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To name or not to name: Criteria to promote economy of change in Linnaean classification schemes

MIGUEL VENCES^{1,5}, JUAN M. GUAYASAMIN², AURÉLIEN MIRALLES^{1,3} & IGNACIO DE LA RIVA⁴

¹*Department of Evolutionary Biology, Zoological Institute, Technical University of Braunschweig, Spielmannstrasse 8, 38106 Braunschweig, Germany*

²*Universidad Tecnológica Indoamérica, Centro de Investigación de la Biodiversidad y el Cambio Climático, Calle Machala y Sabanilla, Cotacollao, Quito, Ecuador*

³*CNRS-UMR5175 CEFE, Centre d'Ecologie Fonctionnelle et Evolutive, 1919 route de Mende, 34293 Montpellier cedex 5, France*

⁴*Department of Biodiversity and Evolutionary Biology, Museo Nacional de Ciencias Naturales, CSIC, C/José Gutiérrez Abascal 2, Madrid 28006, Spain*

⁵*Corresponding author. E-mail: m.vences@tu-bs.de*

Table of contents

Abstract	202
Introduction	202
The scope of this paper: recommendations, not regulations	205
Ranks, categories, and taxa of the Linnaean system	206
Economy of change: a main priority for biological classification	208
Taxon Naming Criteria (TNC) for taxonomic revisions	209
Priority TNCs: monophyly, clade stability, and phenotypic diagnosability	211
Monophyly	211
Clade stability	213
Phenotypic diagnosability	217
Secondary TNCs: time banding, biogeography, adaptive zone, and hybrid viability	218
Time banding	218
Biogeography	219
Adaptive zone	221
Hybrid viability	221
Accessory TNCs	223
Manageability	223
Hall of fame	224
Nomenclatural stability	225
Community consensus	226
The bad and the ugly: naming of non-monophyletic units	227
Discussion	230
Taxon Naming Criteria in practice: examples from amphibian and reptile taxonomy	230
Monophyly	230
Phenotypic diagnosability	231
Clade stability	231
Time banding	232
Nomenclatural stability	233
Conclusions	234
Acknowledgements	234
References	235

Abstract

The Linnaean classification system provides the universal reference system for communicating about the diversity of life and its hierarchic history. Several limitations that challenge the stability of this system have been identified and, as a result, alternative systems have been proposed since its early inception. The revolution caused by molecular phylogenetics has, more than ever, exemplified that Linnaean classification schemes are subject to a degree of instability that may hamper their significance and communication power. Our analysis of recent changes in the classification of several groups of organisms, with a focus on amphibians and reptiles, reveals two main sources of instability: (i) revisionary, objective (empirical) changes based on the discovery of unambiguous instances of non-monophyly and on progress in the Globe's species inventory, and (ii) subjective changes based on author preferences or on a poor analysis of the advantages and limitations of new classification schemes. To avoid subjective taxonomic instability, we review and elaborate proposals for the assignment of Linnaean rank to clades, and thereby for the naming of these clades as Linnaean taxa (Taxon Naming Criteria: TNCs). These are drafted from the perspective of practicing taxonomists and can help choosing among alternative monophyly-based classifications under a premise of economy of change. We provide a rationale for each TNC along with real and theoretical examples to illustrate their practical advantages and disadvantages. We conclude that not all TNCs lead to equally informative and stable taxonomies. Therefore, we order the various TNCs by the generality of their implications and provide a workflow scheme to guide the procedure of taxonomic decisions concerning the creation or modification of supraspecific classifications. The following criteria are considered primary when naming taxa: (i) Monophyly of the taxon in an inferred species tree; (ii) Clade Stability, i.e., the monophyly of a clade to be named as taxon should be as strongly supported as possible by various methods of tree inference, tests of clade robustness, and different data sets; and (iii) Phenotypic Diagnosability, i.e., ranked supraspecific taxa should be those that are phenotypically most conspicuous although in phenotypically cryptic groups of organisms it can be warranted to name taxa based on molecular differences alone. We consider various other criteria as secondary (i.e., the Time Banding, Biogeography, Adaptive Zone, and Hybrid Viability TNCs) and refute using them as sole arguments for the modification of established classifications or proposal of new ones. Taxonomists are encouraged to be explicit and consistent when applying TNCs for creating or modifying classifications. We emphasize that, except for monophyly, the priority TNCs are not proposed as mandatory requisites of a Linnaean taxon but as yardsticks to allow for an informed choice among various clades in a tree that could alternatively be named as Linnaean taxa. Despite a need for plurality, classifications should avoid deliberately violating any of the three primary TNCs because taxa of unstable monophyly or poor diagnosability reduce the information content and hence the utility of the Linnaean system.

Key words: Linnaean system, taxon naming criteria, taxonomic inflation, taxonomy, phylogenetics, rank, category, nomenclature, divergence times, evolutionary species concept

"It is a truly wonderful fact — the wonder of which we are apt to overlook from familiarity — that all animals and all plants through all time and space should be related to each other in group subordinate to group ..." (Darwin 1859).

"Can you see the shape of a tree developing in your mind as you read this description of the sequence of groupings? It is a family tree: a tree with many branches, each branch having sub-branches, and each sub-branch having sub-branches. The tips of the twigs are species. The other groupings—class, order, family, genus—are the branches and sub-branches. The tree is all of life on Earth." (Dawkins 2011)

Introduction

Taxonomy, the science of identifying, classifying and naming organisms, has undergone fundamental conceptual changes over the last century. For some time, taxonomy has been marginalized and neglected as a mere book-keeping and pigeon-holing activity without epistemological underpinning (Wheeler 2008). In contrast, the emerging new taxonomy is fundamentally grounded on evolutionary theory and increasingly makes use of modern bioinformatic tools (e.g., Wheeler *et al.* 2004; Wilson 2003, 2004; Schram 2004).

The first taxonomic aim, identifying species-level taxa, nowadays follows a conceptual framework that considers species as separate population-level lineages (Simpson 1961; Wiley 1978; Mayden 1997; De Queiroz, 1998, 2007) and relies on the use of multiple lines of evidence to delimit them (Dayrat, 2005; Padial *et al.*, 2010). The second practice, classifying species into higher-level taxa, is currently based on the inference of relationships

following Hennig's (1966) principles of phylogenetics, relying on the concepts of homologous characters and monophyly. The third task of taxonomists is the scientific description of the inferred species and higher-level taxa, an activity that largely follows the classification system originally established by Linnaeus (1758). The last two decades have seen a rise of alternative schemes to name clades in phylogenetic trees such as the PhyloCode (Cantino & De Queiroz 2010) and others (Papavero *et al.* 2001; Bethoux 2007), as well as continued claims to abandon the Linnaean system altogether (e.g., De Queiroz & Gauthier 1992; Ereshefsky 2001; Zachos 2011) or to combine it with new approaches (Kuntner & Agnarsson 2006). Nevertheless, the universal taxonomic communication system is still the one based on the Linnaean principles. Linnaean supraspecific taxa, the ones on which this paper is focused, are currently defined as biological entities in a phylogeny that are assigned to ranked categories such as genera, families, orders, or classes.

Phylogenetic classifications are based on scientific hypotheses and necessarily subject to continuous change in order to implement newly gained knowledge. Among the most prominent examples are higher-level relationships of mammals (Springer *et al.* 2004), which led to fascinating rearrangements such as recognizing the enigmatic Afrotheria, a well-supported taxon including animals as morphologically distinct as elephants, golden moles, tenrecs, or aardvarks. These developments have mainly been triggered by the advent of ever more powerful DNA sequencing techniques, and by bioinformatic tools that allow transforming the increasing flow of molecular data into phylogenetic trees (Boore & Fuerstenberg 2008; Wiley & Lieberman 2011). At the level of species, a similar revolution is taking place with the incorporation and popularization of molecular data as a crucial component of integrative taxonomy (Dayrat 2005; Padiál *et al.* 2010). This led to an enormous acceleration in the rate of species discovery in numerous groups of organisms (e.g., Bickford *et al.* 2007; Pfenninger & Schwenk 2007; Fontaneto *et al.* 2008; Fonseca *et al.* 2010; Poulin 2011; Stuart *et al.* 2006; Oliver *et al.* 2009; Vieites *et al.*, 2009; Jansen *et al.* 2011; Funk *et al.* 2012). Estimates usually agree that only a fraction of Earth's species diversity has so far been inventoried and taxonomically described, with a possible 86% of existing species on Earth and 91% of species in the oceans still awaiting description (Mora *et al.* 2011). Nonetheless, due to methodological and conceptual progress, a full species inventory might for the first time in human history be a realistic perspective (Wheeler *et al.* 2012; Costello *et al.* 2013).

This momentous progress in molecular phylogenetic systematics and accelerated species discovery is leading to important and continuous changes of supraspecific classification in many groups of organisms. Accumulation of new phylogenetic knowledge even proceeds so fast that taxonomists do not keep pace translating it into new proposals of Linnaean classifications (Franz 2005). In fact, for many systematists, the phylogenies themselves are central and it matters little how they are turned into taxonomies (e.g., Felsenstein 2001), a position with which we strongly disagree. A related theme is that the pace of taxonomic descriptions of new species lags behind their initial discovery (e.g. Joppa *et al.* 2011).

Changes of classification schemes necessarily bring about conflicts with the main purpose of Linnaean taxonomy, that is, providing a universal reference system of names of organisms for use in all fields of biology and beyond. Changes in Linnaean taxonomies also affect, besides taxonomists, all other end-users of taxa names (biomedicine, databases, museums, conservationists, GenBank, popular literature, international trade rules etc.). The severity of this problem will decline once that synonymy databases are completed and search engines can retrieve, for instance, all information on a species no matter which genus name has been used in the various original publications. However, where information is summarized for entire supraspecific taxa as for example in many biogeographic or conservation biological analyses, it will be much more difficult to compare results if the content of these supraspecific taxa is highly variable among studies. Confusion due to taxonomic instability thus can become a serious problem consuming public and private resources. Amphibian classification serves as a perfect model to illustrate how a veritable tsunami of classification changes has been gaining force over the past ten years (Hillis and Wilcox 2005; Faivovich *et al.* 2005; Grant *et al.* 2006; Frost *et al.* 2006; Glaw & Vences 2006; Hedges *et al.* 2008; Heinicke *et al.* 2009; Guayasamin *et al.* 2009; Dubois & Raffaëlli 2009, 2012; Wilkinson *et al.* 2011; Pyron & Wiens 2011). In reptiles the changes have been less drastic, but in the course of smaller revisions a large number of novel genus- and family-level classifications have been proposed (e.g., Arnold *et al.* 2007, Vidal *et al.* 2007, 2010; Stanley *et al.* 2011; Pyron *et al.* 2011; Hedges & Conn 2012; Nicholson *et al.* 2012).

The European herpetofauna can serve as a model to quantify this acceleration. We tabulated species lists from seven monographs or series of monographs that stand for certain historical periods, assessed how many species changed genus-level classification from one list to the following one, and then normalized this number by the total

number of species compared and by the years between the two accounts (Fig. 1). In the 19th and early 20th century, changes affected 11–36% of the 75–97 species compared, whereas a major stasis was observed in the 20 years between 1978 and 1997, with only 2% of the species (3 out of 128) changing to a different genus. In contrast, between 1997 and 2010, change affected 31% of all species (45 out of 146), thereby leading by far to the highest number of changes per year of all periods (Fig. 1).

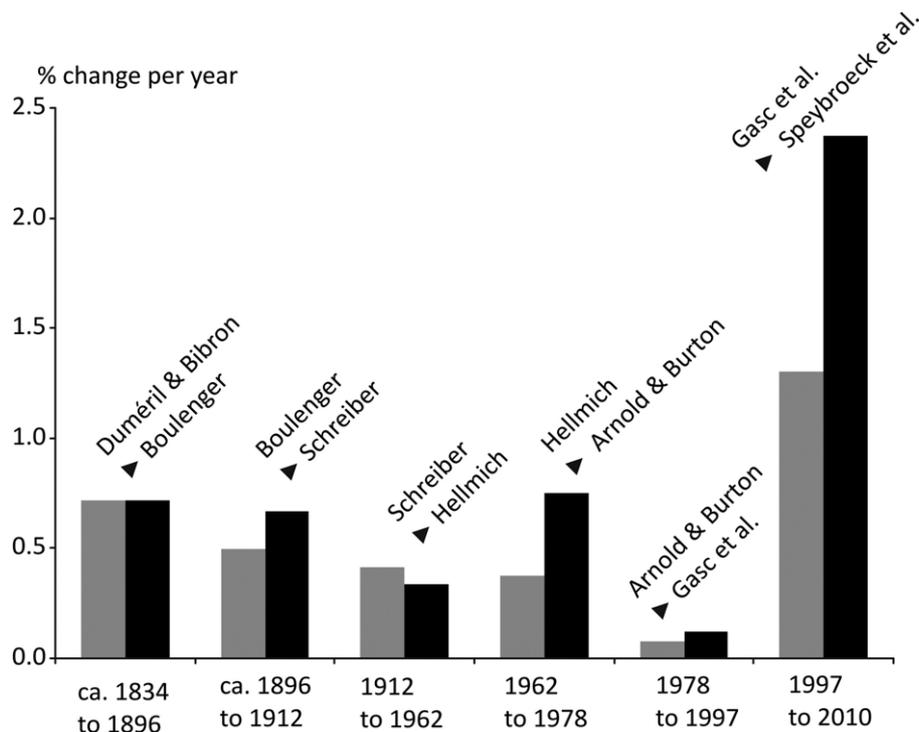


FIGURE 1. Changes of genus-level taxonomy summarized for European amphibians and reptiles. The graph shows the percentage of species that changed genus from one monographic work to the other, standardized per year. After a rather continuous rate of change from 1834–1978, almost no genus-level changes occurred between 1978 and 1997, whereas in the 1997–2010 period the increase was higher than ever before. Black bars indicate values for all pairwise comparisons between the taxon lists of the respective monographs, gray bars show the same trend only for those taxa that already were included in the very first works by Duméril and Bibron and/or Boulenger (with an overall lower rate of change since these early described species comprise several type species of well established genera). Species lists were extracted from the following publications: Duméril and Bibron (1834–1854); Boulenger (1882a,b, 1885a,b, 1887, 1889, 1896a,b); Schreiber (1912); Hellmich (1962); Arnold and Burton (1978); Gasc (1997); Speybroeck *et al.* (2010).

The implications of these re-classifications are manifold. They have extended to numerous species from all geographical areas, and to species that are of special interest to ecologists, conservationists, wildlife managers, amateur herpwatchers, and the pet trade. Differing opinions about their justification and pertinence have raised heated debates in herpetology (e.g., Hillis & Wilcox 2005; Dubois 2006b; Hillis 2007; Vences 2007; Wiens 2007; Frost *et al.* 2008; Pauly *et al.* 2009; Frost *et al.* 2009; Pyron & Wiens 2011). Despite considerable progress towards a consensual taxonomy (Blackburn & Wake 2011), the two most cited online databases of world amphibian species (Amphibian Species of the World: Frost 2012; AmphibiaWeb 2012) still use different classification schemes at the genus and family level for a substantial portion of the anuran fauna.

The enormous progress made in systematics over the last decades has taught biologists that nature is more complex than ever expected: homoplasy is rampant in many groups, and gene trees do not necessarily match species trees. Changes in classification are often necessary and disagreements over these changes unavoidable because the debate usually has two components: (i) empirical arguments, i.e., new phylogenetic inferences suggesting non-monophyly of taxa, or discovery of new species that cannot be accommodated in existing supraspecific taxa, and (ii) subjective preferences of researchers or debates about the appropriateness of data and methods used to infer phylogenies. Given this panorama, rigid classifications are unrealistic (Dubois & Raffaelli 2012) but a reduction of subjectivity in changes of classification is a legitimate goal.

In this paper, we review and develop criteria (Taxon Naming Criteria, TNCs) to enhance an economy of change of supraspecific classifications. Assigning a rank to a taxon often has important consequences, because this taxon (by obtaining a name in the Linnaean taxonomy) will receive increased attention by end-users of the respective classification. We acknowledge the need to replace non-monophyletic classifications if the para- or polyphyly of focal taxa is conclusively demonstrated, but we argue that an informed choice should be made among various alternative monophyly-based replacement classifications. Aiding this choice under the premise of economy of change is the main purpose of the TNCs proposed herein.

The scope of this paper: recommendations, not regulations

Preferences for classification schemes have always been a subject of intense discussions within the scientific community. Sources of discordance include the relevance of the evidence used, concepts and methods, or simply divergent opinions about what within a group of organisms should be a genus, a family, or a higher category. The potential implications of reviewing Linnaean ranks and classification thus extend into a whole variety of fields of biology. In order to prevent any misunderstanding, we consider it important to clearly state the scope of this paper.

First, we focus on the Linnaean classification system. Several methods are available to classify the diversity of life (e.g. phenetic, ecological, phylogenetic) and to translate that organization into a regulated system of words, numbers, or symbols (reviewed e.g. by Hennig 1966; Stuessy 1990; Panchen 1992; Wiley & Lieberman 2011). Of these, especially the PhyloCode (Cantino & De Queiroz 2010) has been explicitly proposed as an alternative to Linnaean classification. Although some of our conclusions and proposals would also apply to the naming of clades under the PhyloCode, we do not aim to provide a review of alternative classification systems. Our main goal is to identify and reduce sources of subjective instability under the Linnaean system. We furthermore herein take a mainly zoological and neontological perspective based on our own expertise. Nevertheless, many of our recommendations would also apply to the supraspecific classifications of other organisms.

