

Species as Ranked Taxa

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Abstract.—Because species names play an important role in scientific communication, it is more important that species be understood to be taxa than that they be equated with functional ecological or evolutionary entities. Although most biologists would agree that taxa are composed of organisms that share a unique common history, 2 major challenges remain in developing a species-as-taxa concept. First, grouping: in the face of genealogical discordance at all levels in the taxonomic hierarchy, how can we understand the nature of taxa? Second, ranking: what criteria should be used to designate certain taxa in a nested series as being species? The grouping problem can be solved by viewing taxa as exclusive groups of organisms—sets of organisms that form a clade for a plurality of the genome (more than any conflicting set). However, no single objective criterion of species rank can be proposed. Instead, the species rank should be assigned by practitioners based on the semisubjective application of a set of species-ranking criteria. Although these criteria can be designed to yield species taxa that approximately match the ecological, evolutionary, and morphological entities that taxonomists have traditionally associated with the species rank, such a correspondence cannot be enforced without undermining the assumption that species are taxa. The challenge and art of monography is to use genealogical and other kinds of data to assign all organisms to one and only one species-ranked taxon. Various implications of the species-as-ranked-taxa view are discussed, including the synchronic nature of taxa, fossil species, the treatment of hybrids, and species nomenclature. I conclude that, although challenges remain, adopting the view that species are ranked taxa will facilitate a much-needed revolution in taxonomy that will allow it to better serve the biodiversity informatic needs of the 21st century. [Concordance; exclusivity; gene genealogy; hybridization; monography; phylogenetic nomenclature; species concepts; taxonomy.]

Considering that species-level taxonomy provides the basic reference system for biological diversity, it is unfortunate that biologists have failed to establish an agreed-upon meaning of the term “species.” Calling a group of organisms a species might be taken to mean that it is an evolutionary unit, a lineage, a population, an ecological entity, a morphologically distinct entity, or just a group given a formal binomial name. One could argue that such imprecision over the meaning of species is to be expected and is not undesirable when meaning is established by “language games” (Pigliucci 2003). This perspective implies that the species category is a cluster concept, referring to a set of entities that share a “family resemblance” rather than being tied to any necessary and sufficient attributes. Even if one thinks that family resemblance is the way that meaning is established in everyday discourse, in the context of rigorous scientific communication we can aspire to more precision. But given the range of connotations of the term, how could we settle on a set of necessary and sufficient properties of “species?”

Although a broad diversity of species concepts have been proposed, I would suggest that there is one major axis of variation: species-as-taxa versus species-as-functional units. Species-as-taxa concepts are ones that emphasize the similarities between species and taxa at other ranks and mainly reflect a desire to guide taxonomists in the practice of assigning groups of organisms to species taxa. Species-as-functional-units concepts are ones that emphasize the functional cohesion or causal efficacy of species and generally emphasize the role of the term “species” in evolutionary and ecological theory. The clearest way to distinguish these 2 kinds of concepts is by asking the question: What is it about a group of organisms living at one moment that would

make them one species as to opposed to 2, or many, or a subset of a single species? If the answer is something about their functional integrity (e.g., interbreeding potential) or ecological cohesion, then the concept is “functional.” By this reasoning the biological (Mayr 1969), evolutionary (Simpson 1961; Wiley 1978), ecological (Van Valen 1976), and cohesion (Templeton 1989) species concepts are all functional in outlook. If the answer to the question stresses the same kinds of attributes that are used to delimit higher taxa, then the species concept is taxic in outlook. Thus, the phenetic (Sneath 1976), morphological (Cronquist 1978), diagnosability (Cracraft 1983; Nixon and Wheeler 1990; Davis and Nixon 1992), monophyly (de Queiroz and Donoghue 1988), and genealogical (Baum and Shaw 1995) concepts all use similar grouping criteria for species and higher taxa, making them species-as-taxa concepts. However, some other concepts require some exploration.

The internodal or Hennigian species concept argues that species are lineages (Ridley 1989). At first sight, this concept might seem to align with the species-as-taxa class because modern views of taxa assume that they are, like lineages, natural chunks of the tree of life. However, internodal concepts are usually species-as-functional-units concepts because the limits of a “lineage” at a moment in time are not governed by history, morphology, or similarity, but by functional features. Indeed, internodal concepts are best viewed as versions of the evolutionary species concept (Simpson 1961; Wiley 1978) that stress the temporal extent of species lineages. The same can be said of the unified (or general lineage) species concept (de Queiroz 2005, 2007), which defines species as separately evolving metapopulation lineages, where a “metapopulation refers to an inclusive

population made up of connected subpopulations” (de Queiroz 2007, p. 881). Although, de Queiroz (1998, 2005, 2007) argues that monophyly is a valid criterion for “recognizing” that a metapopulation lineage is separate, this does not make monophyly a necessary attribute of metapopulation lineages. Rather, monophyly is just a secondary feature that is likely to arise if metapopulation lineages have been isolated for long enough. Thus, the unified species concept is a species-as-functional-units concept.

Attempts to reconcile both functional and taxic views under a single umbrella concept are doomed. If both kinds of entities were simultaneously covered by a general-purpose “species,” confusion would reign. It would continually be unclear whether the term was being used to refer to taxa (understood in various ways) or functional entities (of various kinds). One way to defend pluralism is to suggest that different kinds of species should have different monikers, for example, biospecies, ecospecies, and phylopecies (Ereshefsky 1992; Baum 1998). However, although such terms may help achieve more nuanced communication in evolutionary and ecological theory, it is hard to see how these could help in taxonomy. It seems unrealistic to plan on developing multiple parallel taxonomies of life, one for each kind of species—we have a hard enough time maintaining one taxonomic system without trying to juggle 2, 3, or more. So, in the context of taxonomy we should aspire to monism. The term species should be applied to groups of organisms based on evidence that they correspond to some particular notion of “species.” Should this be a species-as-taxon or species-as-functional-unit concept?

At their most basic, species are taxa assigned the rank of species. As a practical reality, the discovery of a new species involves 2 steps, first deciding that a group of organisms constitutes a distinct taxon and, second, deciding that that group is a species rather than a more or less inclusive taxon (subspecies, genus, etc.). And even after their initial discovery, taxa ranked as species may be later recognized at another rank or vice versa. Thus, the practice of taxonomy implies that species is a rank of taxon, thereby supporting the species-as-taxon approach.

Equating species with taxa can also be defended for theoretical reasons. Most modern systematists would agree that taxa are groups of organisms that have a unique common history (i.e., they have the property of monophyly or something like it). In that case, provided species are also taxa, it becomes valid to refer to the position of a species on a phylogeny or the evolutionary relationships of one species to others. In contrast, if species are functional entities of any sort, there is no reason to assume that they will show historical unity, in which case species could not be said to occupy a single position on the tree of life. So, for this reason too, species should be viewed as a rank of taxon even if that undermines the assumption that all species are functional units in ecology and/or evolution.

In order to develop a coherent species-as-taxa concept, we need a clear understanding of what taxa are. Then, we can ask: what makes some taxa, but not others, species? In this paper, I first clarify the concept of a taxon in light of recent advances in analyzing genealogical discordance. I then argue that the assignment of taxa to the rank of species cannot be fully objective without undermining the demand that species be taxa. The recognition that there is nothing distinctive about the species rank aligns with Darwin’s views (Mallet 2008; Ereshefsky 2009).

The concept I present is an update to the genealogical species concept (Baum and Shaw 1995) except with regard to ranking, for which my position is closer to the ideas of Mishler and coworkers (Mishler and Donoghue 1982; Mishler and Brandon 1987; Mishler 1999; Fisher et al. 2007). However, I believe that my formulation adds clarity to previous work by refining the concept of a taxon, and hence species, based on genealogical exclusivity and by enumerating a set of semisubjective ranking criteria. I begin by providing a brief summary of my species concept and then revisit and expand on some important details. I end by suggesting that treating species as ranked taxa will help to revolutionize taxonomy so that it can serve modern needs as a repository of biodiversity information.

