The Hunting of the SNaRC: A Snarky Solution to the Species Problem

Brent D. Mishler* and John S. Wilkins†

We argue that the logical outcome of the cladistics revolution in biological systematics, and the move towards rankless phylogenetic classification of nested monophyletic groups as formalized in the PhyloCode, is to eliminate the species rank along with all the others and simply name clades. We propose that the lowest level of formally named clade be the SNaRC, the Smallest Named and Registered Clade. The SNaRC is an epistemic level in the classification, not an ontic one. Naming stops at that level because there is no currently acceptable evidence for clades within it, not because no smaller clades exist. Later, included clades may be named. They would then become the SNaRCs, while the original SNaRC would keep its original name. We argue that all theoretical tasks of biology, in evolution and ecology, as well as practical tasks such as conservation assessment, are better approached using this rankless phylogenetic approach.

Keywords

species • species concept • monophyly • phenomena • explanation • taxonomy

For the Snark's a peculiar creature, that won't be caught in a commonplace way.
–Lewis Carroll, "The Hunting of the Snark" (1876)

1 Introduction

Species are often thought to be the fundamental units of evolution, ecology, genetics, and/or systematics (Agapow, Bininda-Emonds, et al. 2004; Birky, Adams, et al. 2010; Blaxter, Mann, et al. 2005; Claridge, Dawah, et al. 1997; Green 2005; Hull 1975; Reydon 2005). However, species are empirically unstable objects, being revised regularly. Moreover, they are theoretically unstable as well; discussions over what counts as a species, and what criteria are to be used to delineate one from another, show no signs of abating (Hausdorf 2011; Naomi 2011; Staley 2013; Wilkins 2011). Some have suggested the other extreme: that species are no more fundamental than monophyletic taxa (that is, those having a single common ancestor) at any rank (Mishler 2010), and furthermore that the species rank should disappear as part of a general move to rankless taxonomy (Ereshefsky 1999; Mishler 1999; Pleijel 1999).

*University and Jepson Herbaria, and Department of Integrative Biology, University of California, Berkeley, CA 94720, USA bmishler@berkeley.edu
†School of Philosophical and Historical Studies, University of Melbourne, Australia 3010 john.wilkins@unimelb.edu.au
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As it stands, most taxonomists resist rankless taxonomy and think that ranked taxa, particularly species, represent natural kinds or explanations of biological groupings. Some (Fitzhugh 2005, 2009) even think that delineating taxa such as species are explanations in themselves. Even many of those committed in general to the idea of rankless taxonomy make an exception for species and think that this one taxonomic rank is important to keep (Cantino and de Queiroz 2000; de Queiroz 2005, 2007). Other supporters of rankless taxonomy advocate a consistent treatment of names for all levels of clades under the PhyloCode, the revision of taxonomy proposed to replace the Linnaean scheme (see below). That includes even the levels corresponding to what have been called species (Cellinese, Baum, et al. 2012).

This topic is thus maximally controversial along several axes of opinion. Are species unique entities of biodiversity or are they the same as taxa at higher and lower levels, either within a ranked or rankless nomenclatorial system? If they are unique, what is their supposed uniqueness due to?

2 Background About Species

Since the inception of modern botany and zoology, biologists have had the notion of a "good species," and although it is not universally agreed what that means, each taxonomist has little trouble in identifying these entities in their chosen study group of organisms, through some sort of prototypic approach (Amitani 2015). Such prototypes have a folk taxonomic origin. All societies have folk concepts of living kinds of one kind or another (Medin and Atran 1999), albeit usually not in a formally ranked nomenclature. In most early classifications, taxa were not ranked. While folk kinds are generally nested in a hierarchy, there are no fixed and specified levels or grades of kinds in most folk taxonomies (Atran 1990, 1999), and prior to the early modern period in the life sciences ("natural history"), there was no such rank either (Wilkins 2018). Thus, species were named before there was any biological theory to speak of, first by botanists and later by zoologists. Christian theological considerations impinged on the question of rank early. The need for a species *rank* appears to have arisen as a result of attempts, by Johannes Buteo and Athanasius Kircher in the 16th century (cf. Breidbach and Ghiselin 2006; Buteo 1554; Kircher 1675; Wilkins 2013c), to work out logistically how many kinds (*species* in Latin) were on the Ark. Other pre-Darwinian theorists of classification also viewed higher ranks such as phyla as indicating major elements of God's creative plan (Agassiz 1859). Ranked classifications in general are a late innovation, and one due to professional and historical contingencies in modern biology (McOuat 2001).