Second, although some concepts are revisited to frame our proposal, we here do not approach the adequacy of the Linnaean system from a theoretical perspective (e.g. Eresfhesky 2001). On the contrary, we primarily accept the theoretical incongruences of the Linnaean hierarchy (e.g., use of ranks despite their non equivalence; Wiley 1979; Wiley & Lieberman 2011) (Fig. 2), and review taxonomic instability from the perspective of the practicing taxonomist and other end-users of classifications. Given that classification is simply a necessity whenever dealing with any kind of diversity (Hennig, 1966) and that classification of organisms provides one of the most important bases for biology, we feel that such a practical perspective for naming clades as Linnaean taxa is often underestimated by systematists proposing changes in classifications.

Third, we here largely focus at supraspecific classification rather than alpha-taxonomy. The increasing species numbers resulting from new discoveries and taxonomic inflation (Isaac *et al.* 2004) clearly constitute another source of taxonomic instability on which we have recently commented (Köhler *et al.* 2005, Padial & De la Riva, 2006). Here, we only consider taxonomic changes at the species level when they affect supraspecific classifications (i.e., due to type-based nomenclatural rules).

Fourth, we do not aim to introduce any new obligatory regulation that could for instance be integrated into the Code of Nomenclature. In order to complete the inventory of life on Earth, flexibility and creativity of taxonomists are more relevant than new restrictions; such an approach explains the enormous success of *Zootaxa* (Zhang 2008), a journal that allows for a substantial plurality of concepts, methods and formats. While we argue that economy of change is important, we are also aware that decisions on classification changes need to be taken on a case-by-case basis. Given the complexity of the evolution of organisms, we have no doubt that situations will regularly arise in which the criteria and priorities proposed herein will be overruled by other arguments in favor or against specific classification schemes. Which weight to give to which TNC in specific cases will necessarily remain as a source of dispute, in some cases even among the authors of the present paper, and the inherent subjectivity of favoring one classification scheme over the other can be reduced but never fully eliminated.

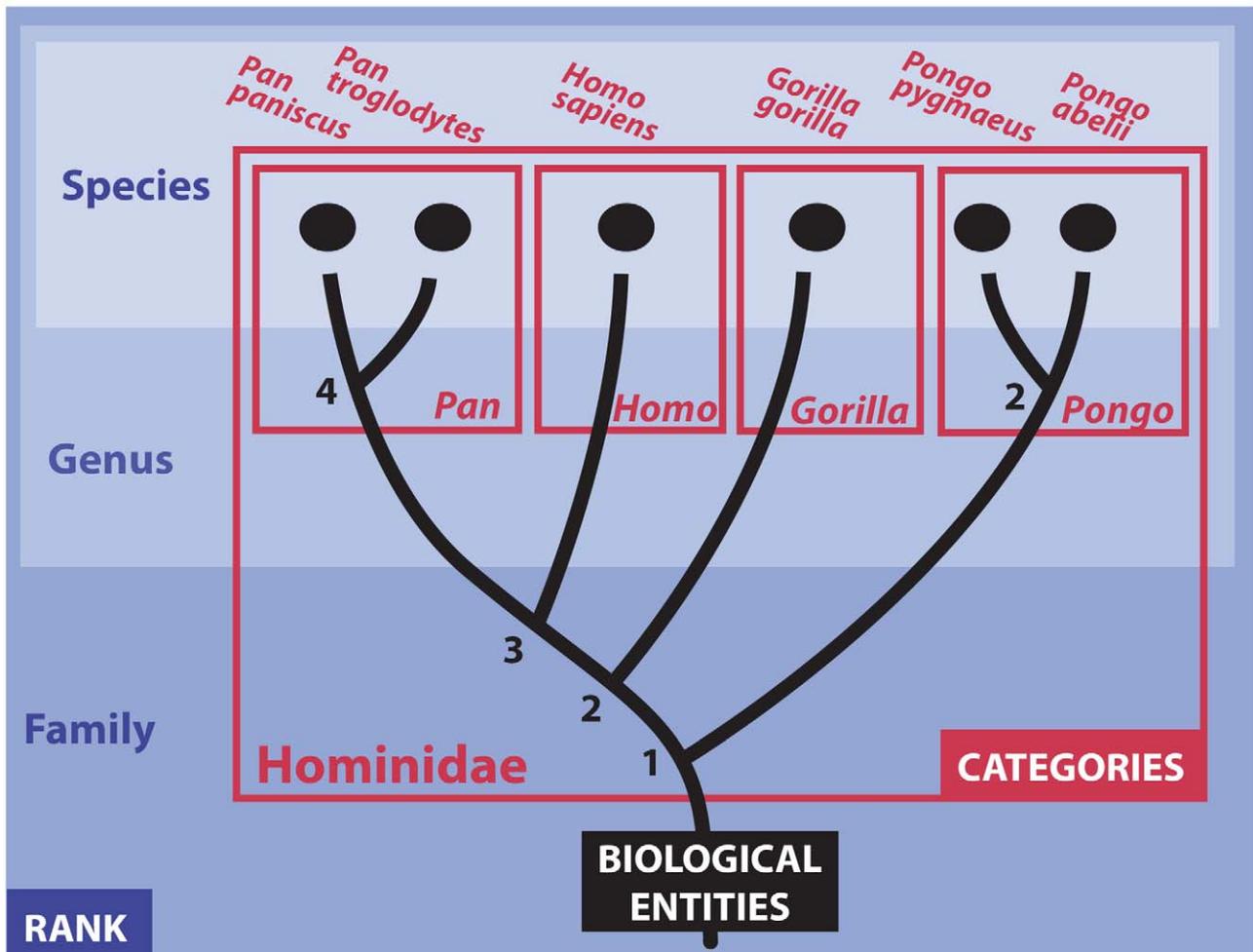


FIGURE 2. Schematic graph showing the Linnaean rank and phylogenetic hierarchy for three categories (species, genus, and family). All components of the genus category have the same rank in the Linnaean system, although the respective clades (nodes) are not equivalent in the hierarchy delimited by the asymmetric phylogenetic tree. For instance, the genus *Pan* is in the genus category, but has hierarchical level 4 in the phylogeny, whereas *Pongo* is also in the genus category, but has hierarchical level 2. This same hierarchical level 2 also applies to its sister group, i.e., the clade containing the genera *Gorilla*, *Homo*, and *Pan*. In the terminology used herein, assuming that the tree correctly reconstructs the evolutionary relationships among the organisms included, all clades can be considered as taxa, but we mostly use the term taxon to refer to Linnaean taxa, i.e., those clades that actually correspond to a Linnaean category and are named accordingly. Note that historically, a taxon was just any group of organisms that received a name in a taxonomy, without necessarily being monophyletic, but herein we use the term explicitly in its definition as corresponding to a clade in the phylogeny of life.

Ranks, categories, and taxa of the Linnaean system

Phylogenetic classifications are regulated systems of words created to communicate about the main levels of organization in the tree of life. We recognize those levels in the phylogeny as taxa that are natural monophyletic groups. Since phylogeny is hierarchic, hierarchic classification schemes such as the Linnaean system perfectly fit its purpose (Hennig 1966).

The Linnaean system relies on a series of categories (species, genus, family, etc.) of a certain hierarchical rank. A clear distinction between taxon, category and rank is important for the following discussion (see also Dubois & Raffaëlli 2012). A natural taxon (a species or a supraspecific monophyletic group) is a biological entity or historical group that exists or has existed and corresponds to a clade in the phylogeny of life. A category is a group of things regarded as having a shared characteristic. A rank is a position in a hierarchy. The ranked categories of the Linnaean system have the goal of grouping taxa at the same rank (but see Fig. 2). Thus, *Homo*, *Pan* and *Gorilla* are

all taxa (natural groups) assigned to the genus rank, and therefore belong to the genus category. The term clade denotes a monophyletic group in any phylogenetic tree. A clade might be chosen for naming it as a taxon, but only if the respective tree is considered to correctly reflect the evolutionary relationships of the organisms included. Herein, we use the phrases "naming a clade as a taxon" and "taxon naming" for the two-step decision of (i) considering that a certain phylogenetic tree correctly infers evolutionary relationships among the organisms included, and of (ii) including in a taxon all the species and lower-ranked taxa that correspond to a certain clade in this tree.

Despite this clear difference between taxa and categories, there have been attempts to confer biological or historical reality to the categories themselves (at least to some of them; see below), or to identify biological properties that would unequivocally characterize taxa of the same rank. Especially for the genus category, various criteria have been proposed (and applied) based on a supposed biological reality of this category (Stuessy 1990). For instance, a survey among botanists at the beginning of the last century revealed that genera were often considered to be biological entities while species were not (Anderson 1940). Also, more recently, researchers have concluded that genera are natural evolutionary units separated by discontinuities and even coined a specific term—geniation—for the putative process that produces new genera (Dubois, 1981)

Along with others (e.g., Forey *et al.* 2004; Orthia *et al.* 2005; Wiley & Lieberman 2011), we here follow the view that supraspecific Linnaean ranks have no inherent biological meaning except that only monophyletic taxa should be classified. Changes in classification, therefore, have a mandatory component –if new data demonstrate that the current classification contains non-monophyletic taxa, changes are needed. There is however also a subjective component in changes of classification because researchers might prefer certain monophyly-grounded classification over others. Only species can be considered to a certain degree equivalent to each other because they correspond to the same level of biological organization. Attempts to use Linnaean categories under the assumption that taxa of the same rank (other than species) reflect a particular level of biological organization and are therefore equivalent, are unrealistic (Bertrand *et al.* 2006; Laurin 2010). Therefore, discussions about classification schemes should not be aimed at identifying criteria that would unambiguously assign a particular rank to a taxon. Instead, it is important to provide explicit criteria for choosing which of the multiple clades of a phylogenetic tree (i.e., which of all of the clades in a tree) are to be ranked in a Linnaean category and thus named as a Linnaean taxon. Criteria are also needed to decide when and why proposing a new classification scheme is sufficiently justified by a new phylogenetic hypothesis. We argue that many of the previously proposed criteria to make taxa of the same rank comparable increase in practical value if considered as Taxon Naming Criteria (TNCs), in part corresponding to what Wiley (1979) referred to as "conventions".

However, this does not imply that all supraspecific ranks are fully equivalent, or that they carry the same amount of information. Tradition plays a role here, as in any convention. First, ranks obviously are hierarchical—the rank of genus is subordinated to the rank of family and, therefore, the category family can contain genera but the category genus can never contain families. Second, there are various other practical distinctions to be made among categories, summarized in Table 1. As an example, the genus is part of the binomial species name and is always used in any communication concerning the species, such as determination keys, species inventories or conservation legislation. As such, there is no doubt that the genus is of particular importance among the supraspecific categories, and changes in this category should be exerted with particular caution to satisfy what we consider a highly important premise: minimizing the amount of taxonomic change and its impact on the communication function of taxa names. A further distinction among supraspecific categories is that the nomenclatural priority principle only applies to family-group and genus-group categories (and to species-group categories, of course), but not to categories of higher rank (see our discussion below on proposals by Dubois 2006a, 2011).

TABLE 1. Main Linnaean categories in zoology and their main characteristics from the practical perspective advocated herein.

Category	ICZN Code applies	Characteristics from a practical perspective
Subspecies	Yes	Might be used for convenience, useful to denote local populations diagnosable by some characters, which, however, do not necessarily identify them as independent lineages. Not the primary focus of the present paper.
Species	Yes	The only category corresponding to a real, objective level of biological organization (a population-level lineage with an independent evolutionary trajectory). Important category because is used as basic unit in numerous fields of science and society. Not the primary focus of the present paper.
Other species-group nomina (e.g., superspecies)	Yes	Might be used for convenience to denote complexes of closely related species.
Genus	Yes	The only category beside species that is reflected in the species binomen; therefore, changes in genus category have higher impact than those in higher or intermediate categories and should be applied with care.
Other genus-group nomina (subgenus, supergenus)	Yes	Much less prominent categories than the genus. Might be convenient categories to name taxa before the phylogeny is fully resolved and/or when phenotypic diagnosability is poor, i.e., when important future changes of classification are to be expected.
Family	Yes	Quite often used in the non-taxonomic literature. Therefore, changes in family classification should be applied with care.
Other family-group nomina (subfamily, superfamily, tribe)	Yes	Less prominent categories than the family. Might be convenient categories to name taxa before the phylogeny is fully resolved and/or when phenotypic diagnosability is poor, i.e., when important future changes of classification are to be expected.
Higher categories (order, class, phylum and intermediates)	No	Some higher categories are well established in biology and society. Changes in their classification should therefore be applied with care and only when their monophyly is rejected and the new topology is robustly supported.
Unranked nomina	No	Convenient to name clades in a phylogenetic tree even if their monophyly is not yet robustly supported and future changes of classification are thus to be expected. Also convenient to reflect relationships in a formal classification without changing well-established names of included clades, avoiding intermediate ranks (such as "subsuperfamily" or similar).

Economy of change: a main priority for biological classification

Supraspecific categories are efficient tools to denote taxa and, thereby, to communicate information on their monophyly and position in the Linnaean hierarchy relative to other, more or less inclusive taxa. Their usage also allows to rapidly confer information on traits that might characterize them. If appropriately defined, these ranked taxon names in the Linnaean system allow discussing evolutionary trends, patterns of geographic distribution, or the expression of morphological, genomic or physiological traits across organisms without having to enumerate and list all species to which a certain characteristic applies. Linnaean names can also provide efficient means for legislators to protect an array of different species. For example, the action of listing the frog tortoise family Testudinidae or the lizard genus *Phelsuma* in an appendix of the Convention on the International Trade in Endangered Species (CITES) immediately regulates trade in all newly described species or yet undescribed species falling into these categories. Field guides and species inventories typically list species separated by families and especially by genera, given that the genus name is an inherent part of the Linnaean binomen of a species. A similar situation of even more direct impact is the use of scientific names to accurately denote pathogen or pest species (e.g., Gordh and Beardsley 1999). Last but not least, taxonomists themselves make extensive use of supraspecific categories in their daily work and revisionary publications. New species are typically first assigned to a family and a genus, and then compared to other species within these groups.

Linnaean names can serve as an efficient mean of communication only if they are relatively stable over time. We agree with Dubois & Raffaëlli (2012) in that any classification of a group of organisms is a step along the progress of knowledge and often will be replaced by a better one as new data arise. However, the idea of taxonomic and nomenclatural stability is not just a praise for ignorance as claimed by Dubois (2007) and Dubois and Raffaëlli (2012), but expresses a legitimate concern. While most taxonomists will agree that it is necessary to keep adapting classifications to novel phylogenetic knowledge, reluctance to accept new classification proposals often arises from objections towards the data or methods on which these changes rely, or doubts about the strength of the underlying evidence. Permanently shifting contents of supraspecific categories, and frequent changes in the genus-level classification will cause confusion, especially where these names are being used beyond the taxonomic community. As early as about 1860, the botanist G. Bentham in an unpublished manuscript cited by Stevens (1997a) suggested that "*Established combinations should be maintained where new ones present no very decided improvement.*" Linnaeus himself wrote in 1751 "*The names of the plants ought to be stable [certa], consequently they should be given to stable genera*" (see Stafleu 1971). Also, the Code of Zoological Nomenclature includes a statement, albeit a rather weak one, on this issue: "*Since it is the object of nomenclature to denote each taxon by a name which is unique, unambiguous and universal, an author should not change the prevailing usage of names, or the sense in which they are used, unless this is required for scientific reasons (i.e. the reclassification of taxa); it is of especial importance that a name should not be transferred to a taxon distinct from that to which it is generally applied.*"

Herein, we adhere to this philosophy by advocating an economy of taxonomic change. This differs from the principle of economy of names, i.e., the attempt to organize taxa in a way that minimizes the amount of ranks and names needed (Wiley 1979; Brooks *et al.* 1984). We obviously agree that it is impractical to name all clades in a phylogenetic tree as taxa, implying the need of a selection of clades for naming, and that redundant naming (e.g., a subfamilial classification with a single genus in each subfamily) is superfluous. But our main focus is a different one. Economy of change applies when one monophyly-based classification is to be replaced by another equally monophyly-based classification, or when different monophyly-based classification alternatives are conceivable to replace a previous classification that turned out to contain non-monophyletic units. In such cases, taxonomists should carefully consider whether the advantages of a new scheme outweighs its disadvantages in terms of compromising taxonomic stability in the particular group of taxa. Most crucial is to select taxa for ranking and naming such that change is minimized compared to the previous classification. Economy of taxonomic change also means appraising the susceptibility of a new classification to future instability, taking into account the amount and conclusiveness of evidence by which it is supported.

Taxon Naming Criteria (TNC) for taxonomic revisions

Many of the criteria that we propose are inspired by Wiley's Conventions for Annotated Linnaean Classifications (Wiley 1979; Wiley & Lieberman 2011). These conventions were established to apply phylogenetic principles to Linnaean classification (Hennig 1966), which we fully endorse. Table 2 reproduces the nine conventions in their updated form (Wiley & Lieberman 2011), along with comments about how these conventions relate to our own proposals that will be detailed in the next sections. Especially important for our purpose is Wiley's suggestion of minimizing taxonomic decisions when building or modifying classifications. Several other conventions refer to the treatment of polytomies, fossils, and stem taxa. Although perfectly valid from a theoretical point of view, these conventions are often difficult to apply in the taxonomic practice. For instance, systematists nowadays only rarely dare to identify a fossil as direct ancestor of an extant taxon, and therefore rather include fossils as terminals in the phylogenetic analyses (following Farris 1976), equivalent to the extant taxa (e.g. Eernisse & Kluge 1993; Müller *et al.* 2011; Ruane *et al.* 2011). Furthermore, many methods of phylogenetic inference, especially those using large amounts of DNA sequences, only rarely produce trees with real polytomies, but rather suggest clades as optimal which then however may receive only poor support values. Whether and when considering such cases as polytomy, and possibly apply convention 5 (see Table 2), will be a matter of debate.

