifies the choice of name and definition for this taxon. Indeed, the goal of the *PhyloCode* is to stabilize the delimitation of each taxon as close as possible to its recent usage and, if possible, to its older usage. The aim

of the *PhyloCode* is also to ensure that taxon delimitation changes only when our objective knowledge about biodiversity requires it (as when we discover new taxa or revise our phylogenies) and that these changes make sense in an evolutionary context and given the nomenclatural and taxonomic history of each taxon.

Phylonoms covers a great variety of taxa that collectively represent much of the extant biodiversity, but the number of taxa defined in this monograph reflects both the distribution of systematists (charismatic taxa such as vertebrates and angiosperms are much better represented than unicellular eukaryotes) and the problems in establishing and rooting the Tree of Life. Thus, among the basal taxa, *Pan-Biota* (the total group of biological organisms that have ever lived on Earth), *Biota* (its corresponding crown group) and *Eukarya* (all eukaryotes) are defined. No taxon names for the large taxa of bacteria and archaea are included. Within the eukaryotes, several taxa of unicellular organisms are defined, such as *Euglenozoa* and *Foraminifera*, but all these very basal taxa form only the first of eight sections of *Phylonoms*. The second section includes photosynthetic eukaryotes, such as *Rhodophyta* and *Chlorophyta*, while embryophytes form the next two sections, the fourth of which is dedicated to angiosperms. In these two sections, names of well-known taxa such as *Embryophyta*, *Hepatica*, *Tracheophyta*, *Spermatophyta*, and *Coniferae* (section three), as well as *Angiospermae*, *Magnoliidae*, *Monocotyledonaea*, *Rosidae*, and *Campanulidae* (section four), among others, are defined. The last four sections deal with metazoans, the last three of which are reserved for vertebrates. Of these, the seventh section deals with synapsids and the eighth with reptiles (including birds). Some of the familiar metazoan taxon names that are defined include *Metazoa*, *Porifera*, *Cnidaria*, *Bilateria*, *Protostomia*, *Lophotrochozoa*, *Brachiopoda*, *Cephalopoda*, *Insecta*, *Deuterostomia*, *Chordata* and *Cephalochordata* (section five), *Gnathostomata*, *Osteichthyes*, *Actinopterygii*, *Teleostei*, *Tetrapoda*, *Amphibia*, and *Amniota* (section six), *Synapsida*, *Mammalia*, *Monotremata*, *Primates*, and *Carnivora* (section seven), and finally *Reptilia*, *Diapsida*, *Testudines*, *Lepidosauria*, *Archosauria*, *Dinosauria*, *Aves*, and *Apodiformes*, among others (last section). This selection of the names of the largest and best known clades gives an idea of the diversity of the taxa represented, which thus cover the whole tree of life, but in a rather unequal way, with an obvious gap for prokaryotic organisms, which are almost absent from this monograph.

Great care has been taken to ensure that certain definitions apply only under certain phylogenies, in order to better respect the conceptualization, sometimes old but still popular, of many taxa. Thus, the definition of the taxon *Lissamphibia* (Laurin et al., 2020) is: “The smallest crown clade containing *Caecilia tentaculata* Linnaeus 1758, *Andrias japonicus* (Temminck 1836), *Siren lacertina* Österdam 1766, and *Rana temporaria* Linnaeus 1758 but not *Homo sapiens* Linnaeus 1758 or *Eryops megacephalus* Cope 1877 or *Diplocaulus salamandroides* Cope 1877.” Note that in addition to including as internal specifiers a gymnophionan (an apodan amphibian), two urodeles (because the affinities of sirenids have long been controversial), and an anuran, which is sufficient to precisely delimit *Lissamphibia* under most published phylogenies, the definition includes an amniote, a temnospondyl, and a lepospondyl as external specifiers. This ensures that under phylogenies accepted by only a few systematists that imply that extant amphibians are polyphyletic (e.g., Anderson et al., 2008; Pardo et al., 2017), the name *Lissamphibia* does not apply. Indeed, this taxon has always been conceptualized as excluding amniotes and Paleozoic stegocephalians, even temnospondyls and lepospondyls, which form the lissamphibian stem group under various phylogenies (e.g., Bolt, 1969; Ruta & Coates, 2007; Mann et al., 2019; Marjanović & Laurin, 2019; Laurin et al., 2022). This ability to limit application of a name to a given set of phylogenetic contexts is unique to PN because in RN, each author has great freedom on how to name each taxon (and may even change taxon names from one study to the next, even in the absence of discovery of relevant new taxa or changes in the reference phylogeny). This feature ensures that under PN, a given name remains associated with a fairly precise taxonomic concept.