Only after Darwin did the question "What makes a species a species?" come into general discussion. It emerged particularly after Johanssen's failed "pure lines" argument during the Mendelian revolution, in which he held that species were pure gene lineages (Wilkins 2010, 2011). The species problem, as it came to be known, became a central issue of the Modern Synthesis with Dobzhansky (1935, 1937). Prior to the Mendelian revolution there was a "species question" (*What is the origin of species?*), addressed by Darwin, but not a "species problem" (*What are species?*) (Wilkins 2013b).[1] Darwin, who addressed the species question, clearly thought species were simply less transient varieties and left the species problem at that; evolution did not license ranking. Many subsequently concluded (erroneously) that Darwin thought were no such things as species, when what he really thought was that the species *rank* was arbitrary (Mishler 2010; Wilkins 2018).

1. The observation is due to Jody Hey (pers. comm.). Contrary to Mayr's and others' characterizations, Darwin did not intend to define species, but to explain why they existed.

Taxa are supposed, in any biological classification, to represent or name natural groupings, and *monophyly* is the modern criterion of a natural group in phylogenetics. This criterion, however, admits of more than one interpretation, in part depending on whether the monophyletic group is thought of as *synchronic* (representing a single time slice across lineages descended from a common ancestor) or *diachronic* (representing the historical causal relations between a common ancestor and its descendants). In other words, is the ancestor included in the group (diachronic) or not (synchronic)? The diachronic view that a group is monophyletic if it includes a single historical common ancestor we might call *dia*monophyly (Vanderlaan, Ebach, et al. 2013). The synchronic view that monophyly is a property of extant or extinct taxa in a simple relationship to each other, such that a group of specimens are more closely related to each other than to an outgroup, we might call *syn*monophyly.

However, what are commonly regarded a "good species" are often not monophyletic under either definition. Named species can be formed by repeated speciation (Turner 2002) or by hybridization between other species (Bogart 2003; Rieseberg 1997). Or particular species may have an incomplete coalescence of genetic lineages or haplotypes (Beltrán, Jiggins, et al. 2002; Després, Pettex, et al. 2002).

Mayr made an important distinction between species as particular *taxa* and species as a general *category*. Mayr held that both a given species taxon and the species category were natural and therefore real (Mayr 1996). Others (known as species nominalists) have held that neither species taxa nor the species category are natural or real (Hey 2001, 2006; Pleijel 1999; Vrana and Wheeler 1992). Still yet others (e.g., Darwin, Mishler) have held that species as individual taxa can be natural but that the species category (the rank) is unnatural. Let us first consider these three approaches to the species category, or rank, before offering a solution in terms of monophyly.

Approaches to Species as a Category

1. Theoretically defined species: Mayr formulated and promoted a theoretical account of the species category, the Biological Species Concept (BSC), which many biologists adopted uncritically. Widely held during the twentieth century, this is the view that a group of organisms is a species if and only if it satisfies a theoretical criterion, specifically that it is reproductively isolated. One major problem with a theoretically-defined species account such as this is that it excludes groups that are empirically regarded by biologists as "good species" but which do not satisfy its criterion. Examples include asexual organisms (Bogart 2003; Lodé 2013; Moritz and Bi 2011), mostly asexual (yet occasionally prolifically exchanging genes) microbial organisms (Ochman, Lerat, et al. 2005; Wilkins 2007a), and, as mentioned, hybridizers.