The Taxon Naming Criteria that we propose deviate from and expand Wiley's approach because, as discussed above, they are formulated from a practical rather than theoretical perspective and with the focus to minimize change, not necessarily to minimize names. Our emphasis on diagnosability, and on the stability of the phylogeny on which classificatory decisions are based, follows initial suggestions by Guayasamin *et al.* (2009).

TABLE 2. Commented list of the proposals of Wiley & Lieberman (2011), largely following Wiley (1979), for conventions for an annotated Linnaean classification.

Convention No	Convention text	Comments
1	The Linnaean Hierarchy will be used, with certain other conventions, to classify organisms.	While other classification systems such as the PhyloCode may be useful for certain purposes, we agree on the usage of the Linnaean Hierarchy as universal reference system to classify the diversity of life.
2	Minimum taxonomic decisions will be made, whenever possible, to construct a classification or to modify an existing classification. (i) No empty or redundant categorical ranks and associated taxon names will be used unless necessary to show the sister-group relationship of a small clade or single species relative to its sister. (ii) The ranks of well-known taxa will be retained whenever possible.	A pivotal convention fully endorsed herein. It agrees with the spirit of our paper that suggests a high priority for stability of classification and economy of change.
3	Terminal taxa in asymmetric trees may be placed at the same hierarchical rank and listed in order of their branching sequence.	A necessary convention because otherwise, a high number of different ranks would be required to translate a tree into a Linnaean classification (see Fig. 2).
4	Entirely fossil clades should be noted as such.	A useful convention in cases where such fossil-only groups are included in the classification.
5	Monophyletic groups that form polytomies are given appropriate equivalent rank and placed <i>sedis mutabilis</i> at the level of the hierarchy at which their relationships to other taxa are known.	This convention is somewhat equivalent to the Clade Stability TNC proposed herein. Our criterion uses various arguments to assess clade stability because, in practice, there is rarely a clear distinction between unambiguously polytomous vs. dichotomous nodes, given different methods of phylogenetic inference and clade support.
6	Monophyletic taxa of uncertain relationships will be placed in the hierarchy <i>incertae sedis</i> at the level and ranks at which their relationships are best understood.	This convention is useful in the framework of a comprehensive taxonomic revision of a group where some enigmatic taxa could not be studied. However, we suggest that, as a default, current Linnaean classification schemes should be considered as consisting of monophyletic units, and changes or <i>incertae sedis</i> status assignments be applied only when new explicit phylogenetic hypotheses become available.
7	A group whose status as monophyletic is unknown or suspected may be included in a phylogenetic classification if its status is clearly indicated by placing the name in shutter quotes to indicate that all included taxa are actually <i>incertae sedis</i> at the level of the hierarchy at which the taxon is classified. Such a group will not be accorded a formal rank.	See above. This convention is useful in cases where an explicitly phylogenetic classification of a group is proposed and where a few taxa could not be included in the study. However, as the status of the majority of Linnaean taxa has probably not yet been thoroughly tested from a phylogenetic perspective, for standard classification purposes we suggest to assume monophyly as default.
8	A stem species of a supraspecific taxon will be classified in a monotypic genus and placed in the hierarchy in parentheses at the side of the supraspecific taxon of which its descendants are parts.	A useful convention in cases where a stem species has been unambiguously defined. However, in practice, this will probably only rarely be the case.
9	Taxa of hybrid origin will be classified with one or both parental species and its hybrid nature (apart from any nomenclatural rules applied) will be indicated by placing the names of the parental species, if known, besides the hybrid's name in parentheses.	Hybrid species or clades arisen by hybridization belong simultaneously to two clades. If they arose from parental species belonging to different supraspecific taxa, they should, in the Linnaean system, be assigned to only one of these, depending on the most relevant phenotypic or genotypic synapomorphies (Fig. 3). Mentioning the parent species can be useful in hybrid species representing terminal taxa, but is not practical if these have further diversified.

Priority TNCs: monophyly, clade stability, and phenotypic diagnosability

Monophyly

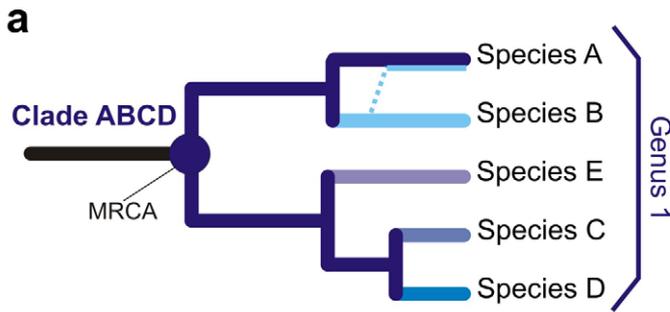
There is now uncontested consensus in the scientific community that the classification of organisms should try to reflect as close as possible their phylogenetic relationships. It must be kept in mind that this goal cannot be fully achieved in a Linnaean system because the same rank can be applied to clades that are at different levels of the phylogenetic hierarchy—sister groups do not necessarily have the same rank (Convention 3 of Wiley; Table 2). For instance, the sister group of one genus can include several other genera (Fig. 2). Leaving aside this necessary inconsistency, it is however an achievable requirement of the highest priority that any named taxon should correspond to a monophyletic group (= a clade: an ancestor and all of its descendants; e.g. Hennig 1966; Wiley 1979; Wiley & Lieberman 2011) in the respective species tree (although it might be paraphyletic in one or several gene trees if explainable by biological phenomena such as introgression or incomplete lineage sorting; see below). We define this requirement as the Monophyly TNC.

Several phenomena and methodological limitations can confound our inferences on monophyly of supraspecific taxa. Phenomena of incomplete lineage sorting and of introgression can lead to non-monophyly of gene trees of particular species in phylogenetic analyses and therefore polyphyly and paraphyly of gene genealogies for particular taxa are widespread (Funk and Omland 2003; see Shimada *et al.* 2008; Brown & Twomey 2009, for examples in frogs). Humans, for instance, have apparently partially admixed with three different archaic forms of *Homo*, among them the Neanderthal that sometimes has been considered as a different species, and traces of these admixtures are still present in extant *Homo sapiens* genomes (Green *et al.* 2010; Reich *et al.* 2010; Hammer *et al.* 2011). Such hybridization does not necessarily compromise the status of species as independent evolutionary lineages, and they are only potentially relevant for supraspecific classifications if the species hybridizing now or in the past belong to different supraspecific taxa (see below and Fig. 3). In fact such hybridization and introgression events have been reported between species belonging to different genera and even different families in some groups of organisms such as turtles, birds, and some plants (e.g., Owen 1941; Montagu 1950; Knobloch 1972; Karl *et al.* 1995; McCarthy 2006; Fritz & Havaš 2007).

Any successful hybridization event with introgression can lead to a lack of monophyly at the level of genes and individuals, but will also always lead to a lack of reciprocal monophyly (Avice 2000) of the descendants of the two hybridizing units at the level of populations. Therefore, it is necessary to take into account the species tree, and not any particular gene genealogy, when assessing monophyly of supraspecific taxa. The species tree as we use this term here is more a concept (i.e., the tree fully corresponding to the true evolutionary relationships) than a real tree that might be available to researchers. A species tree in many cases can be inferred by coalescence-based analysis of multilocus data sets (e.g., Liu *et al.* 2009); however, inferring the species tree does not necessarily require the use of such methods. It also can be obtained, for instance, by invoking superiority of trees based on nuclear DNA sequences, or allozyme markers, or morphological characters, over a mtDNA-based tree in the light of evidence for mtDNA introgression.

In a strict cladistic framework as it is exemplified by the PhyloCode (Cantino & De Queiroz 2010), monophyly is a defining property of a clade (and thus also of any taxon, i.e., a named clade) and ancestry is defined by the origin of a clade through speciation and not by occasional gene flow from other clades. The paradoxical result is that a species, if seen as populations of individuals, can descend from ancestors belonging to different clades yet the monophyly of the same species seen in a cladistic conceptual framework is not compromised. This cladistic viewpoint, adopted herein, is therefore utterly useful to avoid discussions about horizontal gene flow between species belonging to different supraspecific taxa possibly challenging the monophyly of these supraspecific taxa.

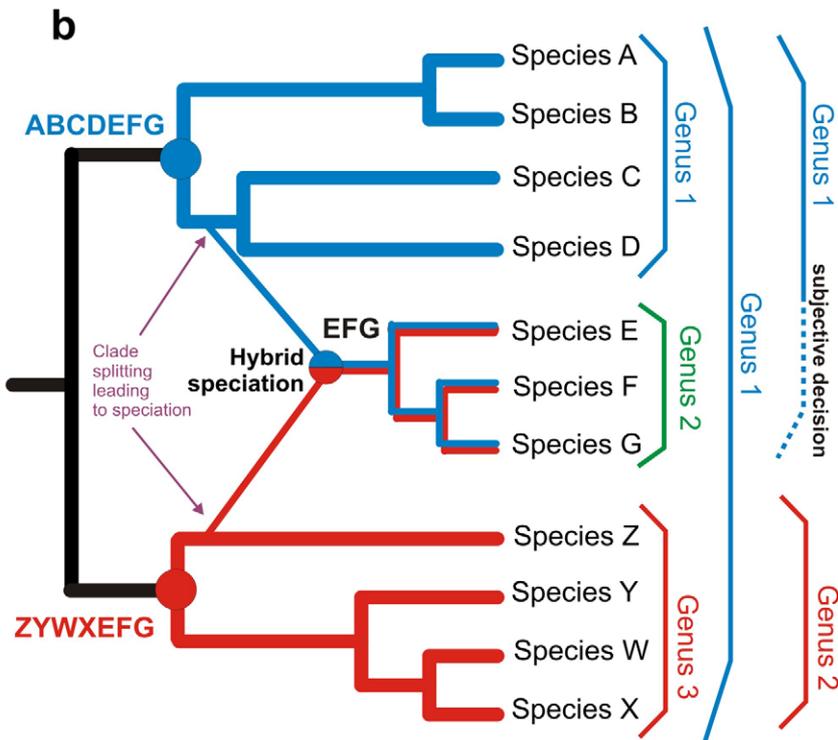
In this framework, only speciation by hybridization, with the hybridizing species belonging to different supraspecific taxa, challenges the monophyly of these taxa (Fig. 3). The solution proposed in Note 2.1.3 of the PhyloCode is to consider a hybrid taxon (originated by hybridization or fusion of two ancestral species) to belong simultaneously to two clades. If such hybrid speciation involves species of different supraspecific taxa, then they may represent a dilemma for the Monophyly TNC, because the cladistic solution cannot be readily translated into Linnaean taxonomy. A single species cannot belong, for instance, to two different genera or families. However, we hold that this practical problem is minor, because we assume that cases of hybrid speciation of species belonging to different genera (or subgenera) are exceedingly rare. In such exceptional cases, it is possible to assign the new species to one of the two genera based on greatest phenotypic similarity, or to merge the two genera based on the Hybrid viability TNC, as explained below and in Fig. 7.



Introgression between two congeneric species

Cladistics: Not relevant for clade monophyly because monophyly does not apply to species

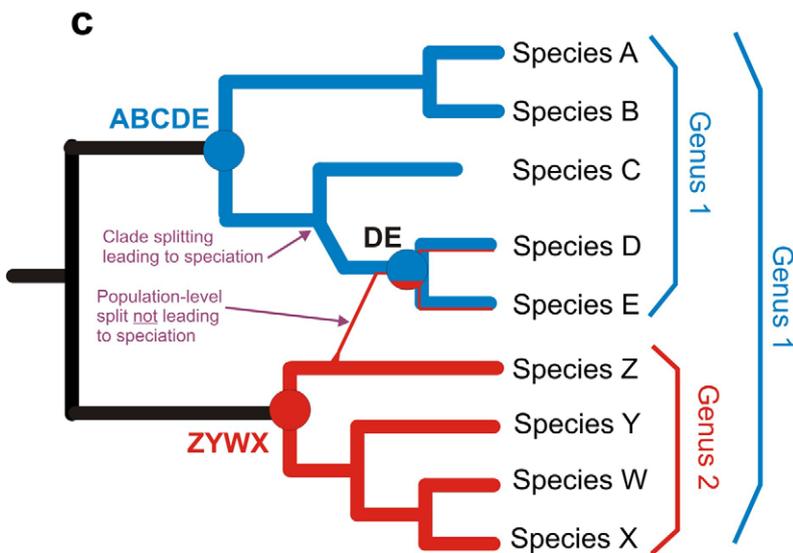
Linnean classification: Not relevant since all species are in the same supraspecific taxon



Origin of a clade (EFG) by hybridization of two species belonging to different genera

Cladistics: Clade EFG belongs simultaneously to two higher clades: ABCDEDFG and ZYWXEFG.

Linnaean: The species in clade EFG cannot be placed simultaneously in two supraspecific taxa.
 Alternatives:
 - Erect a third genus for the hybrid-origin-clade.
 - Include all species in a single genus
 - Include the hybrid-origin-clade in either of the two genera 1 or 2 based on a subjective choice of importance of synapomorphies.
 In a strict interpretation, only the second option leads to a monophyletic genus-level classification.



Hybridization with introgression between species belonging to different genera

Cladistics: Clade DE formally belongs to only clade ABCDE because the hybridization event did not lead to speciation: the ancestor of DE originated (before the hybridization event) by cladogenesis C/DE and hybridized subsequently with Z. From a strict cladistic point of view genus 1 is thus monophyletic although DE shares part of its population-level ancestry with Z.

Linnaean: Classify species D and E in genus 1.
 Alternatively include all species in one genus.

To summarize, (i) species and rarely also genera and families can lack reciprocal monophyly at the level of individuals and genes due to hybridization and introgression, but (ii) hybridization and introgression do not challenge the monophyly of supraspecific taxa. Hence, the Monophyly TNC stands out as the most important taxon-naming criterion for supraspecific taxa.

Clade stability

Monophyly is the first, and the only strict taxon-naming criterion. In other words, no taxon for which there is robust evidence of paraphyly or polyphyly should be named or maintained in a classification. But how to assess monophyly, or evidence for non-monophyly, is more contentious. Given the heuristic nature of tree inference, phylogenetic trees can be flawed and suggest wrong topologies, depending on the quality of the data and appropriateness of the method, the computational power available, the limitations of character and taxon sampling, and biological phenomena.

As a working framework, we suggest that, by default, and if there is not evidence to the contrary, any existing Linnaean classification scheme should be considered as consisting of monophyletic units even if no explicit phylogenetic hypothesis has been proposed for all of them. This seems reasonable given that taxa defined by morphological similarity are often confirmed as being monophyletic by explicit phylogenetic analyses (Jablonski and Finarelli 2009). Such a tacit assumption of monophyly of also phylogenetically untested taxa actually reflects current taxonomic practice although we are not aware of studies that have explicitly stated it. Under this premise, changes proposed on presumed non-monophyly of named taxa require phylogenetic evidence for the alternative classification. In fact, such evidence is nowadays explicitly or implicitly the basis for most proposals of supraspecific classification. A different question is how stable and reliable the underlying phylogenetic hypotheses are.

We thus suggest a Clade Stability TNC that takes into account the stability of the monophyly of the clade corresponding to a certain taxon. This includes the strength of the evidence for monophyly of this taxon but extends further. It encompasses all possible indicators of the probability that future researchers will not recover the taxon as a clade in newly reconstructed phylogenetic trees, thus rejecting monophyly of the taxon and disagreeing with the proposed classification. We here discuss this TNC with examples centered on whether newly discovered clades are stable enough to be considered for carrying ranked taxon names in a revised, newly proposed classification.



FIGURE 3. Introgression (transfer of genetic material between species via occasional hybridization) and hybrid speciation (origin of a new species e.g. by allopolyploidization) can lead to double ancestry of individual organisms and of genes within a species, and thereby challenge the reciprocal monophyly at the phylogeographic level. However, in a cladistic framework, the monophyly of supraspecific taxa is only challenged by hybrid speciation because hybridization and introgression without simultaneous speciation do not cause cladogenesis. The figure shows three different scenarios, their interpretation in a cladistic framework and their consequences for Linnaean classification. (a) Most often, hybridization with introgression (as well as hybrid speciation) will occur among species within the same genus (or other supraspecific taxon), and usually among closely related taxa. Because species in strict cladistic analysis are not considered as clades, the requirement of monophyly does not apply to them and such cases are irrelevant for cladistics as well as for Linnaean classification. (b) Hybrid speciation with parent species belonging to two different genera can be translated into a Linnaean classification in three alternative ways. Classification schemes with two or three genera lead to non-monophyly because not all descendants of clade ABCDEFG and/or of clade ZYWXEFG are included in the respective genera. (c) Hybridization with introgression among species belonging to different supraspecific taxa (in this case genera) also leads to a double ancestry of the individuals forming a species or a clade (and a taxon if the clade is named in a Linnaean classification), but typically in a very asymmetrical proportion. Usually the majority of synapomorphies will clearly link the species with one of the clades and thus provide a useful basis for genus assignment. Notes: (i) The one-genus solution in (b) and (c) is only a feasible means to maintain a monophyletic classification if clades ABCDEFG and ZYWXEFG are sister genera. (ii) Typically phenomena of past hybridization and hybrid speciation are hypotheses derived from molecular data and might often not be strongly supported; obligatorily basing changes of classification on these unstable hypotheses therefore disagrees with stability of classification. (iii) Because in these examples introgression and hybrid speciation apply, at least partly, to extinct ancestral species, the Hybrid Viability TNC to define genera (Dubois 2004) cannot be experimentally applied.