PN has developed well in recent decades, both from a methodological point of view and in terms of adoption by systematists, but much remains to be done, on both fronts. A very small proportion of the taxa regulated by the rank-based codes have been “converted” (redefined according to the *PhyloCode*), many clades remain unnamed (even under RN), and significant controversies remain in PN. For example, some authors like definitions by apomorphies because they seem intuitive and may correspond to the conceptualization of taxa, but the brief history of PN shows that this type of definition leads to a more fuzzy delimitation than those by branch or node (Serenó, 2005). This is related to the conceptualization of characters, which is specific

(within certain limits) to each systematist, as well as to the uncertainty about the history of these characters, which is linked to missing data on their taxonomic distributions and uncertainties about the most appropriate evolutionary models (Laurin, 2023).

NOMENCLATURE IN VARIOUS SCIENCES AND BEYOND

But let us return to the fundamental differences between RN and PN. How similar are these two types of nomenclature to nomenclatures in other fields? Comparisons with folk taxonomies (mentioned at the beginning of this article), stratigraphy, biogeography (including paleobiogeography), geopolitics, and chemistry or physics (concerning the periodic table of elements) show that absolute ranks are used in several other fields, but sometimes informally (they are never mentioned in ethnotaxonomies), they often have an objective basis, especially in geopolitics (e.g., relative legislative autonomy reflects rank, with lesser autonomy characterizing the lowest ranks) and chemistry (e.g., elements are distinguished by the number of protons, whereas isotopes differ by the number of neutrons), and they always play a much smaller role than in RN (Laurin, 2023: 164–165). Moreover, in some fields, these ranks can vary either in time or space, even within a given work (this needs not reflect a difference of opinion among authors). Thus, the rank of paleobiogeographic units can fluctuate in time with their degree of endemism and their geographical extent. Westermann (2000b: fig. 1) showed how the rank of various units varied between those of Province, Subrealm, Realm and even Super-Realm from the Triassic to the Cretaceous. For instance, the “Boreal s. l. / Tethyan s.l.” unit was a Province in the Early Triassic, rose to the Super-Realm rank around the Jurassic/Cretaceous boundary (after considerable fluctuations), before dropping again to the Subrealm rank before the end of the Lower Cretaceous. The rank of lithostratigraphic units varies with their thickness, which changes laterally; for instance, “the Virgelle Sandstone is a formation in western Montana and a member of the Eagle Sandstone in central Montana” (North American Commission on Stratigraphic Nomenclature, 2021: 173). On the contrary, the rank of a given taxon does not vary in space or in time according to any rank-based code (although differences of opinions between authors may lead them to change the rank allocation of a given taxon). For instance, in RN (e.g., Romer, 1966), the taxon *Lissamphibia* is considered a subclass from its Carboniferous or Permian origin (Marjanović & Laurin, 2007; Pyron, 2011), at which time it was represented by only two evolutionary lineages (which have

not been observed but can be inferred by various dating methods) and up to the present day, when 8605 species are recognized (including those that have become extinct in the last few centuries due to our environmental impact), according to Amphibiaweb (accessed 28 March 2023).