The BSC is not the only possible theoretical species concept, of course. For example the Ecological Species Concept (Van Valen 1976) uses filling an ecological niche as a criterion, and the General Lineage Concept (de Queiroz 1999, 2007)[2] uses forming a lineage as a criterion. Both, along with the BSC, have been criticized for empirical vagueness of application and lack of congruence with what are empirically regarded as "good species".[3] Altogether, there are around

2. It is misleadingly also known as the "Unified Species Concept." This term is misleading because, although all species to the extent they are natural objects form lineages, that is also true of taxa at all ranks. It is entirely unclear what kind of lineages uniquely qualify to be named at the species rank. So this conception is unified (and general) just to the extent that it proposes a necessary but insufficient criterion for a natural species concept.

3. "Good species" form the proof of concept for biologists for concepts of *species* (the rank). Every biologist knows what form good species take in their specialty, but each subdiscipline differs in subtle or gross ways from other subdisciplines. See Amitani (2015) for a discussion of this and a characterisation of "good species" as a form of prototypical reasoning.

twenty-eight theoretical definitions of the species category (Wilkins 2018). None match all and only the species taxa empirically identified by taxonomists and ecologists.

The well-known "species-as-individuals" thesis (the SAI or Individualist Thesis) was built on a philosophical foundation: individual species are unique historical objects, held together by theoretically important processes, rather than natural kinds (Gayon 1996; Ghiselin 1974; Hull 1976; cf. Wilkins 2007b). These important processes were most often considered to be reproductive cohesion, although other processes could be involved (see Ghiselin 1997; Mishler and Brandon 1987, for discussion). Under this view, organisms are *parts* of a species, rather than *members* of it, and species are seen as occupying a unique level in the tree of life. This stands in contrast to the philosophical view that there are "natural kinds," in which members of a species share a unique set of traits (Dupré 1981; Hacking 1990, 2007; Khalidi 2013; Rieppel 2010; Wilkins 2013a).

2. Antirealism about species: Another widespread view is that the species category and sometimes also particular species taxa are unreal objects in biology. On this view they are merely conventional terms, names without name-bearers. This is often held erroneously to be the "Darwinian" view (Wilkins 2009, 129ff), although it really came into prominence around 1900 (Anon 1908). This view is also sometimes called "species nominalism," based on the medieval philosophical position of nominalism, which holds that only individual objects exist. This view reached its apogee in the phenetics era in taxonomy (e.g., Levin 1979; Sokal and Crovello 1970), but it still has advocates today.[4]

3. Monophyletic species: Many cladists,[5] but by no means all, have taken an intermediate position, between the two previous views. They hold that individual species taxa can be real objects in biology if they are monophyletic, but also that the species category is neither natural nor uniquely real, since there are monophyletic groups at many levels. This is sometimes called the *phylogenetic species concept* (PSC), although, as with monophyly, there are at least two contenders for the PSC label, one based on historical monophyly (Mishler and Theriot 2000), and one based on diagnostic characters (Wheeler and Platnick 2000). A major problem perceived by some for the PSC is that there is often monophyletic structure below "good species" that leads to potential *taxonomic inflation*, an explosion in the number of species that are described (Isaac, Mallet, et al. 2004; Zachos and Lovari 2013). Likewise, it has been argued by some that the use of a phylogenetic conception based on monophyly could lead to excessive lumping (Staley 2006). Both criticisms result from the fact that the use of monophyly for species needs some criteria external to monophyly to decide which "level" of monophyletic group to rank as species. These external criteria vary from group to group (Mishler and Donoghue 1982), and under this view it is difficult to see species as a unique level in the tree of life (Mishler 1999, 2010).

4. Numerical taxonomy, also known as the phenetics school (from the Greek *phaineros* for "appearance") classified groups according to their "overall similarity." This fell prey to the problems discussed by Nelson Goodman; as he says, similarity is cheap (see Decock and Douven [2011] for a discussion):

> Similarity, I submit, is insidious. And if the association here with invidious comparison is itself invidious, so much the better. Similarity, ever ready to solve philosophical problems and overcome obstacles, is a pretender, an impostor, a quack. It has, indeed, its place and its uses, but is more often found where it does not belong, professing powers it does not possess. (Goodman 1972, 437)

Depending on the characters used, phenetic groups, known as Operational Taxonomic Units or OTUs, could contradict other analyses using different characters of the same organisms.