EXCLUSIVE GROUPS AND SPECIES RANKING

We can assume that every homologous nucleotide position shared by a group of contemporaneous organisms has a single, true tree-like history. This tree has some reasonably high probability of being identical to that of the neighboring nucleotide positions. However, as one increases the spatial distance among nucleotide positions, it becomes increasingly likely that different positions will have tracked different histories. This problem, genealogical discordance, poses a significant conceptual challenge. If different clades can be true for different parts of the genome and if our concept of a taxon is tied to the concept of a clade, then different taxa can be “true” for different parts of the genome. Thus, if our objective were to base taxonomic decisions on the assignment of organisms to clades, genealogical discordance would seem to undermine our endeavor. How can we articulate an ontology of taxa that is meaningful even when genealogical discordance applies?

A set of organisms either forms a clade or does not form a clade on a particular nucleotide position’s true tree. Therefore, there is some actual (if unknown) proportion of the homologous nucleotide positions for which a particular subset of organisms forms a clade. Let us call this proportion the “concordance factor” of the group of organisms (Baum 2007). The concordance factor refers to the probability of drawing a single homologous site at random from each organism and having those organisms form a clade (see Baum 2007, for more discussion). A specified subset of contemporaneous organisms could be a clade for anywhere between

0% and 100% of the genome, corresponding to a range of true concordance factors from 0.0 to 1.0.

Concordance factors can be estimated from multilocus sequence data sets using Bayesian concordance analysis (Ané et al. 2007). This approach assumes that each "locus" is a nonrecombined block consisting of nucleotide positions with a single true genealogy. If there is no systematic difference in the length of loci as a function of their true genealogy, then the proportion of loci having a clade should equal the proportion of nucleotide positions having the clade. This fact predicts that full genomic approaches (which have yet to be developed) and multilocus approaches will yield similar concordance factor estimates in practice.

Let us now define an "exclusive group" as a set of contemporaneous organisms that forms a clade for more of the genome than any conflicting (i.e., overlapping) set of organisms. Thus, an exclusive group is a set of organisms whose concordance factor is higher than that of any set of organisms that includes at least one organism from outside the group and some, but not all, organisms from within the group. Under this definition, a set of organisms can be exclusive even if it forms a clade for less than 50% of the genome, provided that no conflicting clade is true of a higher proportion of the genome. Therefore, this concept of exclusivity, although similar in spirit to that proposed by Baum and Shaw (1995), is much more liberal in that it allows one to recognize divergent tree-like structures when concordance factors fall below 1.0 (see Baum [2007] for more discussion).

I propose that taxa should be defined as exclusive groups of organisms. Thus, assigning an organism to a taxon represents a hypothesis that it forms a clade with all other members of that taxon for more of the genome than any overlapping set of organisms. The nature of this taxon concept ensures that taxa, so defined, will always be hierarchically nested. However, because exclusivity can apply even when a set of organisms forms a clade for only a small proportion of the genome, hierarchical structure (and thus taxa) may exist well below the level that is typically associated with the species rank. For example, a set of 3 siblings might be exclusive while forming a clade for only 25% of their genomes.

The revised genealogical species concept views species as those taxa among a nested series that are designated as being at the species rank. There is no available fully objective ranking criterion for species. The closest would be time since common ancestry (Hennig 1966; Avise and Mitchell 2007), but different parts of the genome can have different histories and hence different times since common ancestry. Furthermore, a strict application of a temporal ranking criterion would likely lead to the recognition of species within species and would also likely rank as species some taxa that do not warrant such a designation for other reasons.

Given the lack of a single, objective ranking criterion, the best we can do is to recognize that there is some ambiguity in the ranking of taxa, but that nonetheless there are certain features that we expect of those taxa (i.e., exclusive groups) that are ranked as species. These

features should each refer to real biological attributes, giving them some measure of objectivity. However, because there are multiple criteria that can be used to rank species (Table 1), and these will sometimes conflict with one another, the ranking of taxa as species is best viewed as semisubjective. These ranking criteria fall into 5 general categories: biological significance, utility, predictive power, robustness, and precedent, as outlined below.

Biological Significance

Species should correspond as closely as possible to units that are perceived to have evolutionary or ecological importance. For example, when 2 or more nonoverlapping taxa occur in sympatry and are not in the process of merging due to interbreeding, they should be ranked as separate species.

Utility

The species rank should apply if at all possible to taxa that are internally homogeneous, can readily be distinguished from other nonnested taxa, and have biological properties that give us a reason to talk about them. It is also helpful if the degree of phenotypic distinction between species has some degree of constancy within a larger group.

Predictive Power

The species rank would generally be applied to taxa about which generalizations can be made. One important facet of the ability to generalize about all the organisms within a species is the expectation that they have a common genealogical history for more than a trivial proportion of their genome. Thus, it would be preferable to recognize as species only those taxa that have a reasonably high concordance factor. This is likely to align with being able to make predictions about the biological properties (morphology, physiology, ecology, distribution, etc.) of organisms in the species.

Robustness

Because of the importance of maintaining the stability of species names, taxa assigned the rank of species should ideally be those whose status as exclusive groups is confidently determined. What matters is not our confidence that the group forms a clade on a given gene tree, but that it forms a clade on more gene trees than any overlapping set of organisms. And it does not necessarily matter how high the concordance factor is. For example, a group with an estimated concordance factor of 0.3 might be acceptable if there is clear evidence that no conflicting clade has a concordance factor over 0.2. Ané et al. (2007) describe how Bayesian concordance analysis permits one to assess statistical confidence that a particular group of organisms forms a clade for more of the genome than any conflicting group.

TABLE 1. Proposed species-ranking criteria

Taxa within species	Species taxa	Taxa including multiple species
	Biologically meaningful	
Ecologically identical to close relatives	Ecologically distinct from close relatives	Ecologically distinct from close relatives
Not composed of ecologically distinct subgroups	Not composed of ecologically distinct subgroups	Composed of ecologically distinct subgroups
When co-occurring with close relatives: interbreeds with them	When co-occurring with close relatives: does not interbreed with them	When co-occurring with close relatives: does not interbreed with them
When close relatives are not in sympatry: interbreeding is possible and leads to fit offspring	When close relatives are not in sympatry: interbreeding is impossible or possible but yields unfit offspring	When close relatives are not in sympatry: interbreeding is impossible or possible but yields unfit offspring
Subgroups can interbreed with each other to produce fit offspring	Subgroups can interbreed with each other to produce fit offspring	Some subgroups cannot interbreed with each other to produce fit offspring
	Utility	
Phenotypically indistinguishable (no fixed differences) from closely related taxa or if distinct, then by “minor” traits (traits that do not diagnose species in related groups)	Phenotypically distinct (with fixed differences) from closely related taxa for “major” traits (traits that diagnose species in related groups)	Phenotypically distinct (with fixed differences) from closely related taxa for “major” traits (traits that diagnose species in related groups)
Without phenotypically distinct subgroups or subgroups differentiated by minor traits	Without phenotypically distinct subgroups or subgroups differentiated by minor traits	With phenotypically distinct subgroups that are differentiated by major traits
	Predictive Power	
Concordance factor low	Concordance factor high	Concordance factor high
Subgroups with low concordance factors	Subgroups with low concordance factors	Some subgroups with high concordance factors
	Robustness	
Not confident that concordance factor is greater than that of a conflicting group	Confident that concordance factor is greater than that of a conflicting group	Confident that concordance factor is greater than that of a conflicting group
No or few subgroups for which we can be confident that the concordance factor is greater than that of conflicting groups	No or few subgroups for which we can be confident that the concordance factor is greater than that of conflicting groups	Some subgroups for which we can be confident that the concordance factor is greater than that of conflicting groups
	Precedent	
Not traditionally recognized as species	Traditionally recognized as species	Not traditionally recognized as species

Precedent

Unless other considerations weigh strongly, taxa previously assigned species rank should continue to be recognized. By maintaining continuity of usage, species-ranked taxa become better units for communicating biological information.