Comparisons with the same fields show that entities are generally better delimited than under RN (Laurin, 2023). This is particularly obvious in geopolitics, where the delimitation is very precise and attempts to change the limits of states have resulted in wars, at least for the last 4500 years, as shown by the Stele of the Vultures (Winter, 1985). Wars, which are often territorially motivated (at least, when they occur between states, rather than internally, as civil wars), are perhaps the most intense expression of attachment to the delimitation of anything that one can imagine. The contrast with RN, in which each author delimits at will each taxon in each study, within the limits imposed by types, ranks, and the principle of priority, is striking (see the example of the taxon *Mammalia* above). Conversely, biogeographic and paleobiogeographic entities are poorly delimited, partly because of the lack of nomenclatural codes in this field, which may result from the absence of learned societies dedicated to biogeography (Westermann, 2000a: 2).

A trend towards better delimitation seems to be visible in various fields. This is especially obvious in geopolitics (state boundaries are now much more precise than in the 18th century) and in geochronology, given that the advent of Global Boundary Stratotype Sections and Points (GSSPs) aims at setting precise boundaries between geological stages (Cowie, 1986; Remane et al., 1996). The evolution of geochronology offers perhaps the most striking parallel to that of biological nomenclature, because in both cases we observe the transition from entities that were not precisely delimited (taxa and geological stages) by a nomenclature that emphasized a single type (a specimen or a section, depending on the field) to nomenclature that precisely delimits these entities (with PN and GSSPs, respectively). In geochronology, this evolution is taking place within the major nomenclature codes (e.g., North American Commission on Stratigraphic Nomenclature, 2021), as these codes have evolved rapidly over the past decades and thus benefited from scientific and technological advances. From this point of view, stratigraphers seem to manage this transition (towards a sharper delimitation of entities) much better than systematists. Indeed, the rank-based codes, particularly the

Zoological Code (ICZN, 1999) and the code used by botanists (Turland et al., 2018) have changed very little; among other things, they still do not require monophyly of taxa (even for supraspecific taxa) and have not been revised in an attempt to delimit taxa. Yet, in the first edition of his book on the origin of species, Darwin (1859: 486), already foresaw that systematists should look for and name clades (which he did not name as such): “Our classifications will come to be, as far as they can be so made, genealogies; and will then truly give what may be called the plan of creation. The rules for classifying will no doubt become simpler when we have a definite object in view.”

THE PAST AND FUTURE OF BIOLOGICAL NOMENCLATURE

This historical analysis, which very briefly summarizes arguments presented in detail elsewhere (Laurin, 2023), has attempted to demonstrate that the development of PN and the advent of the *PhyloCode* are logical, perhaps even inevitable, consequences of the developments of systematics, evolutionary biology, and, more generally, of science in general in the last two centuries. The need for such developments to bring biological nomenclature in phase with current evolutionary theory was outlined long ago by de Queiroz (1988, 1997). The advent of the *PhyloCode* reflects trends in the evolution of nomenclature in various fields (especially obvious in geopolitics and geochronology).

This evolution towards a more precise nomenclature, which delimits entities, divides the community of systematic biologists much more than that of geologists, and one might wonder why most systematists have not yet adopted the *PhyloCode*, given its numerous advantages. Are systematists more attached to their traditions than geologists? This possibility was evoked long ago as a “tremendous inertia” of biological nomenclature that is “great enough to have successfully resisted the Darwinian Revolution” (de Queiroz 1988: 241). This inertia has certainly prevented the draft *BioCode* from being adopted, despite the fact that it is decidedly less revolutionary than the *PhyloCode* in being rank-based. As summarized by Oren (2019: 11), in the last in-depth discussion the draft *BioCode*, which took place in 2005, the participants realized that “there was little agreement among the botanists, zoologists, and microbiologist[,] that progress was limited to attempts to maintain a dialog, and that acceptance of a unified code of nomenclature for all living organisms will probably not happen in our lifetime”. Difficulties in this transition had been predicted by de Queiroz (1997: 138),