5. Cladism is the approach to classification that defines taxa by uniquely shared common ancestry (*monophyly*), as evidenced by shared derived characters. It is also known as *phylogenetic systematics*.

3 A Way Forward: Species Are at Least Initially Phenomena

It is perhaps feasible to adopt a somewhat different approach, in this as in other epistemic matters in science: to take species as *phenomena* to be accounted for.[6] This means treating species as *explananda* (things which need to be explained) rather than as *explanantia* (things which explain). As discussed above, folk taxonomies demonstrate that human cultures generally perceive species as phenomena. Phenomena have been deprecated in the philosophy of science since the theory-observation dichotomy was criticized and abandoned. Recently, though, phenomena have been revisited as a source for scientific discovery (Apel, Dullstein, et al. 2009; Massimi 2008, 2011; Schindler 2011; Woodward 2000). Phenomena represent a relation between the observer/classifier and the world (Bogen and Woodward 1988; Schindler 2011). Observed phenomena can represent real states of the world, but they are dependent upon the pattern recognition capacities of the observer (Wilkins and Ebach 2013). They do not necessarily rely upon prior definitions in order be observed. Some observed phenomena may of course turn out *not* to represent real states of the world; astrological signs or astronomical constellations which are recognized in different cultures are in this category. Phenomena should be treated by science as things to be explained that can be dissolved upon further analysis, and which are often revised.

As an example of a real phenomenon, take a standard philosophical case: mountains. We can identify examples of mountains, but not universally define a category of "mountain" as distinct from "hill" or "plateau." There is no standard height, geological basis, or other property that defines all and only mountains, and what may be called a mountain in Australia, for example, is a mere hill on most other continents. There is no fundamental hierarchical level of "mountainhood"—within what is recognized as a major mountain range there are recognized subranges and individual peaks. Therefore, in terms of the argument in this paper, "mountain" is a rankless concept. Nevertheless, the reality of even an Australian mountain can be demonstrated by the fact that, to get to the other side of it, one must go over, around or through it. Though the *category* is a construct, that does not mean the *individual objects* delineated within the category are constructs.

Phenomenal taxa: Phenomenal taxa are evident groupings of organisms at all levels that have been apparent to folk going back thousands of years. Their perception does not initially rely upon prior definitions—the criteria used are operational and rely on covariances of traits of all kinds, most often the so-called morphological kind.[7] Phenomenal taxa are patterns that call for hypotheses; defensible scientific classifications result when phenomenal taxa are tested, and sometimes dissolved or at least revised on the basis of subsequent assays and phylogenetic analyses.[8]

Phenomenal species: As discussed above, the lowest level of phenomenal taxa can be recognized as phenomenal species, starting with folk classifications (Atran 1999).[9] Species phenom-

6. Existing species concepts (except the conventional ones) define species in terms of some model or process, which is to say, as entities of a particular theoretical kind. To treat species as phenomena in need of explanation is to not beg the question in favour of a prior mechanism, which we take to be a scientific virtue. Thanks to a reviewer for raising this question.

7. Which traits are selected to use for such comparisons depend a lot on prior experience rather than theoretic criteria, in traditional societies as well as in modern taxonomy.

8. See Scerri (2007) for an example from chemistry, the periodic table. The properties of elements were experimentally measured and the periodicity of these properties noted before any theoretical explanation (such as valency theory or electron shells and proton number) was available. Likewise, plate tectonics was observed as a phenomenal pattern before an explanation was offered (Oreskes and LeGrand 2003).

9. There is an extensive literature on folk taxonomy. We simplify here, and are not suggesting that the same basic taxa are recognised in all or even most cultures (Berlin 1973, 1976; Berlin, Breedlove, et al. 1973; Durkheim and Mauss 1963; Medin and Atran 1999; Sousa, Atran, et al. 2002; Zachar 2000).

ena set up the conditions for an explanation, and once these are offered we may revise them, or even dissolve them. Many commonly recognized species turn out not to represent natural states of the world, now that the science of systematics has a good theoretical understanding of monophyly and a good set of empirical tools. New tools have emerged from rapid technological advances in computer hardware and software, and in molecular biology. On the other hand, many commonly recognized species have been confirmed this way.