There is a fundamental difference between species grouping, which is tied to the objective concept of exclusivity, and species ranking, which is tied to a set of semisubjective ranking criteria. The question “Does such and such a group of organisms constitute an exclusive group (i.e., taxon)?” is a question that has a true answer. Either it is a taxon or it is not. We might be uncertain as to the correct answer, and even when we are confident in our answer, we could be mistaken, but there is a true answer. Consequently, scientific data can be used to arbitrate a dispute as to whether a group of organisms is a taxon (and, thus, potentially a species). In contrast, consider the question: “Is such and such a taxon a species?” Supposing that it is a taxon, as implied in the question, there is not an objectively true answer. Although each ranking criterion relates to a

more or less objective property of taxa, the species rank is not defined based on any one criterion, but rather is determined by the judicious balancing of multiple potentially conflicting considerations. Different criteria will often be at odds with one another; for example, a clade may be geographically, and hence reproductively, isolated but lack phenetic or ecological distinctiveness from related taxa. Furthermore, ranking decisions are not made by looking at taxa one by one, but by considering a larger taxon and evaluating the best way to divide it into species such that all organisms are in species. Consequently, although data can be helpful in resolving a dispute about the species rank, there is no underlying ontological claim that can be rigorously tested. The species rank is not a hypothesis, but a judgment. The art of monography is to work within the rigid constraints of genealogical relatedness to find a balance of conflicting ranking criteria that gain the support of other specialists and serve the needs of the user community.

FURTHER IMPLICATIONS

Having now introduced the basics of my genealogical species and taxon concept, I will now expand on some

issues that I have glossed over. In the process, I will discuss and counter some possible objections.

Gene Genealogical Versus Organismic Exclusivity

The use of gene genealogical exclusivity rather than organismic exclusivity as the core of the taxon (and hence species) concept deserves explanation. Gene genealogical exclusivity refers to genetic ancestry and specifically to groups that form clades for a plurality of the genome. As used here, organismic exclusivity refers to descent from common ancestral organisms. There are several ways one might formally define organismic exclusivity, but I have developed (with E. Sober and J. Velasco, University of Wisconsin–Madison) a relatively stringent definition:

A set of contemporaneous organisms, *M*, shows organismic exclusivity if there is at least one organism, *A*, that is an ancestor of all individuals in *M*, such that *A* is also a descendant of all the common ancestors shared by any individual in *M* and any contemporaneous individual outside *M*.

Given this definition, 4 sets of contemporaneous organisms in Figure 1 constitute organismically exclusive groups. Because genetic ancestry is constrained by the paths of parent–offspring descent, organismic and gene genealogical exclusive groups will usually have identical content. So the bracketed groups of organisms in Figure 1 would probably also show gene genealogical exclusivity. Therefore, a substitution of organismic for gene genealogical exclusivity in the taxon concept would not have major consequences in terms of the groups that would actually satisfy the concept. In both cases, there will be a hierarchically nested series of groups satisfying the criterion, thus requiring the application of semisubjective ranking criteria.

Despite the similarity of the 2 concepts of exclusivity, they are not identical and will not always identify the same sets of organisms. Of particular importance, directional selection acting on loci distributed across the genome can result in gene genealogical exclusivity even in a group that does not show organismic exclusivity. Conversely, some groups that show organismic exclusivity may, nonetheless, fail to show gene genealogical exclusivity if patterns of genetic segregation have deviated from Mendelian expectations, as could happen by chance or due to selection. Given the potential for an occasional discrepancy between the 2 kinds of exclusivity, an unambiguous taxon concept should specify which has priority.

Although I can see arguments in both directions, I favor giving primacy to the gene genealogical criterion. Organismic ancestry constrains how genetic ancestry should be structured under Mendelian inheritance and in the absence of selection. When the realized patterns of genetic relatedness deviate from expectation, I think we should recognize taxa based on what actually happened rather than worry about what should have hap-

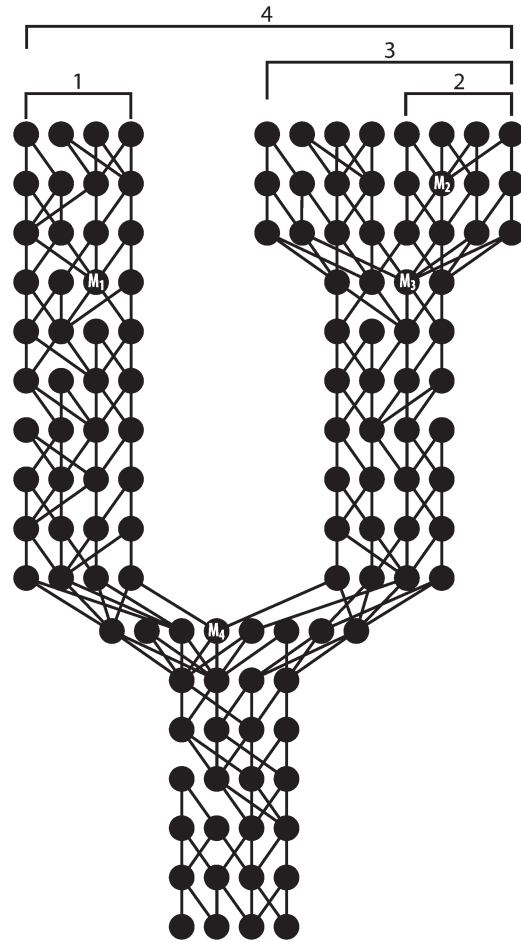


FIGURE 1. A hypothetical pedigree to illustrate the concept of organismic exclusivity. Circles represent individual organisms, each connected by lines to 2 parents in the preceding (lower) generation. For each of the 4 organismically exclusive groups (composed only of organisms in the most recent generation), one ancestral organism *M* is marked. This organism has the property both of being an ancestor of all living members of the exclusive group and of being a descendant of all ancestors shared by members of the group and any contemporaneous organisms outside the group.

pened. In particular, it seems preferable to adopt gene genealogical exclusivity, which is sensitive to a history of selection, rather than organismic exclusivity, which is not. Additionally, gene genealogical exclusivity is more tractable in practice because we can relatively directly evaluate actual genomic ancestry, for example, using concordance analysis (Ané et al. 2007). Thus, I believe that gene genealogical exclusivity provides a more helpful and more tractable criterion for grouping organisms into species and other taxa. Therefore, for the remainder of this paper, the term exclusivity should be understood to mean gene genealogical rather than organismic exclusivity.

Temporal Extent

The definition of taxa, and hence species, adopted here is synchronic: taxa are entities composed only of

contemporaneous organisms. This conflicts with the common viewpoint that species are diachronic: persisting entities with births (at speciation) and deaths (at extinction or speciation). The desire to have species persist through time partly reflects human psychological predispositions: the minute something is given a proper name, or even just pointed out as a particular entity (e.g., “this computer,” “that coffee cup”), we tend to view it as persisting through time. Additionally, the history of treating species as functional units tends to tie us to a diachronic view of species. However, there are good reasons why taxa, including species, should not be treated as diachronic entities.