who suggested that “Replacing the foundation of the nomenclatural system would constitute a **minor revolution**, at least within systematic biology. One might therefore expect that the change will not be made easily” (emphasis mine). Other possible causes of the intense controversy around PN can be invoked. Are systematists less open to change than geologists? Or are they simply victims of circumstances, perhaps because of a poor organization of the societies or committees that regulate the evolution of rank-based codes of nomenclature? Could the current division in the systematic community simply reflect the difficulty of revising rank-based codes to incorporate principles of phylogenetic nomenclature? Indeed, completing such revisions would be more difficult than writing new codes (such as the *PhyloCode*) because RN, as it has been implemented in the rank-based codes, is “in direct conflict” with PN (de Queiroz, 1997: 133). This suggestion is supported by the fact that stratigraphers decided as early as the late 1970s to write a new code (published in 1983), rather than revise the previous 1970 edition (North American Commission on Stratigraphic Nomenclature, 2021: 153), even though the changes to their code were less fundamental than a shift from RN to PN.

Perhaps because of these anticipated difficulties, the *ISPN* moved very slowly, perhaps too slowly, towards implementation of the *PhyloCode*. In the 16 years that passed between the inauguration of the *ISPN* (Laurin and Cantino, 2004) and the publication of *Phylonoms* (de Queiroz et al., 2020), in informal conversations, some systematists (sympathetic or not to PN) asked me if the *PhyloCode* project was dead, probably because only authors of contributions to *Phylonoms* and *ISPN* members were regularly informed of progress on this front. The *ISPN* did release a couple of progress reports, but perhaps the society should have communicated more effectively on this, or perhaps the *PhyloCode* should have been implemented sooner, even if this meant publishing a smaller *Phylonoms* with fewer established names.

A revolution in biological nomenclature was nevertheless anticipated long ago by one of the pioneers of this field, Alphonse de Candolle (1867: 10-11), in this remarkable passage from what is considered the first code of botanical nomenclature:

“However, a time will come when the current plant forms having all been described, herbaria offering certain types, botanists having made, undone, sometimes remade, raised or lowered, and above all modified several hundred thousand groups, from classes to simple varieties of species, the number of synonyms having become

infinitely more considerable than that of the valid taxa, science will need some great renovation in its principles. This nomenclature, which we are trying to improve, will then appear like an old scaffolding, formed of parts painfully renewed, one by one, and surrounded by debris made up of all the rejected parts which will form a more or less embarrassing clutter. The edifice of science will have been built, but it will not be sufficiently free from all that has served to raise it. Then, perhaps, there will arise something completely different from Linnaean nomenclature, something which will be imagined to give stable names to definitive groups.

This is the secret of the future, and of a future that is still very distant.” (My translation of the French original.)

A similar (though less eloquent) statement is found in one of the first zoological codes, which was adopted by the *American Ornithologists' Union* (1886: 5). This quote from de Candolle (1867) describes well the current challenge facing biological nomenclature, even though it was published more than 150 years ago! But perhaps de Candolle was looking even further into the future, as we still do not have “definitive groups”! Nevertheless, this passage suggests that pioneers of RN, such as de Candolle and the authors of the code of the *American Ornithologists' Union* (1886), among others, might have appreciated the development of PN, or at least, they would have seen it more favorably than most of the current members of the *International Commission on Zoological Nomenclature*! The future of biological nomenclature will ultimately be decided by the entire systematic community. More than a century elapsed between the publication of Darwin's *Origin of Species* and the acceptance by most systematists that supraspecific taxa should be monophyletic; how long will it take for the systematic community to accept that phylogeny, rather than artificial “Linnaean” categories, should be the guiding principle of our nomenclatural system? Will that community facilitate, or delay the nomenclatural revolution that appears to be underway?