There is an old distinction between an *explanandum* and an *explanans,* or roughly the phenomena and the theory. In these terms, species do not explain anything; instead they set up the problem that theoretical explanations solve. Species are *explanantia*. It used to be said that theories "save" the phenomena; this came to mean that they would solve the problems posed by explaining the phenomena (Hacking 1983, 222f). The advantage of the phenomenal approach is that it is empirically driven but not absolutely ranked.

4 Rankless Taxonomy

As indicated briefly above, the systematics community has reached a consensus that monophyly is the best criterion for a *natural group*[10] in classification. This consensus comes from several important criteria of classification (Mishler 2009; Wilkins and Ebach 2013), including information content (summarizing what is known about organisms), predictivity (what is not yet known about organisms), and function in theories (capturing entities involved in important natural processes). The latter tracks causal relations (e.g., evolution from common ancestors) even in the absence of detailed knowledge of those causes.

Given the adoption of monophyly as the basis of classification, many empirical and theoretical problems have arisen with the current codes of nomenclature with their mandated taxonomic ranks. There are not enough ranks to name the thousands of levels of clades that have been discovered, and instability is introduced when groups at the "same" taxonomic rank are found to be nested inside of each other. Most importantly, it is impossible to precisely specify a named clade with only one type specimen (de Queiroz and Gauthier 1992, 1994). The idea of removing ranks from nomenclature has developed as a response to these perceived problems, and has gained much support and much criticism.

The major attempt to develop a rankless code of nomenclature to date is the PhyloCode (Cantino and de Queiroz 2000). Its basic philosophical foundation is that all groups should be natural (monophyletic), rank-free, and uniquely identified. Though there are no ranks, there is still hierarchy, as names are nested within names. The PhyloCode uses two or more type specimens (called "specifiers") to triangulate precisely to the clade being named. All new names are registered in a database (REGNUM[11]) with associated metadata including specifiers; the hierarchical nesting of clade names is thus clear, and a name can be applied stably into the future.

However, even within the PhyloCode community there is vehement controversy about species (see discussion in Cellinese, Baum, et al. 2012). The PhyloCode as it stands retains species as a special level and explicitly excludes the normal application of uninomial names to clades recognized at the traditional species level. This, despite the obvious paradox of a code designed for rankless classification retaining one rank as privileged! This issue is an area of active debate, and it is unclear how it will be resolved in the long run in the PhyloCode. Regardless, for the solution to the species problem proposed here, we argue in favor of the application of concepts of monophyly and rankless phylogenetic classification "all the way down."

10. In taxonomy, a *natural group* is a real fact about the organisms' interrelationships. It is contrasted to *artificial groups*, which are merely conventional, or based upon arbitrary characters.

11. http://www.phyloregnum.org/

5 Capturing the SNaRC

What *are* the natural objects of taxonomy? If monophyly is the criterion, then we must recognize and name the most differentiable clades based on the data available, and the assays used (that is, the differentia that we can access as characters and character states). These were mostly morphological traits prior to the molecular revolution, and subsequently mostly gene sequences; but the methodology remains the same. Taxa, including species, are first recognized as phenomena, then tested by phylogenetic analysis.

Following the principles of rankless taxonomy and the synchronic definition of monophyly, the smallest named clade should be treated like other levels and given a formal (uninomial[12]) name registered in a database. These we call the *Smallest Named and Registered Clades* (SNaRCs).[13] Note that this is the smallest level in a hierarchical classification of clades in an *epistemological* sense rather than an *ontological* one. These are the finest-scale clades that can be convincingly demonstrated with *current* data; no claim is made that they are the smallest clades that exist in that group. Further research in the next generation may well find clades within what was regarded as a SNaRC in the current generation (in short, new biodiversity has been discovered). In that case, the finer ones are now the SNaRCs but the original clade retains its name. Thus, the completely rankless naming system is much more stable than the current codes of nomenclature which use a binomial and one type specimen. Currently, if a species is split into finer species taxa, the binomial name must move to one of the finer taxa, causing endless problems with using species names to organize databases and match comparable data.