The genealogical definition of a taxon specifies that the organisms in question are contemporaneous, making species (and other taxa) synchronic entities. Can we remove the requirement that organisms be contemporaneous? Thus, the definition of taxon is a group of organisms (living or dead) that forms a clade for a plurality of the genome. A minor argument against such a move is that we would be lumping different kinds of relatedness: some pairs of organisms are related as ancestor and descendant (an asymmetric relationship), whereas other pairs are related by common ancestry (a symmetric relationship). But this heterogeneity does not seem like a devastating problem because the former can be considered as a special case of the latter in which the last common ancestor of a pair of organisms is one of those 2 organisms.

Another problem with a diachronic version of exclusivity is that it renders it impossible to place all organisms into a species (or any other mandatory rank). For example, if one decided that exclusive groups should be ranked as species, named A and B, then any organism that is ancestral to both A and B could not be in any species because all the clades/taxa of which it is a part will include species A and B and thus cannot also be ranked as a species. Thus, a time-extended view of taxa disallows the use of any mandatory rank, including species (Brummitt 2002). Nonetheless, one could do without mandatory ranks. So, again, this issue alone would not invalidate diachronic exclusivity.

There is one major and, so far as I know, insurmountable problem with a diachronic version of exclusivity: if you include organisms close to branching events, then no exclusive groups exist. This is because some organisms close to lineage branching events will show equivalent relationships to organisms in different lineages. So, when you look at the full set of gene trees for all organisms, no sets of organisms will show gene genealogical (or even organismic) exclusivity. Including ancestral organisms tends to result in exclusive groups slipping away into a sea of overlapping, nonexclusive groups. Thus, although it would have little effect if the concept of “contemporaneous” were extended to encompass tens or hundreds of generations, the inclusion of more ancient, ancestral organisms would make the concept unworkable.

The fact that we cannot apply the exclusivity criterion to time-extended entities of more than trivial evolution-

ary duration does not, in itself, rule out the existence of diachronic species (Baum 1998). A synchronic entity can be associated with a diachronic counterpart by connecting successive synchronic “slices” into diachronic “worms.” The idea is that if we apply a synchronic criterion of individuation in multiple successive instants of time, then the synchronic entities in adjacent time slices can be linked into a time-extended entity. Do diachronic counterparts of synchronic species exist?

In the original version of the genealogical species concept (Baum and Shaw 1995), the species rank was objective, corresponding to a concordance factor of 1.0. This allowed one to imagine connecting the species-ranked groups in each successive slice of time to make a time-extended species lineage (Baum 1998). However, in the revised concept used here, the species rank is no longer objective, which introduces a significant problem. Once species-ranked taxa have been delimited in adjacent time slices, there is nothing to say that the species rank has been assigned equivalently. So, there is no conceptually rigorous basis for linking particular taxa in successive slices of time as being continuations of the same diachronic species. Once we admit that ranking is nonobjective, then linking synchronic entities into diachronic worms becomes nonobjective too. This means that taxa (including species) are best viewed as groups of contemporaneous organisms that do not exist through evolutionary time.

One reason biologists have been troubled by a synchronic view of species is because of a continued commitment to species as causal players in evolution. However, my explicit objective here is to define species as taxa, hence “products” of evolution. In this context, the lack of diachronic existence is not a problem. Indeed, it may be a necessary feature of a product of evolution that it lacks diachronic existence (Lee and Wolsan 2002). Evolution is an ongoing process that is constantly changing the entities that exist in nature. The products of evolution evolve. Maybe, then, it is inevitable that our taxon concept implies only synchronic existence.

Fossils

The synchronic nature of taxa and species poses little practical problem for neontological systematics. However, my species concept may seem to pose problems for paleontologists. Empirically, the estimation of concordance factors for fossils poses major, perhaps insurmountable, problems. We are unlikely to have access to molecular data for fossil organisms, making it difficult to rigorously evaluate exclusivity. Additionally, because species (and other taxa) are delimited with reference to contemporaneous organisms, it will be problematic to establish species status when only a minuscule proportion of the organisms living at a point in time is known (and we generally do not know if different fossils were actually contemporaneous).

At the conceptual level, an evolutionary lineage composed of similar-looking and related organisms

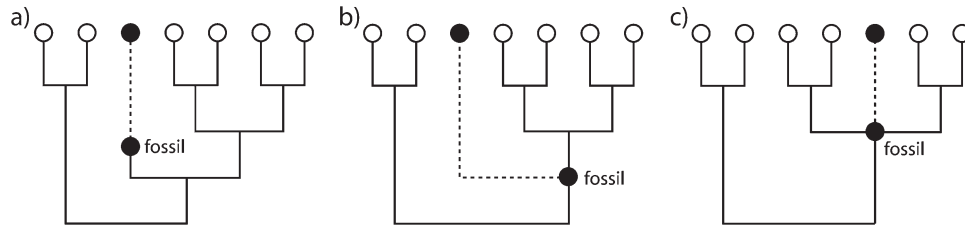


FIGURE 2. The classification of fossils alongside living organisms. Whether fossils are extinct terminal branches (*a*), portions of internal branches (*b*), or organisms drawn from nodes (*c*), they can be treated as though they are extant organisms that have not changed since the time of fossilization. Only in the first case will multiple fossil organisms constitute an exclusive group relative to living taxa.

distributed through time cannot be equated with a species because species, as defined here, do not exist through time. Although this implication may jar with prevailing views of species, we should ask if it is sufficiently problematic that we should abandon the genealogical conception of taxa.

Some fossils are dead-end branches of the tree of life (Fig. 2*a*), whereas others are ancestral to living organisms (Fig. 2*b,c*). In the former case, there is no real detriment to treating the fossils as though they are living organisms that have remained unchanged for a long time (this also applies to recently extinct taxa like *dodos*): we can assign them to taxa (including species) as though they were extant.

Can fossils situated on an internal branch (Fig. 2*b*) be treated similarly? This differs from the preceding case in that these fossil taxa are not expected to have any apomorphic traits. More importantly, if the fossil organisms lived at different times, some could be more closely related to descendants than to earlier specimens from the same fossil taxon. This becomes even more complex when a fossil is situated at a node (Fig. 2*c*). In that case, different members of the fossil taxon could be more closely related to different descendants of that node, undermining the unity of the fossil taxon.

Given the importance of talking about fossils and their evolutionary kinship, I think one should aim to give species names to those fossil organisms that are

not linear ancestors of later fossils or extant organisms (Fig. 2*a*)—although use of a convention to indicate that the species are not extant is warranted. However, there should be no requirement that every fossil be assigned to a species. In particular, fossils that are likely to be ancestors (Fig. 2*b,c*) might better be treated using some other conventions to indicate where they fit on the tree of life. But given the rarity of fossils that are direct ancestors of living organisms and, even more so, fossils situated at internal nodes, the vast majority of fossils can safely be treated as though they are extant but unchanged.

Hybridization

Hybridization between taxa that were until recently members of distinct taxa has widely been perceived to be a major problem for any phylogenetic species concept (and many other concepts as well). As a basis for discussion, consider a hypothetical example. Figure 3*a* shows a true concordance tree for a set of tips sampled some time in the past when each taxon had a high concordance factor. Given that species are just one of a nested series of clades, it does not matter for this discussion whether the individual tips in the figure are ranked as species or are grouped with other tips into more inclusive species. Figure 3*b,c* show the 2 coprimary concordance trees (Baum 2007) that exist now, given that a hybrid individual or hybrid species, H, was formed by hybridization of organisms that were in C and D in Figure 3*a*.