We see the Clade Stability TNC as composed of various subcriteria, and in addition to those discussed herein there might be other such indicators of stability. The clade underlying a supraspecific taxon fulfills this TNC better than another one when: (i) it is supported in a phylogenetic tree derived from an analysis using an optimization method, (ii) it receives a support from one or several clade support metrics stronger than another clade that could be alternatively named, (iii) neither different data sets nor analytical methods provide high support for its non-monophyly, (iv) species sampling in the analysis supporting it is broader, (v) it is congruently supported by a higher number of independent sets of data, and (vi) it is congruently supported by a wider array of different analytical methods. Several of these subcriteria have been proposed before, e.g., numbers (i) and (ii) by Schulte *et al.* (1998), and (i), (ii), (iv), and (v) by Guayasamin *et al.* (2009).

One point is pivotal to emphasize, and we do so here and will repeat ourselves in some of the sections below: By proposing these subcriteria to assess clade stability we do not defend that any kind of data or analytical method is necessarily superior. Neither do we suggest that congruence among methods or data is a necessity to infer a correct biological hypothesis. There always will be some characters, data sets, analyses or rationales that will support a clade and others that refute it, and only a careful and integrative consideration of the various subcriteria here can yield a rationale for higher or lower stability of a certain clade. Again, our approach is a practical one: if supported by many available data sets and methods, the probability is lower that the proposed phylogenetic hypothesis—and the classification based on it—will be challenged and changed by other researchers favoring any particular method or data. Additionally, analytical flaws or data errors are less probable to pass unperceived. In short, given the many options of clades of a tree to which ranks can be assigned (and which can thus be named as Linnaean taxa), it is preferable to choose the uncontested ones.

Subcriterion (i): The taxon is recovered as a clade in an explicit phylogenetic analysis. Recognizing and diagnosing a supraspecific taxon by a unique putative synapomorphy, or in some cases even by a unique combination of phylogenetically unpolarized character states, can be interpreted as implying its monophyly and thus satisfying the Monophyly TNC. We suggest, on the contrary, that a hypothesis based on an explicit analysis resulting in a phylogenetic tree is desirable, and that higher taxa for which the classification is being changed ought to be represented in that tree. This criterion implies that putative synapomorphies are tested, and can be supported or rejected by character congruence during character optimization. We acknowledge that different kinds of data might require different methods of tree reconstruction, and researchers differ in their preferred approaches. Plurality in these approaches is therefore necessary, but optimization methods such as, for instance, Maximum Parsimony, Maximum Likelihood, or Bayesian Inference are preferable while phenetic methods such as Neighbor-joining must nowadays be considered as insufficient.

Subcriterion (ii): Robust clade support. Clades that are to be considered as Linnaean taxa should receive a relevant support from one or several analyses of repeatability or robustness of the phylogenetic hypothesis, such as decay index, bootstrap or jackknife proportion, or posterior probability. Researchers may provide an explicit rationale to define what is to be deemed as relevant support (see e.g., Felsenstein 1985b; Hedges 1992; Hillis & Bull 1993 for bootstrapping; Felsenstein 1985a; Debry 2001 for the decay index; Zander 2004 for a comparison of various metrics). Even stronger cases can be made by employing state-of-the art tests that take an explicit falsification approach (Schulte *et al.* 1998) by comparing the preferred hypothesis with alternatives (e.g., Shimodaira & Hasegawa 1999; Shimodaira 2002), and by verifying an adequate signal to noise ratio in the data set (Wägele & Mayer 2007).

Subcriterion (iii): Absence of evidence for non-monophyly. The absence of any data set or tree support metric that strongly contradicts monophyly is an important condition to consider monophyly of a taxon. Evidence for non-monophyly exists for instance if the clade corresponding to a taxon is supported with high bootstrap values in the analysis based on one gene, but the analysis of another gene yields equally high bootstrap support for another clade which places some of the taxon members elsewhere in the phylogeny. While in some instances such a situation can be convincingly explained by biological phenomena (e.g., introgression or different mutation rates across loci), typically such contrary evidence should serve as a cautionary flag against naming a taxon, because it highly increases the probability that other researchers with other data sets might recover a different phylogenetic topology and, thus, prefer a different classification. This subcriterion is related to subcriterion (v) (see below).

Subcriterion (iv): Dense taxon sampling. Completeness of taxon sampling is known to be an important factor influencing the accurateness of phylogenetic inference (e.g., Wheeler 1992; Zwickl & Hillis 2002; but see e.g. Rosenberg & Kumar 2001; reviewed by Nabahn & Sarkar 2012). When proposing a new classification, the reliability and taxon coverage of the underlying phylogenetic hypothesis is of importance and, therefore, a dense

taxon sampling is preferable. Another important argument is that a patchy taxon sampling will lead to numerous species that cannot be reliably allocated to supraspecific taxa, reducing the value of a new classification. Thus, it needs to be carefully considered whether a new phylogenetic hypothesis with stronger clade support but much fewer terminal taxa than previous hypotheses should actually serve as basis for a change in classification. Whenever possible, all terminals considered in the previous phylogenetic hypothesis (tree) on which the currently accepted classification is based should also be included in the new phylogenetic hypothesis so that their relationships are actually tested. Also, it is preferable that representatives of all name-bearing supraspecific taxa (i.e., type species of genera and type genera of families) be included in the phylogeny, including types of higher taxa that are considered to be junior synonyms in the old or new classification scheme. The optimal scenario is one of full taxon coverage. However, given that only a small portion of species are suspected to be known for most higher taxa, increasing species sampling in phylogenetic analysis will constitute a major source of irremediable taxonomic instability in the future.

Subcriterion (v): Support by independent data sets. We are convinced that the support for a taxon is more stable when it comes from analysis of different independent sets of data. Again, we emphasize the spirit of practical applicability guiding our arguments and terminology. We are well aware that, in phylogenetics, a main assumption is that each character serves as an independent hypothesis of evolution (Kluge and Farris 1969; Felsenstein, 1973), and ensuring this assumption is met constitutes an important task, especially for morphological characters (e.g., Maglia *et al.* 2004). However, independence of characters can be challenged by various factors. While the different nucleotides in the DNA sequence of one gene are independent regarding their mutational history and, thus, suitable for phylogenetic inference, all of them are likely to share the same genealogical history. Any event of introgression, for example, has probably affected all of these nucleotide sites in a similar way, and the species tree inference will therefore be equally biased. Any set of characters—genetic as well as phenotypic—might have been influenced by the same selection pressure or neutral process during the evolutionary history of an organism. Even disparate phenotypic characters might be pleiotropically influenced by the same genes, and genes might be linked in their heritability to different degrees.

Hence there is no doubt that the degree of dependence and linkage of different characters and markers varies and can often be objectively assessed. For instance, in terms of shared genealogical history, nucleotides from two molecular markers on different chromosomes will be more independent than nucleotides from neighboring genes on the same chromosome, and these will be more independent than nucleotides on the same organellar genome that are inherited largely without recombination.

In our rationale, if a phylogenetic hypothesis is supported by analysis of various character sets with a low degree of dependence or linkage, it serves the Clade Stability TNC.

Cautionary words are necessary, again, to emphasize that we here do not plea for any special method of phylogenetic analysis. In phylogenetics, arguments for all-evidence approaches have been brought forward (Eernisse & Kluge 1993; reviewed in de Queiroz *et al.* 1995), and DNA sequences of different genes are typically concatenated or analyzed in concert using coalescent approaches (e.g., Liu *et al.* 2009; Degnan & Rosenberg 2009). On the other hand, the advent of phylogenomics has triggered arguments that adding more sequence data is not enough to produce more reliable trees (Phillippe *et al.* 2011). In contrast to these methodological discussions, our claim for separate analysis complementing combined approaches of each unlinked genetic marker, or of different sets of morphological data, comes from the practical perspective. We argue for the importance of "repeatability of clades" (Chen *et al.* 2003) in analyses of data sets that are as independent as possible and maybe have been gathered by different methods, based on different materials, and by different researchers. In our view, this is important to predict the probability of future studies using different data sets coming up with deviant phylogenetic hypotheses. This argument includes even the very trivial point that analytical flaws and laboratory artifacts such as confusion or mislabeling of samples and of sequences, inclusion of pseudogenes or paralogues, or alignment artifacts, have a higher probability to be detected by such separate analyses. This point has been made particularly clear in a recent review of phylogenomic methods (Phillippe *et al.* 2011) that emphasized the comparison of single-gene trees to the tree obtained by concatenated data, as a means to detect errors in alignments due to contamination or paralogy. The simple consequence is, the more a clade is repeatable, the more should it be preferred over a less repeatable clade for naming it as a Linnaean taxon.

Subcriterion (vi): Support by independent analytical methods. With a very similar rationale as in the previous subcriterion, we suggest that clade stability increases if different methods of phylogenetic inference are

concordant in supporting it. Even more than in the use of different sets of data, it is highly disputed which the most appropriate phylogenetic analysis method is. Discussions have revolved especially around the use of parsimony-based approaches vs. likelihood-based (including Bayesian Inference) approaches (e.g., reviews by Steel & Penny 2000; Sober 2004). Independent from our own preferences and opinions on this matter, we suggest to preferably name clades as taxa for which support is consensual across methods, ideally reflected by at least one likelihood-based and one parsimony-based analysis in cases of data sets where these two approaches can reasonably be applied. We are aware that different data sets can require different methods, and that, for instance, not all methods can satisfyingly accommodate morphological characters which are crucial for paleontologists. If a clear phylogenetic signal of unambiguous synapomorphies is present in the data set, it is probable that all methods will infer the same tree. However, rather than venturing into such a methodological discussion, we formulate also this subcriterion from our practical perspective. If phylogenies are not consensual among methods, then researchers will tend to disagree over the preferred phylogenetic topology and propose different classification schemes, not serving stability. First attempts have been made to develop computer programs searching for phylogenies using more than one criterion at once and selecting trees on which, for instance, maximum parsimony and maximum likelihood converge (Cancino & Delbem 2010).

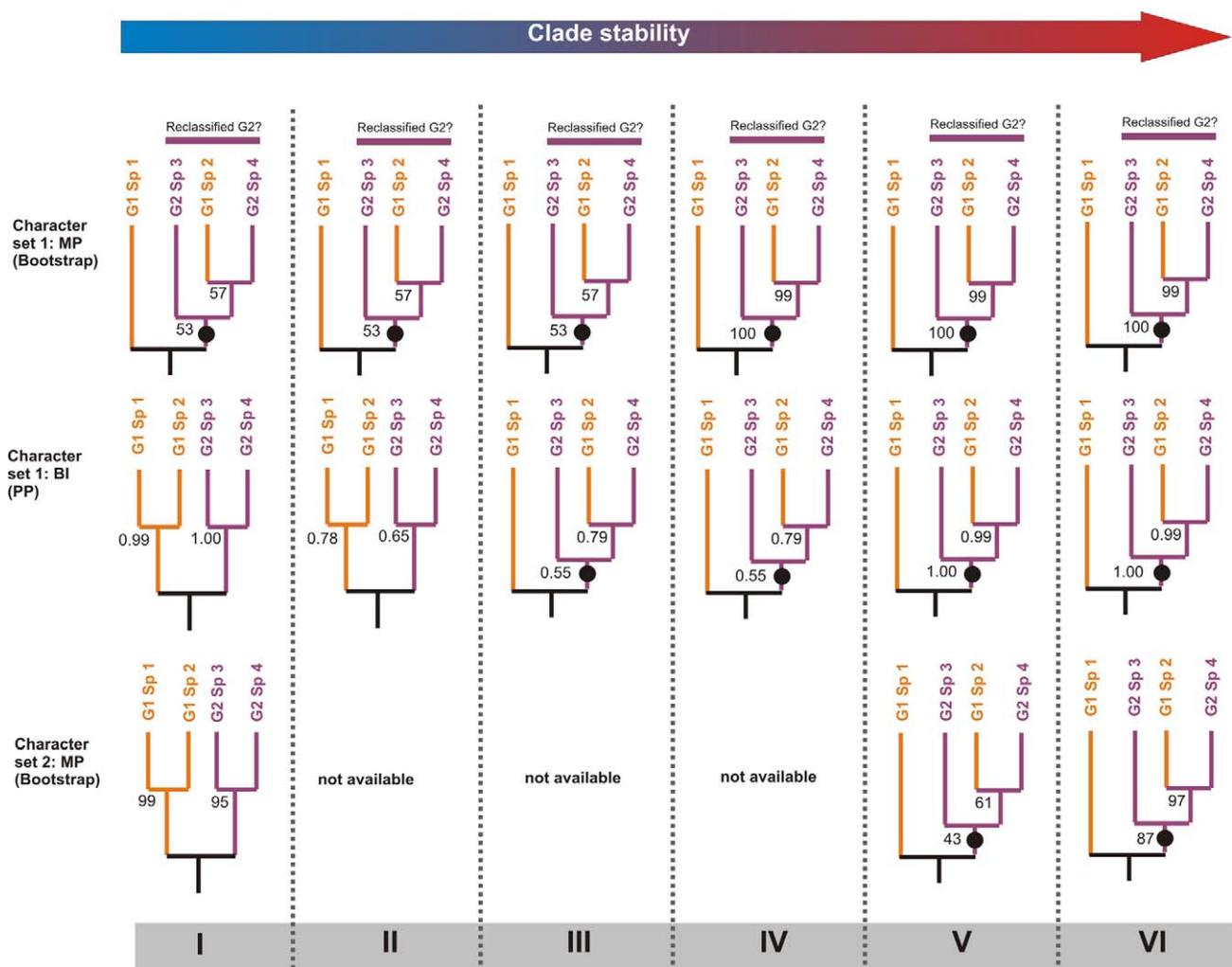


FIGURE 4. Non-exhaustive series of examples of the outcome of tests of monophyly of a certain taxon. The upper row indicates the main analyses that indicate paraphyly of genus 2 (G2), based on the Maximum Parsimony optimality criterion and non-parametric bootstrapping. Clade stability for a reclassified genus 2 (marked with a black circle, including species 2, 3, and 4), rises with increasing clade support in the main analysis (upper series of trees). Clade stability for this reclassified taxon furthermore depends on the congruence with a second analysis method (here as example, Bayesian inference, middle series of trees) and with a second, largely independent set of characters (lower series of trees). Note that the trees do not represent different reanalyses of the same data; each set of trees (I–VI) is just an example of which kind of evidence a researcher could face when deciding on reclassifying genera 1 and 2.

Subcriterion (vii): Support by high-quality data sets. While the methods of choice for phylogenetic inference (e.g., likelihood vs. parsimony) is subject of ongoing debate, the quality of analyses and underlying data can also be scrutinized using a number of objective criteria. Indicators suggesting that a molecular phylogeny might be unreliable include contamination problems and data from misidentified samples (e.g., Phillippe *et al.* 2011; in herpetology, see discussion by Blotto *et al.* 2012 of some data used by Pyron & Wiens 2009), low quality sequence reads, character matrices with large amounts of missing data, or failure to follow the best practice as recommended for a specific analytical method. Furthermore, also phylogenies based on unvouchered samples, with vouchers in private (non accessible) collections, and with doubtful assignment of samples to species should be used only with care to develop proposals of new classifications. Hence, clade stability might be deemed higher when a clade is supported by high quality data not suffering from the restrictions mentioned.

In some cases it could make sense to consider stability not only of the focal taxa, but of the overall emerging classification. Orthia *et al.* (2005) suggested avoiding naming taxa—even if they are robustly monophyletic—within trees that are not well resolved in cases where this leaves a paraphyletic residual of species that cannot be grouped into well-supported taxa at the same level. Strictly following this guideline could severely impede taxonomic progress because phylogenetic trees that are fully resolved with robust support for all clades are rare. However, taking into account stability of the overall phylogenetic hypothesis can serve as a further argument when discussing and applying the Clade Stability TNC in alternative classification schemes and justifying classification proposals on a case-by-case basis.

Phenotypic diagnosability

Phylogenetic classifications are word summaries of our best estimate of phylogeny. As summaries, classifications only highlight those relationships that are deemed more important or are more obvious. Historically, classifications have tried to highlight the most important body plan changes that took place during the evolution of a group. Patterns were sometimes so evident that still today many groups recognized by taxonomists have their counterpart among common names (ducks for Anatidae, frogs for Anura). Formalizing this rationale, we argue that ranked taxa, as communication tools, should maximize the information they carry especially on the phenotype of the contained species. Given that ranked taxa serve as communication tools among biologists, as well as between biologists and society, it is desirable that the content of a taxon can be easily grasped phenotypically also by non-taxonomists, such as in ducks and frogs used as examples above, although it is obvious that very often this is not possible.

Field biologists and ecologists work on species inventories, and when they cannot identify an organism to species they attempt to identify it at least to genus or to family levels. When taxonomists revise a species or describe a new one, they first need to assign their target species to a genus or to another higher taxon. Subsequently, they provide a comparison and diagnosis to distinguish the target species from all other species in that higher taxon. To compile a useful diagnosis, the inclusion of phenotypic characters is essential in most groups of organisms, and this conveys the importance of having phenotypically well-defined higher taxa. Linnaeus already considered a genus to be the smallest "kind" or "sort" recognizable without much expert study, a natural group recognizable by some definite attribute (Cain 1956). Hence, a careful analysis of the phenotypic characters and a good choice of characters used for diagnosis of any Linnaean taxon are essential, although this should by no means lead to classifications decoupled from the results of phylogenetic analyses (Franz 2005).