It is important to note, however, that the cladistic concept of *monophyly* is itself in need of refinement. Horizontal transfer (reticulation) is much more common in nature than realized twenty years ago (see a nice summary by Mallet, Besansky, et al. 2016). Despite having been presented as such (e.g., Wheeler and Platnick 2000), reticulation is not just a problem for the species level; clades at all levels can be subject to horizontal transfer.[14]

In the modern genomic world, because of the mounting evidence of horizontal gene transfer at all levels, monophyly can no longer mean monophyly of a group of organisms on every gene tree (as assumed by earlier generations of cladists, before there were data to the contrary). We would have few to no monophyletic groups, at any level, in that strict sense. Rather, monophyly refers to an ensemble characteristic of organismic descent as discussed by Baum (2009). Monophyly refers to the *preponderance* of gene lineages making up a clade (using the clade-lineage distinction from Mishler 2010; see Figure 1). Gene lineages that don't match the pattern of descent shown by the majority of lineages need a different explanation (e.g., horizontal transfer or incomplete lineage sorting) than the majority. We note this is analogous to the distinction

12. If monophyly is the key, then the name or structure of the including clade is not relevant to the identification of that smallest (currently known) clade. Hence a genus name, giving a binomial, is not necessary.

13. This is similar in some respects to Pleijel and Rouse's notion of a Least Inclusive Taxonomic Unit, or LITU (Pleijel and Rouse 2000), in that there is no rank that is fundamental. They say "Identification of taxa as LITUs are statements about the current state of knowledge (or lack thereof) without implying that they have no internal nested structure." However, with SNaRCs we restrict the naming of terminal taxa to entities regarded as clades, by requiring the author of a SNaRC name to present evidence of monophyly. The LITUs of Pleijel and Rouse (2000) are less restrictive "groups which at present are not further subdivided," leaving open the option to name "metaphyletic" groups (to use the terminology of Mishler and Brandon 1987), or potentially even paraphyletic groups. LITUs are thus purely nomenclatural entities. The SNaRC concept is an extension of the LITU concept, in that it refers to some causal processes presumed to have caused monophyly (while remaining agnostic as to what specific processes have done so).

14. Horizontal genetic transfer can occur in a number of ways, summarized by (Soucy, Huang, et al. 2015). However, it is notable that this usually offers a different phylogeny and recovers different taxa for the *gene* tree, not the *taxon* tree (Degnan and Rosenberg 2009).

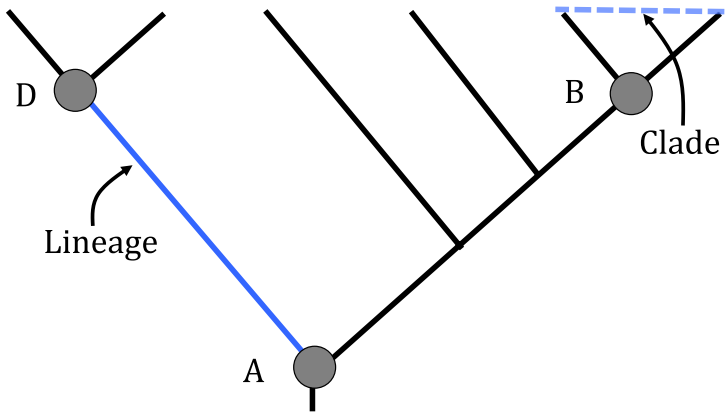

Figure 1: **The distinction between clades and lineages.** A clade is a synchronic, monophyletic set of lineage-representatives, where monophyly is defined as "all and only descendants of a common ancestor" (represented by B in this case). A lineage is a diachronic ancestor–descendant connection (between A and D in this case): "species" in the de Queiroz sense (redrawn from Mishler 2010).

people have made for a long time between homology and homoplasy (Mallet, Besansky, et al. 2016; Nixon and Carpenter 2011); in fact, horizontal gene transfer is best viewed as a type of homoplasy.