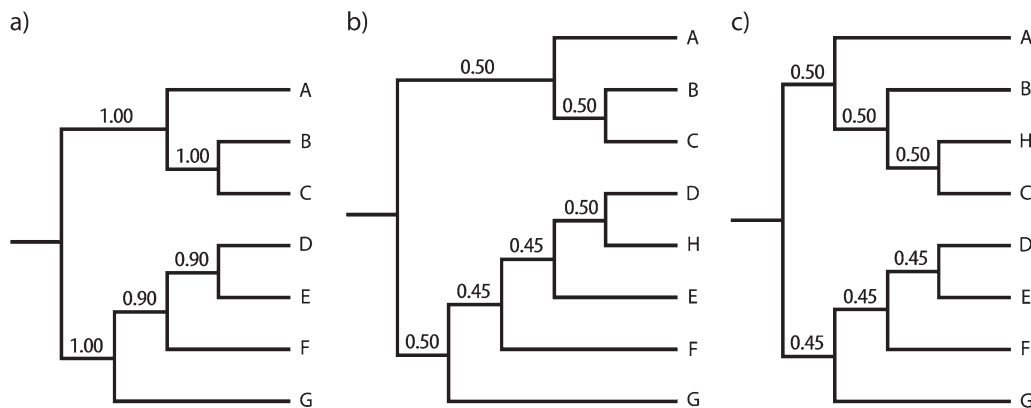


FIGURE 3. Concordance trees before and after hybridization. (*a*) Before hybridization almost all the genomes have tracked the same tree-like history, as shown by clade concordance factors of 0.9–1.0. Hybridization of tips C and D, to yield a new taxon H, generates 2 coprimary concordance trees (*b,c*), one with H sister to C and one with it sister to D. All clades that include one but not both parental taxa (C and D) have their concordance factors reduced by half as a result of hybridization, a phenomenon called trickle-down discordance.

The first issue you might note is that, following hybridization, no sets of organisms have concordance factors greater than 50%. Hybridization of 2 tips greatly reduces the concordance factor of not just the hybrids, but all taxa that include one but not both parents—a phenomenon we may call “trickle-down discordance.” The resulting low concordance factors are deceptive—a set of clades with concordance factors of 0.5 could reflect just 2 true gene trees differing only in the placement of one hybrid organism, that is, very little discordance. Trickle-down discordance is an artifact of trying to summarize a bimodal distribution of genealogical histories with a single statistic. This cautions us that concordance factors provide only an imperfect summary of the full distribution of gene histories, but it is not relevant to the claim that taxa should be equated with exclusive groups of organisms.

The second issue to note is that the set of taxa (including species) we would recognize will differ depending on which of the coprimary trees (3b, c) we used as a basis for classification. If we used tree 3c, we would group H with C and could, for example, rank B + C + H as a species. If we used tree 3b, we would group H with D and might recognize D + H + E + F as a species. These are quite different classifications, raising the question of how either could be defended.

A pragmatic response is to allow that one or the other scheme be picked at random as the basis for taxon delimitation. This will tend to yield taxa that are formally (if marginally) exclusive. For example, taxa such as H + D, H + D + E, and H + D + E + F, recognized under tree 2b, have low concordance factors, but there is no conflicting clade that is true of “more” of the genome. Rather, conflicting clades tend to have equal concordance factors. In this case, selecting a coprimary concordance tree at random as a basis for classification would not misinform us as to the true genealogical structure.

However, although the arbitrary classification of hybrids with one or the other parent may not create misinformation, it does obscure information—namely hybrid ancestry. If the hybrids could be identified as such (the practicalities of which will be discussed shortly), the dual affinities of chimeric organisms or taxa could be reflected in taxonomic practice. In order to understand how the ability to identify hybrids would impact taxonomy, we need to consider 3 alternative situations.

In the first situation, hybridization happened a long time ago, with subsequent interbreeding among hybrids and their descendants but no backcrossing to either parent. In this case, we expect organisms of hybrid ancestry to form a clade on almost all gene trees. Although different gene trees may place the hybrid taxon with one or the other parental taxon, the hybrid itself is an exclusive set of organisms. In this case, we can recognize and name the hybrid just like any other taxon and could, thus, rank it as a species. If its hybrid status were recognized, this taxon could be placed in 2 places in the classification, once with each parent, perhaps with the hybrid symbol being used to indicate its dual parentage.

In the second situation, hybridization has been recent or recurrent, but, again, there has not been backcrossing with the parents. This results in a set of individuals of hybrid ancestry each of which is related to one or the other parental taxon by a different subset of genes. In this case, the set of hybrid individuals is not an exclusive group and cannot be viewed as a species or any other rank of taxon. Instead, the individuals are best viewed as a set of hybrid organisms that simultaneously occupy 2 places on the tree of life. If the chimeric nature of these organisms was recognized, they could be discounted from the normal rules of classification. They would not need to be assigned to species and they could be pruned off concordance trees, thereby counteracting trickle-down discordance.

The final situation to consider is one like the preceding, except that there has been backcrossing and introgression of genes into the 2 parental taxa. The degree of introgression is potentially variable: from a localized hybrid swarm to complete secondary fusion of the formerly distinct taxa into a single gene pool. However, regardless of where on this spectrum they sit, neither the “pure” parents, nor the hybrids, nor the set of both parents plus the hybrids will form an exclusive group. So what should we do?

Pruning the complex (parental forms plus hybrids), as recommended in the preceding situation, is not advisable in this case. Backcrossing means that the parental taxa have lost their identity—they have effectively gone extinct by secondary fusion. This means that we cannot list “parents” when labeling individuals as hybrids. Therefore, instead of just recognizing their hybridity and excluding them from standard classification, it would be preferable to diagnose the 2 historical signals and recognize that the complex represents an admixture of 2 exclusive taxa. We could recognize and name the 2 virtual “pure” taxa (maybe at the species rank) even if all individual organisms were admixtures to some degree.

The preceding discussion begs the question of how hybrids could be recognized. Given a genealogical perspective, a hybrid taxon is a set of organisms that occupies, more or less symmetrically, 2 spots on the tree of life. It is worth stressing that hybrid taxa are defined here based on the distribution of gene genealogies rather than in terms of a particular historical process of formation. If, for example, hybridization occurred, but later all genetic material from one parent was lost, then the taxon may have an evolutionary history of hybridization, but it would not be a contemporary hybrid taxon.

Is there an objective criterion by which hybrid taxa can be identified based on their gene genealogies? I am not aware of any fully developed method. However, I suspect that it might be possible to use an information compactness criterion (as in Ané and Sanderson 2005) to see if the full distribution of gene trees can be more efficiently described when a putative hybrid is treated as 2 virtual taxa that can attach to the rest of the tree in either of 2 places. If this or some other defensible criterion could be developed, it would become possible to

objectively identify hybrid individuals and taxa. This is important if taxonomy is to deal satisfactorily with some difficult cases of hybridization. For this and other reasons, an important avenue for future genealogical theory is the development of a theoretical framework for the genealogical identification of hybridity.

Nomenclature

The species-as-taxa concept espoused here is motivated by the view that it is useful to assign some taxa to the rank of species so as to provide points of reference for scientific communication. For this goal to be met, we must be able to attach names to species-ranked taxa in such a way that communication is not impeded. To see if this is possible, we need to consider in parallel 2 nomenclatural systems: rank-based nomenclature (embodied in the traditional codes) and phylogenetic nomenclature (embodied in the *PhyloCode*).

In rank-based nomenclature, the content of a species taxon is set by reference to a type and a diagnosis. The latter is idealized as a list of characters that differentiate the species from its closest relatives, but it does not provide an essentialist “definition” of the species. Rather, a diagnosis is provided as a window into the thinking of the name’s author. Thus, as with other taxa in rank-based nomenclature, the meaning of a species name is basically determined just by reference to a type and the rank of species. The question, “Is organism *x* in species *y*?” is answered by asking if *x* is in the “species” that includes the type specimen of *y*.