We therefore propose the Phenotypic Diagnosability TNC as a criterion for choosing clades to which Linnaean ranks and thus taxon names should preferentially be assigned. We do not restrict this criterion to morphology, but rather follow Dawkins' concept of the extended phenotype (Dawkins 1982) to include, for instance, conspicuous behavioral characters. The suitability of characters to conform to this TNC increases the more they are discrete, conspicuous, and readily observable in live and in preserved specimens of different sexes and life-history stages. Besides, it might be argued that characters that are immediately obvious and do not require special conditions or skills to be scored are preferable. This especially concerns taxa that are prominent and of high public interest. Efficiently and unambiguously communicating about such taxa is important beyond specialists. Defining a genus or family by a substitution in position 234 of a nucleotide alignment does not serve this purpose, but a clear, externally and where possible macroscopically visible character does (see Brower 2010 for criticisms regarding an

example at the species level). A character such as the presence or absence of webbing in a frog is preferable over the presence of an often faintly recognizable outer metatarsal tubercle, but the latter is preferable over any character in internal anatomy that requires dissection of the specimen to be assessed. If differences are only on the molecular level, using less prominent ranks such as subgenera might be a better choice to flag discontinuities. Lumping can be better than splitting to reach the goal of well diagnosable taxa at prominent ranks such as genus or family. However, we also acknowledge that groups of organisms exist where phenotypic differences are extremely subtle or only visible by detailed anatomical study, and therefore of limited value for field surveys or for perception of a taxon by non-specialists (e.g., many soil nematodes). In such cases, defining taxa on the basis of molecular synapomorphies is warranted and secondary TNCs (see below) might increase in importance.

It is rarely realized that diagnoses of taxa as used in the taxonomic practice fall into different categories that also differ in their utility for the end-user of the respective classification. The favored situation is that of a taxon of absolute diagnosability. In this case, a combination of character states, whether apomorphic or plesiomorphic, is shared by all species included in the taxon, and this combination is not found in any other species (Fig. 5). Ideally, one or several of these character states are unique synapomorphies not shared by any other organism. In general it is preferential that as many of the diagnostic character states as possible are synapomorphies, even if not unique (i.e., states might be fully diagnostic in their combination but each of them might have convergently evolved in other taxa).

In contrast to this situation, taxa might only be relatively diagnosable from their closest relatives (sister groups). For instance, all species in one species-rich taxon might be diagnosable from all species in its sister taxon by one synapomorphic character state, but the same character state also occurs in a few species of a third, remotely related taxon. Such situations are not rare at all. For instance, Drewes (1984) considered the reed frog family Hyperoliidae (including the genus *Leptopelis*) as monophyletic on the basis of their unique unfused carpalia and tarsalia, which he did not observe in any other ranoid frogs. However, it is now well established that *Leptopelis* is nested within the Arthroleptidae (e.g., Frost *et al.* 2006; Roelants *et al.* 2007; Blackburn 2008). The character state of unfused carpals and tarsals can probably still be used for a relative diagnosis of *Leptopelis* from its sister taxon, but alone does not serve any more for an absolute diagnosis, neither of *Leptopelis* nor of the Hyperoliidae. Such a setting of relative diagnosability is still superior to a total absence of diagnosability, but it will often need biogeographical evidence or other kind of data (e.g. molecular) for a correct placement of species. Clearly, the favored situation, especially for prominent ranks such as genus and family, is that of an absolute diagnosability.

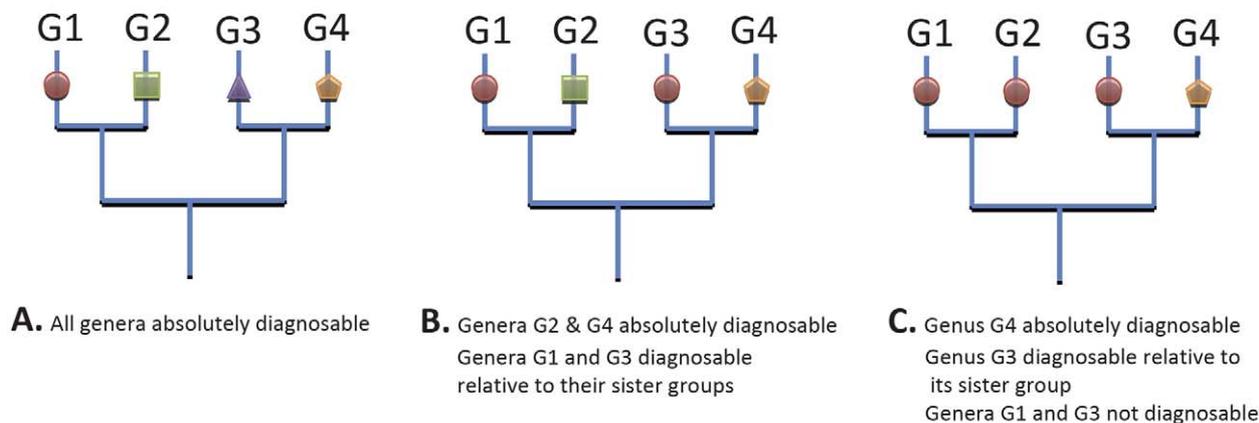


FIGURE 5. Examples for various kinds of diagnosability of a taxon. G stands for genus, symbols and colors for particular character states in one or several characters used for diagnosis.

Secondary TNCs: time banding, biogeography, adaptive zone, and hybrid viability

Time banding

It is appealing to consider evolutionary age as a criterion to determine the absolute rank of taxa to be named, and to

apply this criterion to homogenize taxonomies. Hennig (1966) analyzed the pros and cons of this criterion and supported it. He proposed that clades that originated during the Precambrian should be considered as phyla, Cambrian-Devonian clades as classes, Carboniferous clades as orders, Triassic-Early Cretaceous clades as families, and Miocene clades as genera. Because his approach was purely based on reference on the fossil record, which is scarce or nonexistent for most taxa, it has long been a practical impossibility to use evolutionary age as a uniform criterion in classifications. The advent of molecular techniques that allows not only to reconstruct phylogenies but also to estimate divergence times (Hedges *et al.* 2006; Hedges & Kumar 2009), has led to a renaissance of this part of Hennigian theory. In particular, Avise and co-workers have emphasized the large inconsistencies that exist across the classification of organisms in the absolute age of taxa of equal rank (Avise & Johns 1999; Avise & Mitchell 2007; Avise & Liu 2011). These authors suggest temporal banding (assigning the same rank to taxa of the same geological age) and time-clipping (using codes for each taxon to denote the geological episode when it originated). Information on clade age has been used in many classifications, also in herpetology, but rarely as an exclusive and compulsory criterion.

On the other hand, a multitude of examples exists across the tree of life, including amphibians and reptiles, where taxa are in the same ranked category but have radically different ages (e.g., Fig. 6). Rapid radiations or stasis occur depending on the intrinsic nature of groups and the particular circumstances (ecological, biogeographical, etc.) under which they evolved. In a classification, in our opinion, reflecting this variation is more informative than absolute age. Hence, attempting to standardize rank by age might feed some biological information into the Linnaean system, but at expense of other kinds of information and of the main purpose of this system: to facilitate communication.

Furthermore, inferring clade ages is a science of constantly evolving methodology, both regarding the algorithms to infer time-trees and the underlying fossil constraints (Bromham & Penny 2003; Kumar 2005). Although in some well-studied groups such as vertebrates a certain consensus about clade ages appears to emerge, e.g., in mammals and amphibians (Hedges & Kumar 2009), in most other groups of organisms the application of molecular clocks is still in its infancy. Depending on calibrations, algorithms, and sampling, drastically different estimates of clade ages can be obtained (Bromham & Penny 2003). We support Zachos' (2011) opinion that time banding and time clipping as an obligatory procedure would be deleterious in taxonomic practice although we reject his conclusion to abandon the Linnaean ranks altogether. Within some well studied groups, and if alternative classifications of equal clade stability and phenotypic diagnosability exist, it might be useful to use a Time banding TNC as additional cue to select among these alternatives, in order to have taxa of the same rank characterized by a roughly similar evolutionary age. For instance, Talavera *et al.* (2012) propose what they call a taxonomy-friendly temporal scheme where age intervals rather than fixed age limits are applied, in accordance with the particularities of each group and with the goal to preserve as much as possible traditionally defined taxa and thus taxonomic stability.

Biogeography

Biogeographical arguments might be brought forward to decide on assigning certain taxa to ranked categories. Linnaean ranks might be preferentially applied to taxa restricted to certain continents, biogeographic realms, biogeographic regions, or islands. For instance, although biogeography was not explicitly invoked, of various alternatives to split the previously cosmopolitan lizard genus *Mabuya*, the scheme initially chosen (Mausfeld *et al.* 2002) applied one genus name to each continental radiation (i.e., Africa, South America, Asia, plus one more genus from Cape Verde). Other examples have been mentioned where improved geographic unity was used as an argument to redefine genera (Stuessy 1990). Such a classification facilitates species identification and taxonomic work because only taxa from within a geographically well-defined geographical region need to be compared. On the other hand, in some cases, it might be seen as useful to name a clade as taxon that spans over two or more geographic units, with the aim to emphasize its dispersal potential or biogeographic history. We feel, however, that there will only be few occasions in which this TNC in any of its variants will be usable as main argument to favor one classification alternative over another.

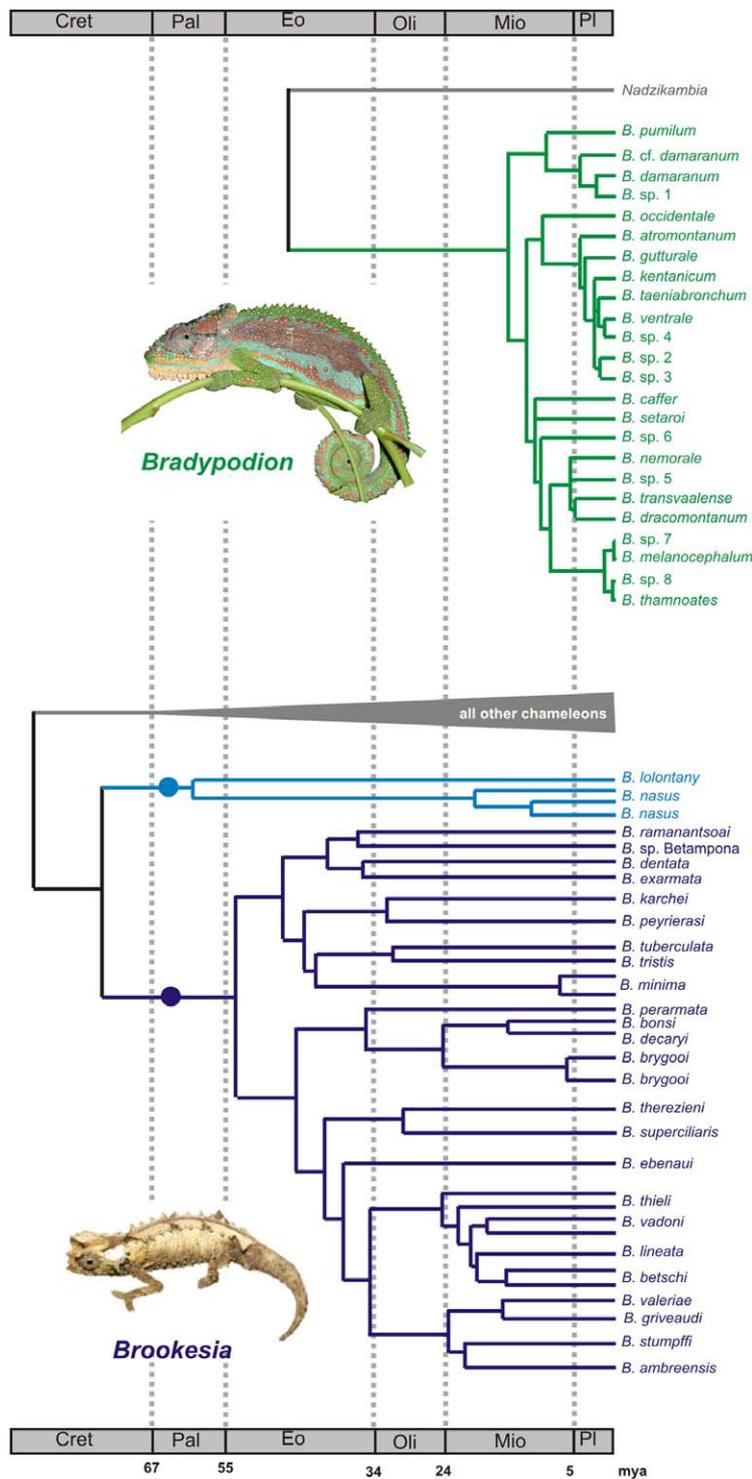


FIGURE 6. Pros and cons of the time banding criterion as exemplified in two related reptile genera with radically different patterns of temporal diversification. Both the African *Bradypodion* and the Malagasy *Brookesia* are well diagnosable and clearly monophyletic units. While *Bradypodion* diversified in the Miocene-Pliocene, *Brookesia* dates back to the Cretaceous. Several morphologically extremely similar sister species of miniaturized *Brookesia*, such as *B. tuberculata* and *B. tristis* have an age almost doubling that of the entire genus *Bradypodion*. Attempts of adapting classification on the basis of age would mean an extreme oversplitting of *Brookesia* with numerous non-diagnosable genera, or merging *Bradypodion* into a larger unit of unstable monophyly and low diagnosability. Within *Brookesia*, arguments might in the future be brought forward that the *B. nasus* group (light blue) should be recognized as a distinct genus and the two sister clades would obtain the rank of genus (light and dark blue dots). This decision would bring an even more stable monophyly and better diagnosability. However, such a splitting would still leave units of much older age than *Bradypodion*. Abbreviations: Cret = Cretaceous; Pal = Paleocene; Eo = Eocene; Oli = Oligocene; Mio = Miocene; PI = Pliocene + Pleistocene + Quaternary. Timetrees redrawn after Tolley *et al.* (2006) and Townsend *et al.* (2009, 2011).

Adaptive zone

The adaptive zone criterion dictates that a clade occupying a distinctive adaptive zone should be assigned to a ranked category and thus named as Linnaean taxon. Simpson (1944) defined an adaptive zone as a set of ecological niches that may be occupied by a group of species exploiting the same resources in a similar manner. Inside such an environmental space, species can evolve phenotypically and speciate, but those species evolving too close to the zone's margins will have selective disadvantages and get extinct. Mayr (1950), discussing hominid evolution, suggested that species in a genus should "occupy an ecological situation which is different from that occupied by the species of another genus, or, ... they occupy a different adaptive plateau". With reference to the genus *Homo*, Wood and Collard (1999) modified this definition so that paraphyletic taxa are not allowed (i.e. a subordinate clade occupying an adaptive zone cannot have the same or higher Linnaean rank that a superordinate clade containing it), and the adaptive zone occupied by a genus does not need to be unique (not differing from all other genera) (see also Cela-Conde & Ayala 2003). Maggenti (1989) applied this concept to genera and families of nematodes. In herpetology, a few authors have made reference to the adaptive zone as criterion to delimit genera (e.g., Heyer 1969; Martin & Watson 1971; Vences *et al.* 2001), and especially Inger (1958) has elaborated on the subject. For instance, the different larval and adult adaptations of Asian toads (e.g., genera *Peltophryne*, *Pedostibes*, *Ansonia*, and others) were mentioned as examples indicating different adaptive zones of these taxa. Their classification in different genera was therefore deemed to be useful also to ecologists.

A main problem with this criterion is the difficulty in defining what an adaptive zone actually is, and objectively establishing its boundaries. Furthermore, we expect this criterion will be of limited applicability because, in most cases, invasion of a new adaptive zone will be linked to the evolution of certain phenotypic adaptations (sometimes key innovations) that lead to an increased phenotypic diagnosability of a taxon—for instance in tree frogs that occupy an arboreal adaptive zone and are characterized by enlarged discs of fingers and toes, broad heads, large eyes, and a number of osteological characters. Hence, the Adaptive Zone TNC will typically be just a reinforcement of the Phenotypic Diagnosability TNC. In some cases, however, we might observe that sister clades with phenotypically similar or polymorphic traits have radiated in two different adaptive zones (like arid vs. humid biomes). In such cases, we suggest the Adaptive Zone TNC can be invoked as additional support for assigning a Linnaean rank and taxon names to those two clades. As we have argued before, we consider the placement of all supraspecific Linnaean ranks as an arbitrary decision, and therefore suggest that the Adaptive Zone TNC should not be limited to the genus rank, but might in some cases also be used as secondary criterion to assign other ranks.

Hybrid viability

As mentioned previously, several researchers have argued that the rank of genus is characterized by universal biological properties that can be used to unambiguously identify which taxa deserve that rank (e.g., review by Anderson 1940). Defined in this way, the category genus would become an objective category based on a universal property or set of properties shared by its contained members. For example, genera would always correspond to those clades grouping species occupying a certain adaptive zone (see above), or to clades distinguished from others by a particularly large gap in morphological variation of their contained species. Others (e.g., Dubois 1981, 1987, 1988, 2004) went even further to defend that genera are the result of a biological process (geniation) that leads to the evolution of a particular level of biological organization that we call genus. Dubois suggested using the theoretical or practical ability of species to hybridize as an indicator for their belonging into the same genus. In practice, he proposed an asymmetrical rule to identify genera: successful hybridization demonstrates that two species belong into the same genus, but failure of hybridization does not demonstrate that two species belong to different genera. In an extension of this concept, he proposed that animals of radically different developmental pathways (such as larval vs. direct development in amphibians, or matrotrophy vs. lecithotrophy) will likely be unable to hybridize, and that such different developmental pathways should be used as a criterion for genus delimitation except if hybridization among them has been positively demonstrated (Dubois 2004).