If there is no majority consensus pattern of lineage descent, then there is no good evidence of a clade, and one is below the SNaRC level given current knowledge. Just like clades at all levels, SNaRCs should not be recognized and named based on a single gene's evidence, but rather on congruence among the majority of gene trees and other types of phylogenetic characters available. SNaRCs are the finest-scale clades named at a given point in time, and they can be counted and used in comparative analyses as long as one keeps in mind the caveats that: (1) they are not comparable to each other in time depth, or biologically significant properties, or amount of evolutionary change, and (2) they may well be subdivided in the future, given more knowledge. Keeping these warnings in mind, SNaRCs can be used as a better starting point than species for scientific studies of biodiversity, in ways described below.

6 Using SNaRCs in Systematic, Evolutionary, and Ecological Studies

Studies in such areas as systematics, conservation biology, population genetics, macroevolution, community ecology, and biogeography currently use "species" as a unit of biodiversity in their respective investigations. For example, in ecology, species are used as a stand-in for niche occupiers or trophic nodes. But species are a poor surrogate for biodiversity under an evolutionary worldview. They are at best one level on the tree of life, and there are clades both larger and smaller than named species. Furthermore, a large proportion of currently named species are not units on the tree of life at all, in that they are not monophyletic.[15] All of these factors can potentially confound process studies. Thus phylogenies and rankless phylogenetic taxonomies provide

15. This is to be expected, since monophyly is only a relatively recent desideratum (for some) in taxonomy, many species were named before the cladistics revolution, and a large number of practicing taxonomists still do not accept monophyly as a desideratum.

a better theoretical framework than species do for all of these disciplines, and better practical methods for such purposes as conservation assessment as well (Mishler 2010).

Some complain that knowledge in their particular study group is too limited to take a phylogenetic approach to taxonomy. But even if sampling is poor, one can still build a phylogeny with the specimens one has, and this act is no more methodologically suspect than the typical approach to such a situation, which is building a phenogram (a similarity-based classification). Science is about sampling, and one does not need to have sampled every clade in one's group to make the first phylogeny. Phylogenies are hypotheses to be tested by future sampling. Likewise, lacking molecular data is not an excuse to avoid phylogenetic classification including naming SNaRCs. Perfectly good phylogenetic hypotheses can be built using morphological characters. True, it is likely that SNaRCs named with morphological synapomorphies may be particularly subject to subdivision once molecular data are available, but subdivision does not falsify them if they remain monophyletic according to the new data.

Fisher (2006) is a groundbreaking example of in-the-trenches taxonomy using SNaRCs. Her monographic study on a group of tropical mosses relied on all the traditional data-gathering methods: field work making new collections, searching herbaria and literature, measuring morphological characters, sequencing DNA from examplars, etc. Once she had a phylogeny, she named the best supported nodes on the tree, as any cautious taxonomist would do. Not all nodes were named; some did not have enough support to be worth naming. For all clades that were named, including the terminal-most clades (i.e., the level formerly treated as species), she provided uninomial PhyloCode-style names. She placed earlier binomial names in synonomy as appropriate, to allow a connection to the literature and herbaria. For example, the clade *Revolutus* (a SNaRC in our terminology) has *Syrrhopodon revolutus* and *Syrrhopodon microbolax* listed as synonyms. She provided a key to the SNaRCs in the normal manner for practical use in identification. Thus, all the important contributions of a systematic monograph are present for use in other studies.

This example shows it is possible, and indeed more precise, to do standard monographic taxonomy using rankless classification all the way down. As long as we take into account synonymies with traditional taxa, to allow linkages with past literature and databases that use traditional ranked names, there is no barrier to rankless taxonomy. In fact, removing the ranks forces users to consider the nature of clades they compare instead of relying on a false correspondence of ranks.