Given the concept of species advocated here, species are taxa. While not clades in the simplistic sense of monophyletic groups for the whole genome, taxa are clades in the looser sense of forming clades for a plurality of the genome. Thus, the application of a name to a species taxon can be achieved using the same kinds of phylogenetic definitions that are used to attach names to other clades (de Queiroz and Gauthier 1990, 1992). For example, one could define the species-ranked taxon, *Homo sapiens*, as including all extant (and recent historical) organisms that form an exclusive group that includes Charles Darwin, say, but not certain designated specimens of chimpanzees, bonobos, or gorillas. The use of branch-based, node-based, or other kinds of phylogenetic definition instead of, or in addition to, diagnoses would certainly go some way toward improving the clarity of species taxonomy.

Although genealogical species can be named under the rank-based codes, such a system of nomenclature is not optimal because it is premised on ranks, including the rank of species, being objectively real. Under the rank-based codes, the association of a species name with a clade will last only so long as that clade continues to be ranked as a species. For example, imagine that we have provided a node-based definition of a clade that includes some horned animals within *Equus* and have assigned this clade the rank of species, giving it the name *Equus unicornus*. Suppose that a clade that is sister to *E. unicornus* is later discovered. If it were judged nec-

essary to assign the species rank to the larger clade that includes both *unicornus* and the newly found organisms, this expanded species would have the name *E. unicornus* (because it is a species including the type of *E. unicornus*). In the process, the original “*E. unicornus*” clade has been deprived of its name. This shows that, under rank-based nomenclature, changing rank assignment results in a name applying to a new clade—even when the clade it originally applied to remains a valid, exclusive taxon.

Given that phylogenetic nomenclature, with its emphasis on phylogenetic relationships, is so well aligned with the genealogical species concept, it is unfortunate that the current version of the *PhyloCode* (www.phylocode.org) forbids one from treating species as ranked exclusive taxa (Dayrat et al. 2008). Articles 3 and 21 of the *PhyloCode* stipulate that species names are governed by the traditional ranked codes. Furthermore, species epithets cannot be converted into phylogenetically defined clade names (Article 10.9): “A clade name may not be converted from a preexisting specific or infraspecific epithet (ICBN and BC) or a specific or infraspecific name (ICZN).”

At first glance, you might think that the reason that the *PhyloCode* excludes species is that “species” is a rank, and the *PhyloCode* is incapable of handling ranks. However, this is not the case. Phylogenetic nomenclature is neither rank-based nor rank-free (de Queiroz 1997), as made clear in Note 3.1.2 of the *PhyloCode*: “This code does not prohibit, discourage, encourage, or require the use of taxonomic ranks.”

To illustrate how it would be possible to treat species as a rank of clade within the framework of phylogenetic nomenclature, consider a hypothetical phylogeny with 12 tips, each corresponding to an exclusive group of organisms from a single population (Fig. 4). These and all clades in this tree have been named. Figure 4a shows an original classification that achieves exhaustive assignment of all 12 tips to 3 ranks: species (indicated by a lowercase first letter), genus (indicated with an asterisk), and family (indicated with a plus sign). Given this classification, it might be convenient to refer to organisms by reference to the genus and species clades to which they are assigned, yielding pseudobinomials, for example, *Tardis magnifica* and *Vogon horridus*. It should be stressed that the genus name is used merely as a partial clade address and is not part of the species name (as it would be in rank-based nomenclature).

Now suppose that a subsequent authority, while accepting the same phylogenetic relationships, concluded that all the terminal populations should be ranked as species. This would not change the name of any clade, but now the annotation of species rank (in my example, the use of lowercase) shifts to the new species-ranked clades (Fig. 4b). For the sake of illustration, suppose that the same author also shifted the genus rank—splitting **Vogon* into **Ovalis* and **Ultra*. Now, under this new classification, the names of species have changed, especially when combined with their generic clade address (e.g., *Tardis magnifica* has been split into *Tardis angustifolia* and *Tardis bellissima*, and *Vogon ovalis* has been

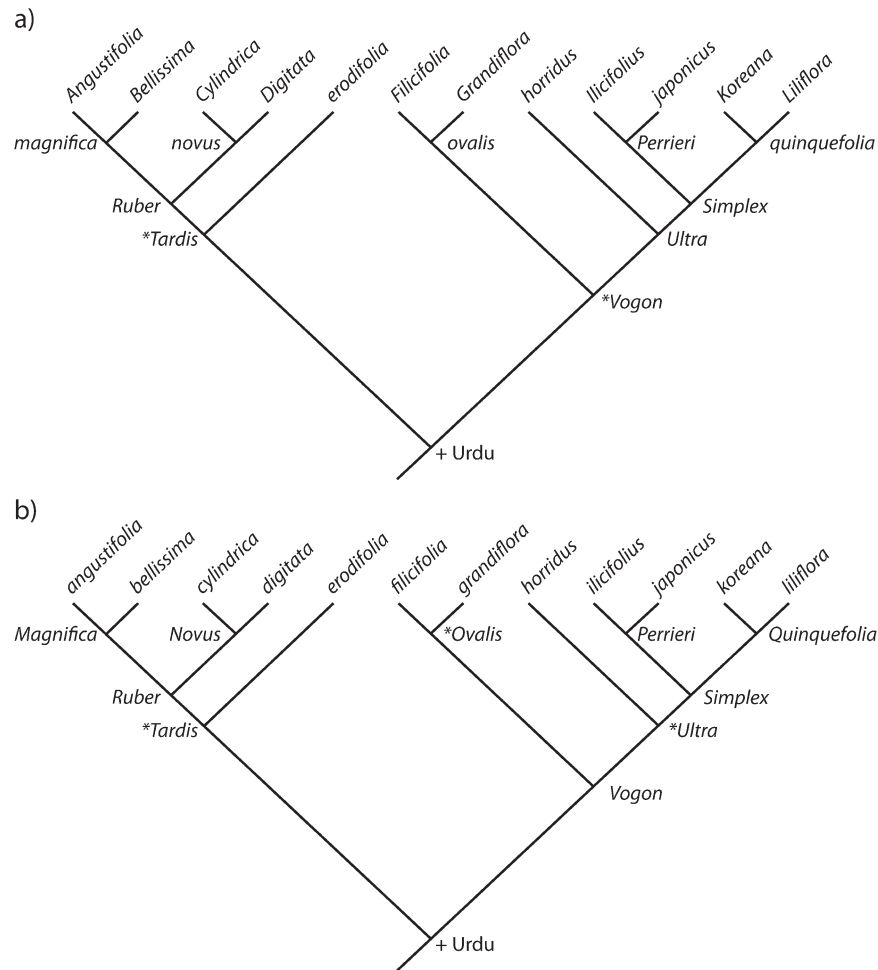


FIGURE 4. Phylogenetic nomenclature with species as ranked clades. It is assumed that all tips (taxa) and clades have been attached to names using clade definitions but that, in the 2 versions, different clades are assigned to different ranks. Taxa assigned to the species rank are written in lowercase, whereas taxa at all other ranks (above and below species) have their first letter capitalized. Genera are marked with an asterisk and families with a plus sign. Note that despite changing ranks, all clades have the same names in the 2 cases.

split into *Ovalis filicifolia* and *Ovalis grandiflora*). This shows the undesirability of changing rank assignments whimsically, which is why precedent is such an important ranking criterion. However, although the names of species, genera, etc., have changed, the composition and name of every taxon have remained stable.

This example illustrates the point that phylogenetic nomenclature can, in principle, accommodate ranks, including the rank of species, and that it does so in such a way that rank is nomenclaturally neutral. So why does the PhyloCode exclude species names?

Some years ago there was division among proponents of phylogenetic nomenclature as to whether species names should comprise just species epithets (uninomials) or a fusion of the traditional generic names and epithets (Cantino et al. 1999). But this dispute has been largely resolved in favor of uninomials, primarily due to some empirically worked out examples (Dayrat 2005; Dayrat and Gosliner 2005). Instead, the decision to exclude species from the PhyloCode rested on practical concerns and one strong philosophical position.