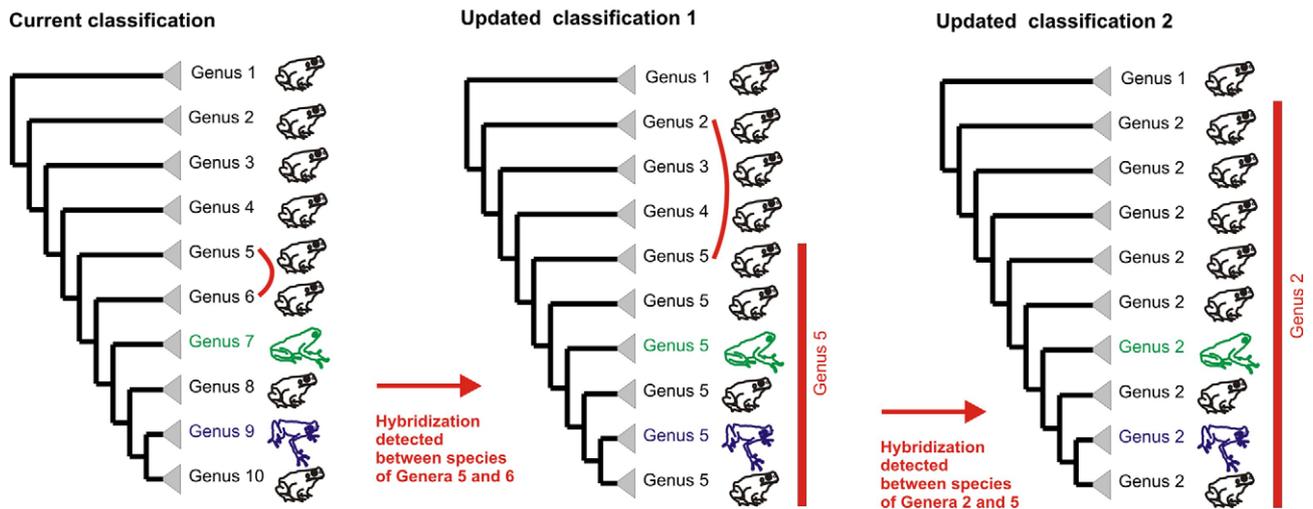


FIGURE 7. Example of how a strict application of the hybrid viability criterion to define genera threatens stability. The trees are a simplification of the phylogeny of the family Bufonidae (Van Bocxlaer *et al.* 2009, 2010). "Generalized" large toads are arranged paraphyletically along a main branch of Eurasian and African taxa, together with several genera of distinct morphological, ecological and life history adaptations that have traditionally been considered as distinct genera (symbolized by blue and green color). Following a phylogenetic classification, also all other separate clades are to be considered as genera. As soon as hybridization among members of two of these phenotypic groups is detected (such as the real case, *Bufo bufo* and *Pseudepidalea viridis*) these two genera (as well as all genera in their respective sister clades) should be included in a single genus, including those morphologically highly divergent taxa that have typically been considered separate genera in bufonids (e.g., *Ansonia* and *Pedostibes*). However, as soon as hybridization is later on demonstrated between one member of this newly defined genus and a more basal one, generic allocation of all included taxa again needs to be revisited. Note that many of these genera are species-rich, and evidence for (captive or natural) hybridization will only occasionally be found, leading to a long-term instability of the generic arrangement.

As we have made clear above, we disagree with concepts that consider supraspecific ranks in the Linnean hierarchy as biologically meaningful, and thus we refute any universal and mandatory criterion to assign ranks. Furthermore, we see both theoretical and practical limitations to the hybrid viability criterion. First, hybridization between organisms of species of different genera is an indication that their reproductive traits remain in a plesiomorphic condition. In other words, they have not evolved reproductive incompatibility. Reproductive incompatibility might not arise among all species within a genus or across genera if selective or neutral forces were not at work on those particular traits, as in cases of allopatric speciation. Second, using hybrid viability as a strict criterion will perpetuate instability because it cannot be ascertained at once for all combinations of species and new results will therefore be continuously be reported over time (Fig. 7). It also would require substantial changes already in the established taxonomy of many groups of organisms. For instance in turtles, numerous hybrids among genera are known (Stuart and Parham 2007; Fritz and Havaš 2007), and in birds hybridization in numerous cases affects species of highly divergent morphology considered to belong even into different families (thoroughly reviewed by Mayr, 1942; see also McCarthy 2006). Hybridization has been proven among taxa as phylogenetically deviant as guineafowl, family Numididae (sister to a large clade containing most other Galliformes; Hackett *et al.* 2008, Kimball & Brown 2008) and domestic fowl, family Phasianidae (Owen 1941), which suggest that many reproductive traits have remained in a plesiomorphic condition for those groups. A strict application of the hybridization criterion as defining genera would mean, in these birds, to merge almost 50 genera of partly strongly deviant morphology into a single one, with all the taxonomic confusion and disagreement that this would convey. In short, we consider that the Hybrid viability TNC has serious theoretical and practical limitations and suggest limiting its use to cases in well-known groups when the primary TNCs do not clearly favor one among several alternative classifications.

Accessory TNCs: keeping manageable units, taking special care with prominent taxa and prominent ranks, avoiding unnecessary nomenclatural actions, and considering consensus

Manageability

There is little doubt that the number of undescribed species of eukaryotes is probably at least an order of magnitude higher than the already described species (Mora *et al.* 2011); as a consequence, it is likely that most existing higher taxa will lose their current dimension and manageability during the continuous addition of new species to the inventory of life. Mayr (1942) already argued that large genera are very inconvenient units, and that desirably genera should contain only few species. Clearly, this is an argument that especially refers to genera, as these are the units typically used for taxonomic diagnoses and identification keys. Nevertheless, it might to a lesser degree also sometimes apply to higher taxa (e.g., families) containing too many lower taxa (e.g., genera, species). Such cases can hinder further research simply because the large number of lower taxa makes the whole group difficult to manage for taxonomic purposes and taxonomic revisions (Grant *et al.* 2006). We dub this argument the Manageability TNC.

How many species make a particular higher taxon, say a genus, manageable? There certainly is no universal answer to this question, and by no means should any threshold of minimum and maximum size of any category be defined. Supraspecific classification has the main function to packaging the wealth of species diversity into portions sufficiently digestible by the human brain to serve for communication. Stevens (1997a,b) suggested that classifications function as memorization devices, and recommended that systematists can use gaps that exist in nature (i.e., clades of sufficient phenotypic divergence to other clades) to form taxa of convenient size. Miller (1956) assessed that the human mind on average has the capacity to operate simultaneously with seven (plus/minus 2) items—e.g., words, concepts, or sounds. In general, the mind can effectively remember large amounts of information if it is committed to memory in chunks of five or fewer units (references in Stevens 1997a,b). In many respects, this appears to be reflected in historical and current biological classifications. In birds, a group that has been very finely split early on, the average number of species per genus was estimated between 3–5 by Mayr (1946). In the extant herpetofauna, according to three databases as accessed in July 2012 (Frost 2011; AmphibiaWeb 2012; Uetz 2012), the average numbers are around 13 for amphibians and 8.5 per reptiles (see Table 3), although variation is considerable (the frog genus *Pristimantis* contains 449 species; AmphibiaWeb 2012). Scotland and Sanderson (2004) suggest that the deviance of species per genus values in real data sets from that of models is due to a preference of taxonomists for genera being neither too small nor too large. Humphreys and Linder (2009) observed a recent (1998–2007) trend of recognizing larger genera, which they attributed to a return of broad-scale studies rather than to incorporation of molecular data.

It is obviously impractical to have named taxa such as plant genera with up to 3000 species (Frodin 2004; Horn *et al.* 2012) or the frog genus *Eleutherodactylus*, that before being partitioned by Hedges *et al.* (2008) contained over 700 species, values even higher than the ca. 500 typically observed for folk generics in ethnobiological classifications (Berlin 1992 as quoted by Stevens 1997a). As stated by Mayr (1982: p. 241), the function of a classification to serve as an index to an information-retrieval system imposes constraints on the size of the taxa. Linnaeus himself considered that genera should not have over 100 species, and Frodin (2004) emphasized that their sheer size has made plant "megagenera" difficult, with only few of them having been taxonomically revised since the 19th century.

On the other extreme, monotypic taxa—i.e., genera with a single species, families with a single genus—can be thought of as lacking any information on relationships, biogeography, or phenotypic similarity. Several authors have claimed that monotypic classification units typically should be avoided (e.g., Farris, 1976; Wiley 1979) because they contribute to the proliferation of taxon names that identify no taxon. Although we agree with this point in general terms, we also feel that monotypic taxa do not pose an important limitation for Linnaean classifications, especially taking into account that the system has other more important incongruences that usually are accepted, such as the use of the same rank at different hierarchical levels of the phylogeny (Fig. 2). In fact there are cases in which monotypic taxa are appropriate in supraspecific categories. For example, in phylogenetically deeply divergent relict taxa of high morphological distinctness (and thus, high phenotypic diagnosability), such as in the enigmatic pignose frog *Nasikabatrachus syhadrensis*, or the Mexican Burrowing Toad (*Rhinophrynus dorsalis*) which are the sole representatives of their respective genera and families, with morphologically

completely different sister taxa. Fritz *et al.* (2011) argued that given the existence of a well-pronounced morphological gap separating a given species from its sister clade, only monotypic genera, or higher monotypic taxa, can indicate the extent of the morphological distinctiveness of the included unique species. We hesitate accepting this as a universal rule. But the invoked "large morphological gap" probably would also compromise phenotypic diagnosability of an inclusive taxon including the divergent species, and thus provide an argument for a monotypic higher taxon under the Phenotypic Diagnosability TNC.

TABLE 3. Species and genus counts of extant amphibians and reptiles according to three databases accessed in July 2012: AmphibiaWeb (AmphibiaWeb 2012), Amphibian Species of the World (ASW; Frost 2011), and Reptile Database (Uetz 2012). Note that *Anolis* has recently been split in various genera (Nicholson *et al.*, 2012).

	Amphibians (AmphibiaWeb)	Amphibians (ASW)	Non-avian reptiles (Reptile Database)
Species	6986	6760	9595
Genera	532	529	322
Average number of species per genus	13.1	12.8	8.5
Monospecific genera	128	123	322
Genera > 100 species	8	7	10
Top 3 most speciose genera	<i>Pristimantis</i> (449), <i>Rana</i> (226), <i>Eleutherodactylus</i> (187)	<i>Pristimantis</i> (439), <i>Litoria</i> (197), <i>Eleutherodactylus</i> (185)	<i>Anolis</i> (385), <i>Liolaemus</i> (226), <i>Cyrtodactylus</i> (151)

During discussions with colleagues, we have even been confronted with the radical view that the smaller a taxon is, the less prone it is for further splitting and taxonomic rearrangement. Over-splitting should thus in principle favor stability: once that each species is in its own monotypic genus, there will be no need for further genus-level name changes. However, such an extreme taxonomic inflation would of course reduce the whole essence of the Linnaean system to absurdity.

As a conclusion, there are situations when taxa containing either single or very high numbers of lower-ranked taxa do reflect a particular distribution of variation in nature and thus should be adopted as such in the Linnaean classification system. Monotypic taxa often indicate lineages in which much extinction has taken place and much of the original diversity has not yet been recovered from the fossil record. Over time, as more extant and fossil species are discovered and described, at least some monotypic taxa will lose their monotypic status (e.g., Erdmann *et al.* 1998; Nielson *et al.* 2001; Maciel 2009; Rohland *et al.* 2010; Pombal *et al.* 2012; Barata *et al.* 2012; Castroviejo-Fisher *et al.* 2012). On the other hand, clades that underwent successful and fast adaptive radiations, often with limited or homoplastic phenotypic divergence, are best reflected in classification by being considered as species-rich genera. Therefore, manageability needs to be associated to other criteria, especially phenotypic diagnosability. Species-rich taxa can be advantageous if they are phenotypically homogeneous so that we can readily associate them to a particular phenotype for communication purposes and newly discovered species can be allocated to them without problems (e.g., birds such as *Buteo* and *Falco*, or frogs such as *Leptodactylus* or *Hyperolius*). On the other hand, phenotypically diverse taxa such as the former species-rich frog genus *Eleutherodactylus* or the lizard genus *Anolis* become more manageable when partitioned into multiple genera (e.g. Hedges *et al.* 2008; Nicholson *et al.* 2012).

Hall of fame

If we accept that the main purpose of supraspecific ranked taxa is to facilitate communication by highlighting what we deem important levels in the hierarchy, then it becomes immediately obvious that some taxa as well as some ranks are more prominent than others. Taxa of large body size and commonly encountered in nature such as most vertebrates, those that have a direct impact on humans such as crops, livestock, pets pathogens, and pests, model organism in the life sciences, and taxa of conservation concern, will be more commonly than others the focal

subject of scientific articles, popular media, and of all other sorts of communication. Among supraspecific ranks, the rank of genus is used most often because the genus name is part of the binomial name of a species. Genera are therefore used in all species lists, such as inventories of the faunas and floras of countries, regions or nature reserves, red lists, conservation assessments, DNA sequence repositories such as GenBank, and many more. Besides the genus, also the other main Linnaean ranks—family, order, class, phylum—are more prominent than intermediate ranks such as tribe, subfamily, superfamily, suborder, and others.

We here propose a Hall of Fame TNC, which urges taxonomists to apply more caution, and consider even more carefully the need for economy of change, with increasing prominence of a taxon or rank. For instance, if only an incomplete phylogeny is available and data on phenotypic diagnosability are not complete, but still the need for reclassification is obvious, taxonomists might choose to use a more inclusive, clearly stable and diagnosable clade to be ranked as genus, rather than splitting it into various genera. Subgenera or species groups can then be used to refer to its subunits of partly uncertain monophyly or poor phenotypic diagnosability. This will allow specialists to add more phylogenetic and phenotypic data, to discuss which species is to be assigned to which subgenus, and to determine how these units can be phenotypically diagnosed—without any broader impact of these shifting classifications, because species lists, field guides and conservation assessments use the genus name rather than the subgenus or species group name. In addition, on a level that is even more subjective yet of great importance, usage of low-profile ranks such as subgenera allows taxonomists to follow their ambition to perpetuate their own name by gaining priority as first describer of a taxon in the light of novel yet incomplete phylogenetic findings, but without compromising the universal use of long-lived established genus names. Once sufficient data and consensus of specialists are achieved, and if deemed useful because of other TNCs, some or all of the subgenera can then be elevated to genus level. The same applies to families, where subfamilies may be recognized rather than creating new families. In a similar line of arguments, whenever very prominent taxa are concerned, changes in supraspecific classification (and especially at the genus level) should only be carried out on the basis of highly stable phylogenies and if clearly supported by one or several of the priority TNCs proposed herein.

An illustrative and somewhat extreme example is the genus *Drosophila*. The important model organism *Drosophila melanogaster* is not the type species of this genus and has been found to belong into a different clade than the type species *D. funebris* (O'Grady & Markow 2009). A proposal to fix *D. melanogaster* as type species of the genus *Drosophila* has recently been rejected (ICZN 2010). As a consequence, *Drosophila* in its currently prevailing usage is a non-monophyletic taxon. Under a phylogenetic classification, to maintain *Drosophila* as the genus for *D. melanogaster*, several other genera have to be sunk as its junior synonyms, and the genus will become a barely manageable unit of almost 2000 species. However, we argue that such a solution might in fact be preferable over a change in genus for the species epithet *melanogaster*. Clearly the inevitable consequence of such a change would be renaming this model species, e.g. as *Sophophora melanogaster* (by upgrading its subgenus *Sophophora* to genus). This would not only cause enormous confusion, but might even lead to the rejection of the principles of Linnaean nomenclature by part of the scientific community.

Nomenclatural stability

Supraspecific taxon names in the genus-group and the family-group are regulated by the Codes of Nomenclature, which means that a strict priority principle applies, and all taxa names at these levels are based on types (type species for genus-group taxa, type genera for family-group taxa). However, all taxonomists know that especially for historically described taxa, the status of types can be contentious. Controversy might surround the fixation of type species for genera. Or, such type species themselves might be based on type specimens (holotypes, syntypes) that are in poor state of preservation and thus undiagnosable, or simply lost. For instance, the recent controversy about the appropriate genus and species name for the Aldabra giant tortoise was spurred by disagreement over the identity and locality of a specimen in the Leiden museum that had been designated as lectotype of *Testudo dussumieri* (e.g., Frazier and Matyot 2010; Hoogmoed 2010). We think that there can be cases (see a fictitious example in Fig. 8) in which it can be advisable to choose, other things being equal, a classification that avoids resurrecting nomenclaturally contentious nomina, and rather keeping them as synonyms, thereby leaving them in what could be termed nomenclatural oblivion and following a Nomenclatural Stability TNC. Such an action would prevent subsequent nomenclatural discussions, which not only divert taxonomists from their primary task of

species description and classification, but also lead to a continued instability of the taxa concerned. In the spirit of the Hall of Fame TNC, avoiding the resurrection of an old, forgotten name would be especially important when dealing with a widespread and/or common species whose current name populates collections and literature. Although such a resurrection could be justified on historical grounds, it would have meager usefulness.

We also feel that there can be cases when it might be a justified choice of a taxonomist to simply leave the nomenclature of a group untouched, even if he or she is aware of inconsistencies, until a stable solution is available. This could for instance involve leaving a dubious name (*nomina dubia*) unmentioned and unlisted for a few years if such action then will lead to its justified status as *nomen oblitum*.