The taxonomic situation with orangutans provides a nice illustration of the difficulties with ranked classifications. Over the last twenty years there have been debates over the specific status of Sumatran (*Pongo abelii*) and Bornean orangutans (*Pongo pygmaeus*) (Groves 1986; Hobolth, Dutheil, et al. 2011; Xu and Arnason 1996), based primarily on genomic data (Locke, Hillier, et al. 2011). For most of the twentieth century, primatologists identified one orangutan species (*P. pygmaeus*) and several subspecies. Groves rang the change in 1986 when he declared that the *P. p. abelli* and the Sumatran (*P. p. pygmaeus*) "subspecies" were in fact full species, despite reproductive compatibility (adopting a phylogenetic species concept, Groves 2004). This debate continued until the early 2000s (Muir, Galdikas, et al. 2000; Muir, Galdikas, et al. 1998; Muir, Fleming, et al. 2000; Zhang, Ryder, et al. 2001) when a preponderance of molecular, morphological, and ecological data showed that the phylogenetic structure of the two populations was approximately the same in time and degree as between the *Pan troglodytes* (common chimpanzee) and *Pan paniscus* (bonobo) populations (Locke, Hillier, et al. 2011; Muir, Galdikas, et al. 2000;

Muir, Galdikas, et al. 1998). However, there are still "subspecies" of *P. pygmaeus* (Caldecott and McConkey 2005):

- the northwest Bornean orangutan, *P. p. pygmaeus*;
- the central Bornean orangutan, *P. p. wurmbii*; and
- the northeast Bornean orangutan, *P. p. mono.*[16]

Moreover, there is considerable haplotype structure within the new species *P. abelii* (Kuhlwilm, de Manuel, et al. 2016). As more data become available, the question of specific rank becomes more urgent under the current paradigm, with concerns about taxonomic inflation. However, a rankless taxonomy, with names applied to SNaRCs supported by a preponderance of gene trees using a concordance-based approach (Steel and Velasco 2014), would resolve much of this concern.

Evolutionary and ecological studies are also better done using clades instead of taxonomic ranks. Diversification studies are often done using species number as a proxy for diversity present in a larger clade (e.g., Alfaro, Santini, et al. 2009), but would be better served by looking at phylogenies down to the SNaRC level, since the number of named species is often not comparable across different groups due to differences in taxonomic customs or amount of taxonomic effort. Rather than comparing species, ecological studies would be more rigorously done comparing clades, as in modern approaches to community phylogenetics (Vamosi, Heard, et al. 2009; Webb, Ackerly, et al. 2002). Clades at any level might be filling a specific niche such as a role in a food web. The important question to be addressed is what level in the tree is filling which ecological role. We should not assume that only named species can do so.

Conservation studies should also be based on phylogenetic approaches that take into account branch lengths on trees rather than species counts per se. Faith (1992) pioneered a concept of phylogenetic diversity (PD) that can be used to characterize biodiversity much more accurately than species number. A related metric has appeared more recently called phylogenetic endemism (PE), which is a measure of how range-restricted lineages are (Rosauer, Laffan, et al. 2009). There is a burgeoning school of research called "spatial phylogenetics" that takes advantage of the availability of large-scale phylogenies, and big distributional data sets derived from museum digitization efforts, to look at patterns of PD and PE on the landscape (Gonzalez-Orozco, Pollock, et al. 2016; Mishler, Knerr, et al. 2014; Nagalingum, Knerr, et al. 2015; Schmidt-Lebuhn, Knerr, et al. 2015; Thornhill, Baldwin, et al. 2017; Thornhill, Mishler, et al. 2016). The results from these studies enable rankless phylogenetic evaluations of conservation priorities, as well as studies of evolution, ecology, and biogeography.

7 Conclusion

Whether the PhyloCode accepts the SNaRC approach or not, and regardless of how radical it sounds, it is an important step for systematics to take to best account for the theoretical and methodological advances of the last twenty years. As discussed above, it is possible to do all the theoretical and empirical work biological scientists need to do without species or other ranks, and indeed to do it better.

16. A recent paper now assigns specific status, *Pongo tapanuliensis*, to a central Bornean population (Nater, Mattle-Greminger, et al. 2017)

SNaRCs represent the smallest clades for which we have evidence. These are the *infimae* clades. These may or may not coincide with traditional "good species." However, they are the product of good science, and so we should accept them in favor of naïve classifications. While convention may prefer "good species," these are objects of a refined folk taxonomy, not science. For scientists, phenomena such as species are only a starting point for analysis and explanation.

> For the Snark was a Boojum, you see.
>
> –Lewis Carroll, "The Hunting of the Snark" (1876)

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