A number of practical reasons have been put forward for why species names should not be included in the PhyloCode (Dayrat et al. 2008). Most obviously, the current version of the PhyloCode forbids the same name to be used for more than one clade. This rule would need to be removed if species epithets were converted into clade names because so many traditionally recognized species share the same epithet (Wolsan 2007). Some people fear that systematic communication would be impaired if homonyms were allowed. I believe, however, that we can easily disambiguate homonyms using publication information or partial clade addresses. So, I neither believe that homonymy is such a problem nor believe that this or any other practical concern motivated the decision to exclude species from the PhyloCode.

The core reason that the PhyloCode relinquished species was because the individuals who drafted the document hold that species and clades are inherently different kinds of taxa. The PhyloCode articulates such a position quite explicitly (Note 3.1.1): "In this code, the terms 'species' and 'clade' refer to different kinds of

biological entities, not ranks." Similarly, in defending the treatment of species names in the PhyloCode, Dayrat et al. (2008) state: "Clades and species are regarded as kinds of biological entities under the *PhyloCode*. They are not ranks . . ." They go further and assert that: "Under the *PhyloCode* . . . a species is defined as a segment of a population-level lineage that is evolving separately from other such population lineages" (p. 511). In effect, the PhyloCode has adopted the unified or general lineage species concept of de Queiroz (1998, 2005, 2007). As discussed earlier, this is a species-as-functional-units concept, making it incompatible with the taxic view advocated here. I think it is a mistake to configure the PhyloCode around a single, species-as-functional-units concept. It seems like a major failing of the PhyloCode that it makes it impossible to attach species names to phylogenetically defined clades. The best you could do would be to name clades that you wished to rank as species within the traditional codes and then treat them within the PhyloCode. But, because the name is not attached to the clade, but to the rank of species, there would not be a stable connection between the name and the clade, which is the whole point of phylogenetic nomenclature. It is ironic that the only nomenclatural system that allows one to treat species as clades is rank-based nomenclature, which regrettably treats ranks as though they were objectively real.

CONCLUSIONS AND PROSPECTS

Given the lack of an objective species-ranking criterion that can place all organisms in species-ranked taxa, I have here argued for treating species as a semisubjective rank. The idea is that having identified a set of taxa that are hypothesized to be exclusive, taxonomists should assign taxa to the species rank based on judicious compromises among a set of potentially conflicting criteria. Under this approach, although many species will correspond to functional units in ecology and evolution, it should never be assumed that a species-ranked taxon has functional importance.

There are 2 main responses to the lack of an objective species rank. The first is to argue that because species are not distinct from other taxa, we gain nothing by using the concept of species for a kind of taxon. Instead, we should adopt a species-as-functional-units concept. This has the advantage that one could then aspire to an objective ranking criterion for species (Lee 2003), not that any objective ranking criterion has been identified for any species-as-functional-units concept. But, as I argued in the introduction, defining species as functional units forgets that species exist in the same hierarchy of named groups as other taxa and that we want to believe that each species occupies a unique position on the tree of life. The second response is to abandon the species category entirely: if it is just taxa all the way down, why pick out one taxon for special attention (e.g., Mishler 1999; Pleijel and Rouse 2000; Fisher et al. 2007)? Here I will argue that we need the species rank not because it is objective, but because it (and other mandatory ranks) pro-

vides informatic reference points that facilitate effective communication about biological diversity.

Phylogenetic taxonomy provides a reference system for biological diversity, analogous to longitude and latitude in geography. Both reference systems need a single unambiguous criterion for assigning a unit (geographic feature or organism) to a place in the system. This is why the coexistence of 2 competing longitudinal reference points at Paris and Greenwich was not viable in the long run. Similarly, systematics has now largely adopted a single reference system, evolutionary relatedness, as a basis for defining where an organism fits in the classificatory structure. But why do we need the species rank?

Again, consider the analogy to the geographic coordinate system. The coordinates of Madison, WI, will generally be reported as 43°N 89°W. Doing so places Madison within a 1° square, providing a useful starting point for locating this city. We could provide coordinates within 0.1° (43.1°N 89.4°W), 0.01° (43.09°N 89.37°W), 2° (44°N 90°W), or any arbitrary level of accuracy. However, the degree square provides a conventionally agreed upon first-order summary of the location of geographic feature. The species rank can be viewed similarly: assigning an organism to a species answers the question "Where does this organism fit on the tree of life?" to a conventionally agreed upon, if not explicitly defined, level of accuracy. Likewise, assigning organisms to genera answers the same question, but with lower precision, and assigning organisms to subspecies does so with greater precision.

A significant difference between the geographic and taxonomic coordinate system is that whereas geographic space has an unambiguous scale, in units of degrees, taxonomic space is less readily parameterized. One might wish to use time since common ancestry, but different parts of the genome share common ancestry at different times in the past. One might wish to use degree of phenotypic differentiation, but phenetic similarity cannot be captured on any one true scale (Farris 1982). Thus, the scale of relatedness is less easily defined than longitude and latitude. Nonetheless, although we cannot readily define the size of the phylogenetic neighborhood encapsulated by the species rank, it will tend to be a smaller neighborhood than would be designated by the genus rank (and so on).

Maybe in the distant future we will have new ways to instantly communicate a detailed tree picture without having to name taxa. But, for the time being, the only way to tell somebody where an organism fits on the tree of life is to name the taxa of which it is a part. But there are often too many taxa to name, so we need certain ranks that are established as shared reference points for easy communication. Among these, the species rank has historically been the most important. For that reason, systematics without the species rank is hard to imagine.

The species debate is tiresome, which is why there have been so many calls to set it aside or to agree to disagree (Pigliucci 2003; de Queiroz 2005; Hey 2006). However, the species debate is not just academic. How

we think about species has a very real impact on how taxonomy works. And it is hard to look at the status of taxonomy and conclude that the field is in good shape. We face a crisis of extinction and habitat destruction which can only be kept track of through taxonomic data. Yet the rate at which taxonomic data are generated, for example, the rate at which new taxa are described and named, has barely changed in the last 100 years. This is despite the ready availability of powerful computers and increasingly sophisticated and comprehensive databases of molecular, geographic, and bibliographic data. Whereas other information-rich sciences such as geography and genomics have made huge strides, taxonomy is largely the same as it was 100 years ago. Recent improvements in electronic publishing and data storage are beginning to have an impact (Penev et al. 2008). However, I believe that a more pragmatic and streamlined approach to species taxonomy and nomenclature has the potential to help break this logjam and allow taxonomy to truly enter the information age.

Genealogical history provides the one universal feature of all organisms. Therefore, we should build a database that maintains information on the inferred relationships of very many placeholder organisms tied to raw molecular data and a database of phylogenetic clade definitions and rank assignments. With such a resource, taxa could be named consistently and it would be easy, using molecular data, to quickly determine the taxonomic neighborhood of an unidentified organism. Furthermore, taxonomists would no longer need to publish monographic treatments in the conventionally laborious way—they would just update the databases by adding additional placeholder organisms, increasing the accuracy of the genealogical data, assigning names to newly discovered taxa, and refining ranking so that nearly all living organisms are assigned to species. Such a streamlined structure would be much more democratic and efficient than anything we have today. Just as any scientist can deposit and annotate a sequence in GenBank (subject to editorial oversight), so too would a simple genealogically based database allow many more scientists and amateurs to contribute to the bioinformatic infrastructure. As a result, taxonomy could better serve the needs of scientists, policymakers, and the public.