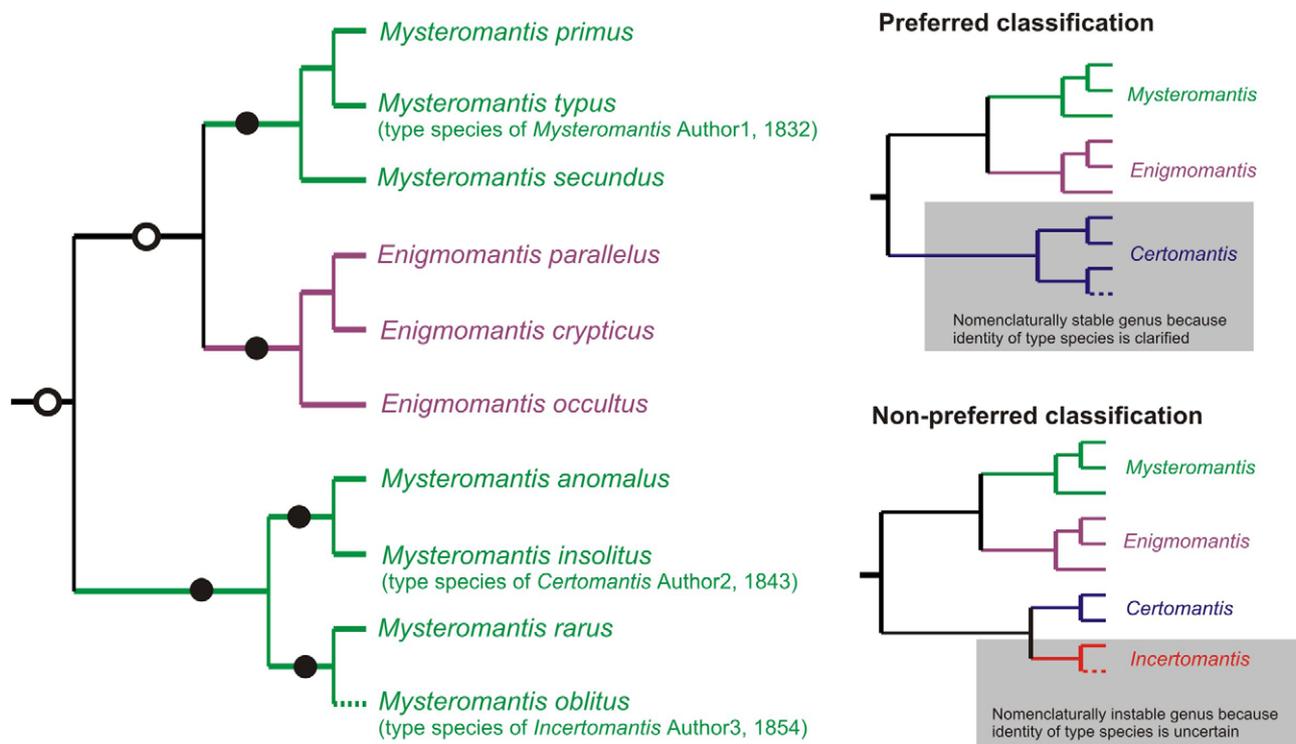


FIGURE 8. Fictitious example of a choice between two alternative classifications on the basis of the Nomenclatural Stability TNC. The large tree on the left represents the current classification and the result of a phylogenetic analysis. Black circles denote clades that are phenotypically clearly diagnosable and of highly stable monophyly; white circles are of highly stable monophyly but low phenotypic diagnosability. The clear paraphyly of *Mysteromantis* mandates a change in classification. Both alternative classifications (on the right) lead to phenotypically diagnosable and monophyletic units. However, the second alternative revalidates a genus *Incertomantis* of unstable nomenclatural status, e.g. because its type species is based on a lost holotype and incomplete description, or on a holotype in very poor state of preservation. It is therefore probable that *Incertomantis* will be completely redefined in the future, and therefore it is not advisable to choose a classification in which this taxon is resurrected.

Community consensus

The criteria here listed as accessory TNCs are not based on biological arguments—i.e., they are not guided by an attempt to charge Linnaean names with biological information. Instead, they are based on the principle to enhance the efficiency of these names in communication. As an ultimate consequence of this principle, it can be advisable to also consider expected acceptance or rejection of a possible classification scheme by the scientific community as an argument to choose among alternative classifications, provided that these classifications are equivalent in terms of the primary TNCs. Often, the expected rejection of a classification by the community will be grounded on good arguments, such as the *Drosophila* dilemma mentioned above—changing the genus name of *Drosophila melanogaster* would lead to considerable confusion in other fields of biology. Another aspect is within the names themselves: we support the claim of Dubois (2011) for taxon names to be "short, simple and euphonious". Such a prevalence of easy nomina can lead to a higher acceptance of a classification by the community, and thus should be favored.

In other cases, however, preference for one or the other classification might be much more subjective, and would extend beyond the "sozonyms" of Dubois (2011), i.e., "*genuinely well-known nomina, having had a documented widespread use in non-specialized publications, in various languages, from various authors in various countries, to designate taxa traditionally recognized in the general scientific and non-scientific literature and in society as a whole*".

We have stated above that subjectivity in classification can never be fully avoided, just reduced. There certainly will be cases where the prevailing opinion among leading specialists for a certain group of organisms rejects any change in classification, sometimes even in the light of evidence for non-monophyly of established taxa. In such cases, new and better classification schemes will anyway be proposed by scientists holding different views. It will then be the majority of end-users to eventually determine which of the competing classifications will prevail. However, far too much time and energy of taxonomists have in the past been wasted in unnecessary disputes over classifications. While adapting to the mainstream opinion is certainly not a desirable strategy in science, we feel that with every new classification proposed it is worth considering whether this proposal will lead to disputes—and thus instability—just because it might oppose an alternative classification that serves equally well the primary TNCs.

The bad and the ugly: naming of non-monophyletic units

A large proportion of the community of taxonomists was for long reluctant to accept the Hennigian proposal of classifications based only on monophyletic groups, and ghosts of this past remain strong today. Several clearly paraphyletic higher taxa are still commonly used in the scientific literature, especially the class Reptilia (in their traditional paraphyletic definition, including lepidosaurians, crocodiles, turtles and many extinct groups, but not birds or mammals), and the superclass Pisces (in their traditional paraphyletic definition, including Chondrichthyes, Actinopterygii, lungfish and coelacanths, but not tetrapods). A search in September 2011 in the Scopus database of scientific articles containing the term "Reptilia" in Title, Abstract or keywords, yielded 652 hits for 2010, and 5014 in the decade 2001–2010. The respective numbers for "Pisces" were 1485 and 11249. Both nomina are still used as major section headings on the websites of taxonomic journals as *Zootaxa* and *Zookeys* as of 2012. "Reptilia" is even part of the title of a specialized herpetological journal, "Amphibia-Reptilia". Attempts have been made to provide phylogenetic definitions of Reptilia, either as equivalent to Sauropsida (Modesto & Anderson 2004) and thereby including birds, or as equivalent to Lepidosauria and thus excluding crocodiles and turtles (<http://www.cnah.org/taxonomy.asp>, accessed September 2011), but these novel definitions have not been widely adopted.

How to deal with such taxa might depend on the robustness of the evidence by which their monophyly has been questioned or rejected. For many species, especially those known only as fossils, too few data are available. Fossil species are often anchored at deep positions of phylogenetic trees and have traditionally been considered as part of a "stem group". Their phylogenetic position is notoriously unstable, which in turn can lead to a highly unstable taxon content of higher-level taxa. Often such species can neither be robustly assigned to any of various alternative clades, nor can their belonging into one of these clades be clearly rejected. The result can be a tree suggesting paraphyly of certain taxa, but with overall low clade stability in the available phylogenetic trees, so that no useful classification scheme can be suggested for these taxa without violating the Clade Stability TNC. In such cases, we suggest as much as possible to use unranked taxa for including these problematic species, and we endorse the convention of Wiley (1979) and Wiley & Lieberman (2011) to use such taxon names in shutter quotes where monophyly is doubtful (see Table 2).

On the other hand, we feel that groups of robustly ascertained paraphyly should not be included as taxa in formal classifications and their use as Linnaean names should be abandoned. It might be argued that some of these paraphyletic groups share a certain amount of morphological, physiological and ecological similarity, and that referring to them in non-taxonomic studies can facilitate efficient communication. In such cases the use of common names might be a solution. Instead of "Reptilia" and "Pisces", reptiles and fishes can be used in a similar way as terms like marine mammals, hemimetabolous insects, or freshwater invertebrates, which can be often found in zoological literature without implying a Linnaean taxon or a clade.

TABLE 4. Taxon Naming Criteria as proposed herein. Note that taxon naming is the process of selecting one out of several alternative clades in a phylogenetic tree for naming it as a Linnaean supraspecific taxon (e.g., genus, family).

Priority Criteria		
TNC 1	Monophyly	The only strict TNC, although exceptions may occur in particular cases of hybrid speciation: All supraspecific taxa must be monophyletic units in the respective species tree (although they might be paraphyletic in any gene tree). Monophyly of a taxon should be assessed by an explicit phylogenetic analysis with adequately dense taxon sampling.
TNC 2	Clade Stability	Those clades selected for naming as taxa in a phylogeny should be supported by as many different independent data sets and analysis methods as possible, and not strongly contradicted by any of them (strong / significant contradictions require a biological explanation to be put forward)
TNC 3	Phenotypic Diagnosability	A taxon to which a Linnaean rank is assigned should be diagnosable and identifiable phenotypically. Preference should be on diagnostic characters that are unequivocally synapomorphic, externally visible in as many sexes and life-history stages of the organism as possible, and recognizable also by non-specialists; however this ideal certainly will not be achievable in many cases
Secondary Criteria		
TNC 4	Time Banding	If equally stable and diagnosable clades are alternatively available for naming as taxa, assign equal taxonomic ranks to clades of similar evolutionary age. Highly problematic if applied universally, but can be useful within well-delimited groups of taxa.
TNC 5	Biogeography	If equally stable and diagnosable clades are alternatively available for naming as taxa, choose clades that inhabit a geographically well-delimited region (continent, archipelago, mountain range, biogeographic region)—or conversely, name clades spanning over two such regions if the goal is to emphasize this distributional pattern and to facilitate communication about it. A very ambiguous criterion that we feel has little practical value in most cases.
TNC 6	Adaptive Zone	Especially applicable at the genus level: If equally stable and diagnosable clades are alternatively available for naming as taxa, assign genus rank to those whose members occupy a set of ecological niches, exploiting the same resources in a similar manner, different from their sister clade. Difficult to apply because adaptive zones are hard to define and usually there will be phenotypic features related to them that are easier to use as criteria.
TNC 7	Hybrid Viability	Especially applicable at the genus level and mostly in well-studied and oversplit groups of taxa: If equally stable and diagnosable clades are alternatively available for naming as taxa, choose the one that includes the most phylogenetically distant taxon known to produce viable hybrids with a nested taxon. Theoretically and practically difficult to apply
Accessory Criteria		
TNC 8	Manageability	If equally stable and diagnosable clades are alternatively available for naming as taxa, choose those that contain a number of taxa manageable for the human mind. Avoid oversplitting and deliberately creating monotypic taxa..
TNC 9	Hall of Fame	Take particular care with taxa that are of high public interest beyond taxonomy and where communication is thus particularly important. The more prominent a rank the more carefully should any change be applied. Intermediate ranks or unranked taxon names can be used preferentially when Clade Stability and Phenotypic Diagnosability TNCs are not sufficiently met.
TNC 10	Nomenclatural Stability	If equally stable and diagnosable clades are alternatively available for naming as taxa, avoid a classification in which unstable names (e.g., because of lost or poorly preserved types) are resurrected from synonymy.
TNC 11	Community Consensus	If equally stable and diagnosable clades are alternatively available for naming as taxa, choose a classification which is favored by the majority of taxonomists and, if applicable, other biologists, e.g. because it conserves the traditional content and definition of prominent taxa, or because of a prevalence of euphonious nomina.

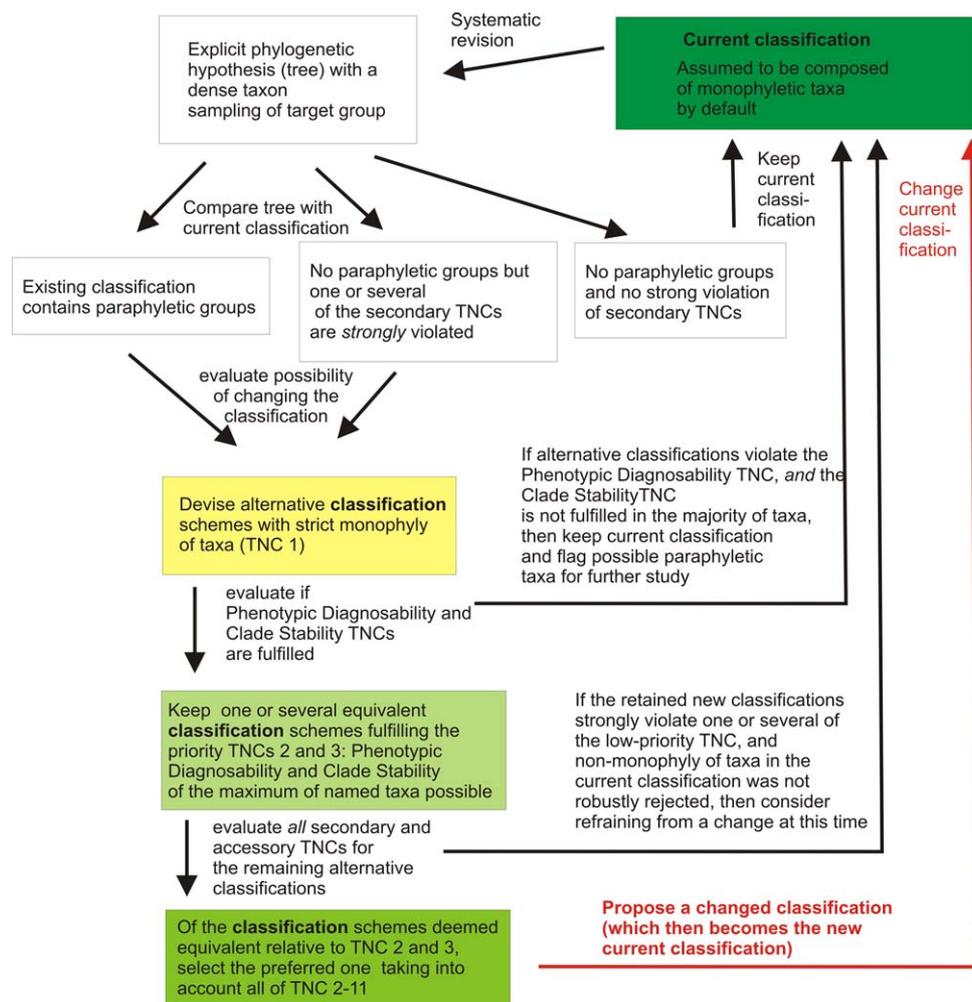


FIGURE 9. Suggested workflow for taxonomists working on supraspecific classification of organisms. We suggest that any revision starts with an explicit phylogenetic hypothesis (a tree), and if polyphyletic or paraphyletic groupings are suggested by the tree, a stepwise procedure should be followed to devise alternative classification schemes reflecting evolutionary history, and choosing among the alternative schemes on the basis of first priority Taxon Naming Criteria, and then the secondary and accessory TNCs.

A valuable claim for the need of better monitoring and possibly regulating higher-taxon names has been made by Dubois (2006a, 2011). We feel, however, that a rigorous application of priority principles to Linnaean ranks above the family would be a wrong track, only leading to additional instability. In taxonomy, the unregulated use of higher taxon names for several centuries, in itself, has led to an ample stock of names of uncertain or disputed authorship and content. Biologists simply have not kept track of the first use of higher taxon names, and this would be the source of an extended period of instability once that mandatory priority-based rules would be introduced. Dubois (2006a, 2011) suggests that sozonyms (names of prevailing usage) should be validated and stabilized even if they do not have priority. But this validation process itself will be a long-lasting, time-consuming, and somewhat futile endeavour. Instead, we suggest as a first step an initiative be started to database higher-level taxa, not within a strict priority-driven framework (e.g., Gérard *et al.* 2006), but rather with the purpose of creating a dictionary which after a starting phase could be automatically completed and updated from literature databases. Such an approach could follow the model of dictionaries for gene name normalization (e.g., Wermter *et al.* 2009). These alleviate the inconsistent use of gene names in different groups of organisms (e.g., Fundel & Zimmer 2006), an inconsistency which is almost unavoidable due to the rampant speed by which new genomes are being sequenced and cross-species homology assessments of genes are changing.

At a lower hierarchical level, a useful alternative to partition species diversity without applying Linnaean ranks are informal species groups. Sometimes these are even expressively named "phenetic species groups". For instance, among Malagasy treefrogs, the *Boophis majori* group, as defined by Glaw and Vences (2006), is known to

be probably polyphyletic, but due to external phenetic similarity its continued use serves to facilitate comparisons, diagnoses, and determination keys, until a comprehensive and well-supported phylogeny of the genus becomes available. In the same way, species groups have been historically broadly used within the taxonomically complex group Terrarana, where over 50 informal groups are currently recognized.