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FIGURES

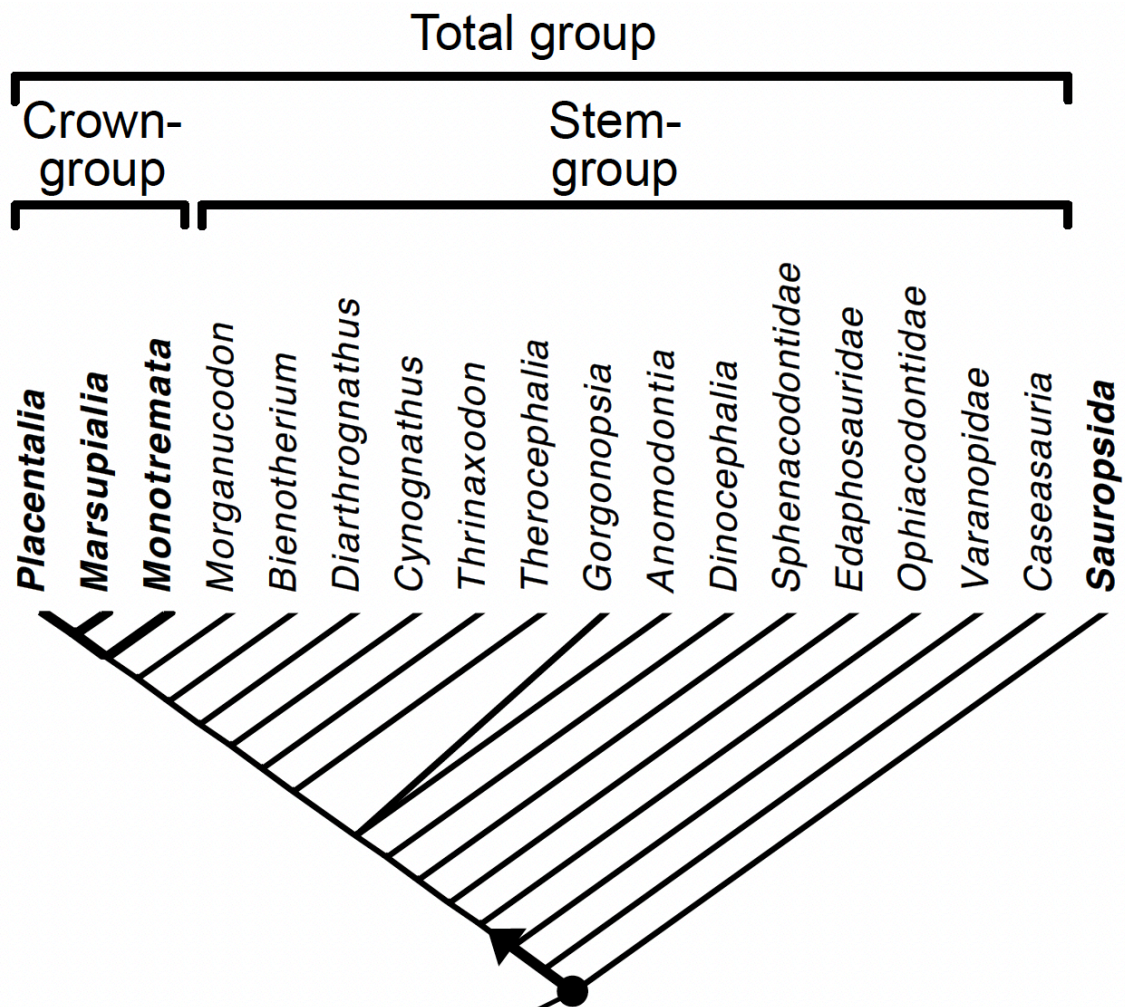


Figure 1: Concepts of crown group, total group and stem group, illustrated by the example of synapsids. The taxon *Mammalia* is the crown group delimited by monotremes, marsupials and placentals (extant taxa are in bold). The stem group (paraphyletic by definition, thus not corresponding to a taxon in phylogenetic nomenclature) includes all extinct taxa (in plain type) more closely related to mammals than to extant reptiles. It includes the synapsids in the traditional (paraphyletic) sense of the term, i.e., the “pelycosaurs” (paraphyletic; from *Caseasauria* to *Sphenacodontidae*) and the “therapsids”, also taken in the traditional and paraphyletic sense of the term (from *Dinocephalia* to *Morganucodon*). The total group, marked by the arrow that extends out of the basal node and by a bracket above, includes the crown group plus its stem; it thus includes *Mammalia* and all the taxa shown here except *Sauropsida*. Similarly, *Sauropsida* is the total group that contains the crown group most closely related to *Mammalia*, namely the taxon *Reptilia*, considered to be a clade that includes birds, in addition the ectothermic extant taxa traditionally considered to be reptiles.

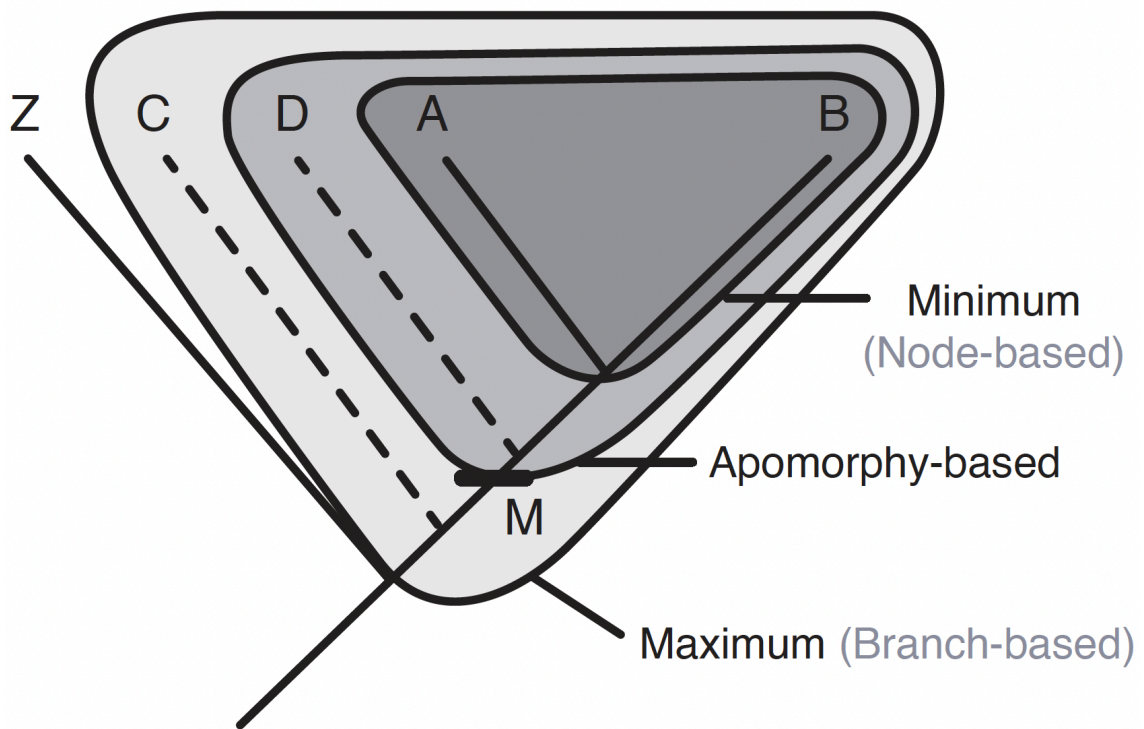


Figure 2. The three kinds of phylogenetic definitions of taxa. These are: “minimum”, formerly known as “node-based”, “maximum”, formerly known as “branch-based”, and apomorphy-based. The letters A–D, M and Z designate specifiers (nominal species, except for M, which is an apomorphy).