To achieve the goal of converting taxonomy into a modern, open, information science, it is necessary that the concept of species be moved, once and for all, out of the realm of mechanistic evolutionary biology and kept fully within systematics. If species status depends on something different than relationships, then we inflate the kinds of data that need to be kept track of and broaden the set of scientists who need to participate in species grouping and ranking. Furthermore, if species were defined as functional entities, or anything but a rank of taxon, then we would have to complicate the system by allowing species to overlap in content with taxa. Within the framework of species-as-taxa, it is also important to give up on the idea that there is an objective way to rank species taxa. Once systematists accept

that species status is a semisubjective decision, they may be less inclined to revise the ranking decisions of previous workers and focus instead on evaluating the exclusivity of species and other taxa. By advocating a shift to monistic grouping (based on exclusivity) and semisubjective ranking, I hope that, in some small way, this paper will help systematics evolve into the sophisticated information science that it needs to become.

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REFERENCES

- Ané C., Larget B., Baum D.A., Smith S.D., Rokas A. 2007. Bayesian estimation of concordance among gene trees. *Mol. Biol. Evol.* 24: 412–426.
- Ané C., Sanderson M.J. 2005. Missing the forest for the trees: phylogenetic compression and its implications for inferring complex evolutionary histories. *Syst. Biol.* 54:146–157.
- Avise J.C., Mitchell D. 2007. Time to standardize taxonomies. *Syst. Biol.* 56:130–133.
- Baum D.A. 1998. Individuality and the existence of species through time. *Syst. Biol.* 47:641–653.
- Baum D.A. 2007. Concordance trees, concordance factors, and the exploration of reticulate genealogy. *Taxon.* 56:417–426.
- Baum D.A., Shaw K.L. 1995. Genealogical perspectives on the species problem. In: Hoch P.C., Stephenson A.G., editors. *Experimental and molecular approaches to plant biosystematics*. St. Louis: Missouri Botanical Garden Press. p. 289–303.
- Brummitt R.K. 2002. How to chop up a tree. *Taxon.* 51:31–41.
- Cantino P.D., Bryant H.N., de Queiroz K., Donoghue M.J., Eriksson T., Hillis D.M., Lee M.S.Y. 1999. Species names in phylogenetic nomenclature. *Syst. Biol.* 48:790–807.
- Cracraft J. 1983. Species concepts and speciation analysis. In: Johnston R., editor. *Current ornithology*. New York: Plenum Press. p. 159–187.
- Cronquist A. 1978. Once again, what is a species? In: Ramberger J.A., editor. *Biosystematics in agriculture*. Monclair (NJ): Allanheld & Osmun. p. 3–20.
- Davis J.I., Nixon K.C. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. *Syst. Biol.* 41:421–435.
- Dayrat B. 2005. Advantages of naming species under the PhyloCode: an example of how a new species of Discodorididae (Mollusca, Gastropoda, Euthyneura, Nudibranchia, Doridina) may be named. *Marine Biol. Res.* 1:216–232.
- Dayrat B., Cantino P.D., Clarke J.A., de Queiroz K. 2008. Species names in the PhyloCode: the approach adopted by the International Society for Phylogenetic Nomenclature. *Syst. Biol.* 57:507–514.
- Dayrat B., Gosliner T.M. 2005. Species names and metaphyly: a case study in Discodorididae (Mollusca, Gastropoda, Euthyneura, Nudibranchia, Doridina). *Zool. Scr.* 34:199–224.
- de Queiroz K. 1997. The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature. *Aliso.* 15:125–144.
- de Queiroz K. 1998. The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and

- terminological recommendations. In: Howard D.J., Berlocher S.H., editors. *Endless forms: species and speciation*. New York: Oxford University Press. p. 57–75.
- de Queiroz K. 2005. Different species problems and their resolution. *Bioessays*. 27:1263–1269.
- de Queiroz K. 2007. Species concepts and species delimitation. *Syst. Biol.* 56:879–886.
- de Queiroz K., Donoghue M.J. 1988. Phylogenetic systematics and the species problem. *Cladistics*. 4:317–338.
- de Queiroz K., Gauthier J. 1990. Phylogeny as a central principle in taxonomy—phylogenetic definitions of taxon names. *Syst. Zool.* 39:307–322.
- de Queiroz K., Gauthier J. 1992. Phylogenetic taxonomy. *Ann. Rev. Ecol. Syst.* 23:449–480.
- Ereshefsky M. 1992. Eliminative pluralism. *Philos. Sci.* 59:671–690.
- Ereshefsky M. 2009. Darwin's solution to the species problem. *Synthese*. doi: 10.1007/s11229-009-9538-4.
- Farris J. 1982. The logical basis of phylogenetic analysis. In: Platnick N., Funk V., editors. *Advances in cladistics: proceedings of the second meeting of the Willi Hennig Society*. New York: Columbia University Press. p. 7–36.
- Fisher K.M., Wall D.P., Yip K.L., Mishler B.D. 2007. Phylogeny of the Calymperaceae with a rank-free systematic treatment. *Bryologist*. 110:46–73.
- Hennig W. 1966. *Phylogenetic systematics*. Urbana: University of Illinois Press.
- Hey J. 2006. On the failure of modern species concepts. *Trends Ecol. Evol.* 21:447–450.
- Lee M., Wolsan M. 2002. Integration, individuality and species concepts. *Biol. Philos.* 17:651–660.
- Lee M.S. 2003. Species concepts and species reality: salvaging a Linnaean rank. *J. Evol. Biol.* 16:179–188.
- Mallet J. 2008. Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. *Philos. Trans. R. Soc. Lond. B.* 363:2971–2986.
- Mayr E. 1969. *Principles of systematic zoology*. Cambridge (MA): Harvard University Press.
- Mishler B.D. 1999. Getting rid of species? In: Wilson R., editor. *Species: new interdisciplinary essays*. Cambridge (MA): MIT Press. p. 307–315.
- Mishler B.D., Brandon R.N. 1987. Individuality, pluralism, and the phylogenetic species concept. *Biol. Philos.* 2:397–414.
- Mishler B.D., Donoghue M.J. 1982. Species concepts: a case for pluralism. *Syst. Zool.* 31:491–503.
- Nixon K.C., Wheeler Q.D. 1990. An amplification of the phylogenetic species concept. *Cladistics*. 6:211–223.
- Penev L., Erwin T., Thompson, Christian F., Sues H.-D., Engel M.S., Agosti D., Pyle R., Ivie M., Assmann T., Henry T., Miller J., Ananjeva N.B., Casale A., Lourenço W., Golovatch S., Fagerholm H.-P., Taiti S., Alonso-Zarazaga M., van Nieukerken E. 2008. ZooKeys, unlocking Earth's incredible biodiversity and building a sustainable bridge into the public domain: From "print-based" to "web-based" taxonomy, systematics, and natural history. *ZooKeys*. 1:1–7.
- Pigliucci M. 2003. Species as family resemblance concepts: the (dis-) solution of the species problem? *Bioessays*. 25:596–602.
- Pleijel F., Rouse G.W. 2000. Least-inclusive taxonomic unit: a new taxonomic concept for biology. *Proc. Roy. Soc. London B.* 267: 627–630.
- Ridley M. 1989. The cladistic solution to the species problem. *Biol. Philos.* 4:1–16.
- Simpson G.G. 1961. *Principles of animal taxonomy*. New York: Columbia University Press.
- Sneath P.H.A. 1976. Phenetic taxonomy at the species level and above. *Taxon*. 25:437–450.
- Templeton A.R. 1989. The meaning of species and speciation: a genetic perspective. In: Otte D., Endler J., editors. *Speciation and its consequences*. Sunderland (MA): Sinauer. p. 3–27.
- Van Valen L. 1976. Ecological species, multispecies, and oaks. *Taxon*. 25:233–239.
- Wiley E. 1978. The evolutionary species concept reconsidered. *Syst. Zool.* 27:17–26.
- Wolsan M. 2007. Naming species in phylogenetic nomenclature. *Syst. Biol.* 56:1011–1021.

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