One Linnaean rank that consistently falls into the non-monophyletic bin is the subspecies. As stated before, in this paper we mainly focus on supraspecific ranks, and an exhaustive review of the subspecies discussion is therefore not our scope (see Haig & Winker 2010 for a summary of discussion regarding subspecies of birds). From the cladistic point of view, the unit of analysis is the species (under the concept of a species as individual; see Mayden 2002; Wiley & Lieberman 2011), and any taxa below the species rank are therefore irrelevant. According to the Evolutionary Species Concept (Simpson 1961; Wiley 1978), any rank below the species is by definition a non-independent evolutionary lineage, and typically will be characterized by having potential or actual regular gene flow with other subspecies. Advocates of the biological species concept typically see the subspecies as an objective taxonomic rank (e.g., Remsen 2010), but we rather agree with Fitzpatrick (2010) who elegantly formulated that trinomial epithets will inevitably be applied to a heterogeneous mix of evolutionary phenomena, thereby precluding genuine standardization of the concept (see also Wilson & Brown 1953). In this pragmatic approach, subspecies are seen purely as a useful convenience (Fitzpatrick 2010), which can be useful to avoid taxonomic inflation at the species level when the species status of allopatric lineages (e.g., on islands) is insufficiently supported (Hawtlitschek *et al.* 2012).

Discussion

Taxon Naming Criteria in practice: examples from amphibian and reptile taxonomy

Reptile and especially amphibian classification offers a rich source of examples for the application of taxon naming criteria as proposed here. In fact, many of our TNCs have been implicitly used in many classifications although they were not typically invoked in detail. In other cases however, we feel that taxonomic disputes and confusion could have been avoided if alternative classifications had been discussed in the light of our primary TNCs.

Monophyly

The central position of monophyly as mandatory requirement for a classification has been most commonly used to justify all of the recently published major classificatory changes in amphibians and reptiles. Usually it was on the basis of molecular data that the rampant paraphyly and polyphyly of traditional taxa became apparent. The splitting especially of the species-rich and supposedly widespread genera such as *Bufo*, *Hyla*, *Rana*, and *Eleutherodactylus* among amphibians, or *Coluber*, *Lacerta*, and *Mabuya* among reptiles, was long overdue and resulted in distinctly more monophyly-based taxonomies. Especially the studies based on rich taxon sampling were helpful, and successfully removed instances of non-monophyly in the traditional genus-level classifications of *Hyla* and other Hylidae (Faivovich *et al.* 2005), dendrobatid and aromobatid frogs (Grant *et al.* 2006), terraranan frogs (Hedges *et al.* 2008), and glassfrogs (Guayasamin *et al.* 2009). As discussed by Brown *et al.* (2011) for the dendrobatids of the former genus *Dendrobates*, these re-classifications reduced the number of species per genus, and because these smaller genera are composed of taxa that are more closely related they usually can be diagnosed more easily using non-molecular synapomorphies.

Similarly, many of the classificatory changes proposed by Frost *et al.* (2006) were badly needed and drastically reduced non-monophyly within groups such as the traditional family Leptodactylidae or the genera *Rana* and *Bufo* sensu lato. Much of the controversies surrounding this and other publications were caused by just a few premature changes, such as the erection by Frost *et al.* (2006) of the new genus *Epidalea* for *Bufo calamita* although this species was not even included in their phylogenetic tree (see Vences 2007). Further disputes arose due to the restriction of some studies to particular analytical methods, which hampered assessment of clade stability (see below). Furthermore, some proposals at the family level were controversially discussed, and we argue below that this was mainly caused by an insufficient consideration of the phenotypic diagnosability of the resulting families.

Problematic were also the conclusions of Ruiz-Carranza and Lynch (1991) and Cisneros-Heredia and McDiarmid (2007), who defined genera based on a combination of few traits, but no objective phylogenetic analysis. Subsequent molecular studies (Guayasamin *et al.* 2008, 2009) suggested homoplasy in the supposed synapomorphies and led to a further modification of the classification. This example illustrates the importance of basing classificatory changes as much as possible on an explicit phylogenetic analysis, in order to be able to assess monophyly and clade stability.

Phenotypic diagnosability

Phenotypic diagnosability has long been mediated by as an important prerequisite for Linnaean taxa in herpetology, although few authors have explicitly emphasized its importance. One example for a balanced discussion and combination of phenotypic diagnosability with various other taxon naming criteria is a recent proposal of a new genus-level classification for lacertid lizards (Arnold *et al.* 2007). This study uses and reports information about monophyly, evolutionary age, hybridization, and morphological distinctiveness, although not specifically focused on the ease of phenotypic diagnosability mediated by the reported morphological characters.

For the genus *Hydromantes*, which contains species of lungless salamanders in Europe and California, a one-genus classification has been preferred over a two-genera classification with a European and an American genus, mainly based on an implicit application of the Phenotypic Diagnosability TNC (e.g., unique structure of feeding apparatus in all species) (Jackman *et al.* 1997).

In other cases, discussions over alternative classification schemes could have benefitted from a more rigorous consideration of this TNC. In reptiles, phenotypic diagnosability has been poorly considered in proposals to partition the originally widespread genus *Mabuya* (Mausfeld *et al.* 2002; Hedges & Conn 2012), probably because these and other scincid lizard taxa are anyway notoriously difficult to diagnose. In amphibians, different views exist concerning whether New World direct-developing frogs are more appropriately classified in one family (as Brachycephalidae; Frost *et al.* 2006) or five families (as the unranked group Terrarana, with the families Brachycephalidae, Ceuthomantidae, Craugastoridae, Eleutherodactylidae, and Strabomantidae; Hedges *et al.* 2008; Heinicke *et al.* 2009), but it certainly is true that in the five-family classification an absolute diagnosis at family level is impossible. A somewhat similar situation was the placement of the morphologically unique Indian frog *Nasikabatrachus* together with its Seychellean sister group (genera *Sooglossus* and *Sechellophryne*) in the family Sooglossidae (Frost *et al.* 2006) rather than keeping both taxa in their own families Nasikabatrachidae and Sooglossidae (Biju & Bossuyt 2003) as in subsequent, revised classifications (Frost 2011).

Guayasamin *et al.* (2009) used phenotypic diagnosability to justify the recognition of seven glassfrog genera within the specious and morphologically diverse clade Cochranellini. An alternative classification could have recognized a single and monophyletic genus (*Cochranella*), with the clear downside that it would have been impossible to morphologically diagnose it from the other genera.

Hedges *et al.* (2008), in their taxonomic proposals for New World direct-developing frogs, and Hedges and Conn (2012) in their partitioning of Neotropical lizards of the former genus *Mabuya*, supported their proposed classifications by the need for Linnaean taxa of having a manageable size. In such species-rich groups the Manageability TNC certainly is of value, but these examples also demonstrate how conflict among different TNC is often unavoidable. In fact, several of the new taxa created in these studies are less phenotypically diagnosable than the original, more inclusive taxon. We hold that in such cases, where monophyly and clade stability are unequivocal in both alternatives, manageability should not be increased on the expense of phenotypic diagnosability.

Clade stability

Arguments corresponding to this TNC have been used by Guayasamin *et al.* (2009) to recognize the glassfrog genera *Sachatamia* and *Rulyrana* (supported by all datasets and inference criteria), instead of a single genus that was supported by only a subset of data (nuclear) and inference methods (Bayesian). Fritz *et al.* (2011) used a similar rationale to advocate the use of three distinct turtle genera, *Emys*, *Actinemys*, and *Emydoidea*. The

concerned species had previously been merged in a single, inclusive genus *Emys* (Spinks & Shaffer 2009), but the monophyly of such an inclusive *Emys* was contradicted by a subset of possible gene trees (Wiens *et al.* 2010) and the respective clade stability thus compromised.

A fully resolved phylogenetic tree with dense taxon sampling, and with clades maximally supported by all analysis methods and data sets, is an optimal basis for proposing a new classification yet typically far from reality. Especially when species-rich taxa are being split the dilemma is obvious—often some parts of a phylogenetic hypothesis are strongly supported and indicate paraphyly of the taxon while other parts of the tree are poorly resolved. Still, a new classification only makes sense if the great majority if not all of the species included in the historical taxon are re-distributed into new monophyletic taxa. This situation led researchers for decades to hesitate partitioning genera such as *Rana* and *Bufo* despite clear punctual evidence for their paraphyly (Frost *et al.* 2006). Naming less stable clades as taxa might be warranted in such cases, but one of the most criticized shortcomings of numerous recent studies is the restriction to single analysis methods and a lack of discussion of congruence among data partitions. For instance, only combined analysis of morphological and molecular data using maximum parsimony was used by Faivovich *et al.* (2005), Frost *et al.* (2006), and Grant *et al.* (2006), and only Maximum Likelihood bootstrapping of concatenated mitochondrial and nuclear DNA sequences was used by Pyron and Wiens (2011). This impeded assessing several subcriteria of our Clade Stability TNC because congruence neither among data partitions nor among analytical methods was reported.

The same applies to another study by Scott (2005) in which a partially new family-level classification of ranid frogs was proposed on the basis of a combined maximum parsimony analysis of morphological data and DNA sequences. Her analysis, besides being based on only short DNA sequences of few mitochondrial genes, clearly violated the Clade Stability TNC in various respects: This study (i) did not assess whether the morphological and molecular data sets would support similar topologies in separate analyses, (ii) only carried out a single (non-model based) analysis method, and (iii) did not consider that several of the clades named as taxa had very low support values (from a jackknife analysis) and would therefore likely be challenged by future analyses.

In the early 1990s, molecular phylogenetic work was still in its infancy, and Kluge (1991) reconstructed a global phylogeny of giant snakes based on morphological characters only. He recovered a sister-group relationship of the Malagasy giant snakes with *Boa constrictor* and reclassified them into the genus *Boa*, although the most parsimonious tree was only slightly shorter than alternative topologies. After 20 years of parallel use of different genus names for these taxa, it now seems clear from molecular data (Noonan and Chippindale 2006) that Malagasy giant snakes (*Sanzinia* and *Acrantophis*) are not at all closely related to *Boa*, and their status as separate genera is therefore widely accepted. A similar example from reptiles concerns the endemic terrestrial tortoises of Madagascar. These contain the small-sized *Pyxis arachnoides* and *P. planicauda*, the large-sized *Astrochelys radiata* and *A. yniphora*, and several extinct giant species. Based on maximum parsimony analysis of a multi-gene data set, Le *et al.* (2006) found *A. radiata* to be more closely related to *Pyxis* than to *A. yniphora*, and thus erected a new monotypic genus *Angonoka* for *A. yniphora*. However, these same authors had in fact recovered a monophyletic *Astrochelys* (with *radiata* and *yniphora*) in a separate Maximum Likelihood analysis. Their taxonomic decision was contested by Fritz and Bininda-Emonds (2007) who reanalyzed the data and found a strong support for a monophyletic *Astrochelys* in their ML and Bayesian analyses. Giant snakes and tortoises both are prominent flagship species for conservation, and changing their genus-level classification would have required particularly strong arguments following the Hall of Fame TNC. The available evidence, however, did not sufficiently comply with the primary requirement of the Clade Stability TNC, suggesting that a careful consideration of these TNCs could have avoided these controversies.

Time banding

This criterion has been regularly used in herpetological classifications, but rarely as the sole and predominant criterion, in accordance with the many problems that its strict application would imply. For instance, Arnold *et al.* (2007) used the age of clades of lacertid lizards (having originated in the Miocene) as one argument for assigning them to the genus category, but also considered morphological synapomorphies and other criteria.

Townsend *et al.* (2011) on the basis of an unexpected but robustly recovered finding from a new molecular phylogeny, found the Seychellean chameleon not related to the genus *Calumma* in which it had previously been

included, but to the ground chameleons of the genus *Rieppeleon*. Faced with the alternatives of including the species in the genus *Rieppeleon* or considering it as belonging to an own, monospecific genus (as *Archaius tigris*), the authors opted for the latter because the divergence between the two clades was similar to that between several other chameleon genera (our Time banding TNC) and because of the distinct morphology and ecology of *A. tigris* relative to *Rieppeleon* (thus a combination of the Diagnosability and Adaptive Zone TNCs). Following the priorities proposed herein, the most important of these criteria would have been diagnosability (the new monotypic genus would be carrying the information of a morphologically very distinct lineage). Strictly applying the Time Banding TNC to chameleons would be highly problematic because morphologically distinct radiations (genera) of these lizards have occurred in very different temporal settings (Fig. 7).

The application of this criterion to some families of salamanders highlights some of its limitations. Blackburn and Wake (2011) recognize Ambystomatidae and Dicamptodontidae for *Dicamptodon* and *Ambystoma* according to an estimate of 100 million years of divergence time. Nonetheless, applying the 100 my criterion to other groups of salamanders, and especially taking into account confidence intervals for divergence time estimates (Zhang & Wake 2009), would lead to major rearrangements and to the splitting into family-level taxa of well-established and diagnosable units. In the specific case of Dicamptodontidae and Ambystomatidae, possible biological and morphological differences among at least their extant representatives (Blackburn & Wake 2011) might be more informative than absolute clade age, and could lead to favoring a two-family solution under the Phenotypic Diagnosability TNC.

This same issue is particularly obvious in Bossuyt & Roelant's (2009) taxonomic interpretation of a global amphibian timetree. These authors propose, relying on time banding alone (i.e., on their opinion that "evolutionary time is an important parameter in conveying useful comparative information in biological classification"), the elevation of a whole set of taxa to family rank. In their timetree, each family-level taxon is represented by a single terminal branch, but some of these taxa contain fast radiations that likely happened soon after the origin of the respective taxon (e.g., Van der Meijden *et al.* 2007). We anticipate that inclusion, in the timetree, of more taxa in the Microhylinae (Microhylidae sensu Bossuyt & Roelants 2009), Gastrophryinae (Gastrophrynidae sensu Bossuyt & Roelants 2009) or Arthroleptidae would reveal additional nodes within the Late Cretaceous to Early Paleogene "time band" deemed indicative for family-level splits (Bossuyt & Roelants 2009), and thus require elevation of even more clades to family rank, thus leading to rampant inflation and instability of amphibian family-level classification.

Nomenclatural stability

One example of this criterion is provided by the classification of European newts in the family Salamandridae. These were long included in the genus *Triturus* until molecular data provided convincing evidence for paraphyly of this genus. Consequently, several former species of *Triturus* were included in the resurrected genera *Lissotriton*, *Mesotriton* and *Ommatotriton*. While the herpetological community started accepting this classification, several authors (e.g., Dubois & Raffaëli 2009; see summary of the complex nomenclatural situation in Schmidtler 2009) noticed that an earlier name was available for one of these newts: the genus *Ichthyosaura* had been historically erected to classify a newt larva that probably constituted the larva of the alpine newt. This species consequently changed from *Mesotriton alpestris* to *Ichthyosaura alpestris*. While correct under strict nomenclatural rules, this resurrection confers several problematic aspects: (i) The name *Ichthyosaura* is highly reminiscent of *Ichthyosaurus* and Ichthyosauria, and of the common name ichthyosaur which is often used in popular writing to refer to this group of extinct marine reptiles. Hence, outside of the taxonomical realm, this name may lead to confusion between these phylogenetically distant organisms. (ii) *Ichthyosaura* had not been used for many decades and would have qualified as a *nomen oblitum* and thus as an unavailable name relative to any other established name such as *Triturus*. This rule did not apply for the sole reason that *Mesotriton* had been resurrected shortly before and had been used as valid name for less than ten years—just a few additional years of usage of *Mesotriton* would have been sufficient to sink *Ichthyosaura* into oblivion. (iii) The use of *Ichthyosaura* for the alpine newt was not the intent of the original describer of the genus who was misled and assumed the larval stage to represent a species different from the adult. In the original description of "*Proteus tritonius*" which later would become the type species of *Ichthyosaura*, this species was even figured next to an adult of "*Triton alpestris*". (iv) Although some

figured morphological characters and the current species composition at the type locality indicate that probably *Ichthyosaura* refers to an alpine newt larva, alternatives (e.g., a fire salamander larva) cannot be fully excluded since no type is preserved. In this case, in the spirit of the Nomenclatural Stability TNC, it would have been more appropriate to leave the nomen *Ichthyosaura* unmentioned and thereby to salvage the classification of these prominent organisms, mentioned in innumerable field guides, species lists and legislations in Europe, from yet another change. This exemplifies the general principle that in supraspecific taxonomy, change does not always equal progress.

Conclusions

Under the premise that nothing in biology makes sense except in the light of evolution (Dobzhansky 1973), current consensus is that classifications must reflect the evolutionary history of organisms and thus consist of monophyletic units only. In the Linnaean system this means that classifications are summaries of phylogenetic trees in which particular clades are highlighted by naming them as taxa and thus assigning them to a ranked category. Therefore, we are confronted with the need to choose, among the many clades of a tree, those that are going to be named and formally ranked. This is not a simple task as the options are many and the criteria are diverse and controversial. However, it is important to keep in mind that the foremost purpose of any taxonomy is to provide a universal and stable system for communication. It is useful to choose classifications that convey additional information such as clade age or hybrid viability, although in our opinion this must not compromise clade stability and diagnosability of ranked taxa. We therefore strongly recommend that—besides the mandatory monophyly of taxa—taxonomists should take clade stability and phenotypic diagnosability into account as prime criteria to choose the clades to which they assign Linnaean ranks and taxon names.

Despite our recommendations and clear preferences for certain TNCs, it also is obvious that some plurality in the naming of clades as taxa, and in the criteria to be applied is crucial. Any classification system based on rigid concepts and mandatory criteria not allowing exceptions cannot account for all facets of the diversity of life. It is obvious that many taxonomists will disagree with the priority settings that we allot to the specific taxon naming criteria. We nevertheless hope that even those colleagues will find it useful to use some of our TNC definitions in their rationale. Such an informed discussion will help reducing subjectivity even if consensus on alternative classifications is not reachable in all cases.

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