12 Getting Rid of Species?

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The debate about species concepts over the last twenty years follows a curious pattern. Rather than moving toward some kind of consensus, as one might expect, the trend has been toward an ever-increasing proliferation of concepts. Starting with the widely accepted species concept that took precedence in the 1940s and 1950s as a result of the Modern Synthesis—the biological species concept (BSC)—we heard calls for change from botanists, behaviorists, and others. Despite the babel of new concepts, the BSC continues to have fervent advocates (Avise and Ball 1990, Avise and Wollenberg 1997) and has itself spawned several new variants. A recent paper by Mayden (1997) lists no fewer than twenty-two prevailing concepts! We can't seem to eliminate any existing concept, only produce new ones.

Why? The obvious conclusion one might draw—that biologists are contrarians who want to make their own personal marks in a debate and thus coin their own personal concepts to defend—is really not the case; this is no debate about semantics. The conceptual divisions are major and real. In my opinion, the plethora of ways in which different workers want to use the species category reflects an underlying plethora of valid ways of looking at biological diversity. The way forward is to recognize this view and face its implications: the basis of the confusion over species concepts is a result of heroic but doomed attempts to shoehorn all this variation into an outdated and misguided classification system, the ranked Linnaean hierarchy. Most of the confusion can be eliminated simply by removing the ranks. The issues that remain can then be dealt with by carefully considering what we want formal classification to represent as the general reference system and then by carefully specifying criteria for grouping organisms into these formal classifications.

To develop this argument, I first make the case for generalizing the species problem as a special case of the taxon problem. For a consistent, general reference classification system, all taxa must be of the same type; species should be regarded as simply the least-inclusive taxon in the system. Then, I review the reasons why phylogeny provides the best basis for the general purpose classification: species should be considered as just another phylogenetically based taxon. Next, I address the recent calls for rank-free classification in general and pursue the central thesis of this paper: *the species rank must disappear along with all the other ranks.* Finally, I explore the practical implications of eliminating the rank of species for such areas as ecology, evolution, and conservation.

SPECIES AS JUST ANOTHER TAXON

In their particular theories of systematics, many authors have made a firm distinction between species and higher taxa (e.g., Wiley 1981, Nelson and Platnick 1981, Nixon and Wheeler 1990; see also the discussion by de Queiroz, chapter 3 in this volume). The idea is that somehow species are units directly participating in the evolutionary process, whereas higher taxa are at most lineages resulting from past evolutionary events. However nicely drawn this distinction is in theory, these arguments have resulted more from wishful thinking than from empirical observations. When anyone has looked closely for an empirical criterion to distinguish the species rank uniquely and universally from all others, the attempt has failed.

One early suggestion was phenetic: a species is a cluster of organisms in Euclidean space separated from other such clusters by some distinct and comparable gap (e.g., Levin 1979). This idea has been clearly shown to be mistaken: phenotypic clusters are actually nested inside each other with continuously varying gap sizes. Current entities ranked as species are not comparable either in the amount of phenotypic space they occupy or in the size of the "moat" around them, nor can they be made to be comparable through any massive realignment of current usage.

Another suggestion for a unique ranking criterion for species is expressed in the biological species concept: a species is a reproductive community separated by a major barrier from crossing with other such communities (Mayr 1982). Like the phenetic gap, this view (nice in theory perhaps) fails when looking at real organisms (cf. Nanney, chapter 4 in this volume). Despite the publication of many conceptual diagrams that depict a distinct break between reticulating and divergent relationships at some level (Nixon and Wheeler 1990, Roth 1991, Graybeal 1995), actual data suggests that in most groups, the probability of intercrossability decreases gradually as more and more inclusive groups are compared (Mishler and Donoghue 1982, Maddison 1997). There usually is no distinct point at which the possibility of reticulation drops precipitously to zero.

Similar suggestions have been made based on ecological criteria: a species is a group of organisms occupying some specific and unitary ecological niche (Van Valen 1976). Maybe species "can define themselves"; we just need to see whether two organisms treat each other as belonging to the same or different species. Again, actual studies show no such distinctive level where ecological interactions change abruptly from "within kind" to "between kind." Cryptic, ecologically distinct groups can be found below the species level, and large guilds of organisms from divergent species can act as one group ecologically in some situations.

Finally, there have been attempts to distinguish species from all other taxa phylogenetically (Nixon and Wheeler 1990, Graybeal 1995, Baum 1992). In this view, species are the smallest divergent lineage, inside of which there is no recoverable divergent phylogenetic structure (only reticulation). Again, nice in theory, but unsound empirically, at least as a general principle (Mishler and Donoghue 1982, Mishler and Theriot 1999). Some biological situations fit the model well (e.g., in organisms with complex and well-defined sexual mate recognition systems and no mode of asexual propagation). However, in many clonal groups (e.g., aspen trees, bracken fern) discernible lineages go down to the within-organism level (the problem of "too little sex"; see Templeton 1989). On the other hand, occasional horizontal transfer events ("reticulations") occur between very divergent lineages (the problem of "too much sex"; see Templeton 1989). In all such cases, a large gray area exists between strictly diverging patterns of gene genealogies and strictly recombining ones (cf. Avise and Wollenberg 1997).

To sum up, we have no and are unlikely to have any criterion for distinguishing species from other ranks in the Linnaean hierarchy, which is not to say that particular species taxa are unreal. They are real, but only in the sense that taxa at all levels are real. Species are not special.

THE NECESSITY FOR PHYLOGENETIC CLASSIFICATIONS

The debate over classification has a long and checkered history, but this essay is not the place to detail the history fully (see Stevens 1994 and Ereshevsky, chapter 11 in this volume). I want to begin with the conceptual upheaval in the 1970s and 1980s that resulted in the ascension of Hennigian phylogenetic systematics (for a detailed treatment, see the masterful book by Hull 1988). Many issues were at stake in that era, foremost of which was the nature of taxa. Are they just convenient groupings of organisms with similar features, or are they lineages, marked by homologies? A general, if not completely universal, consensus has been reached that taxa are (or at least should be) the latter (Hennig 1966, Nelson 1973, Farris 1983, Sober 1988).

A full review of the arguments for why formal taxonomic names should be used solely to represent phylogenetic groups is beyond the scope of this paper, but they can be summarized as follows. Evolution is the single most powerful and general process underlying biological diversity. The major outcome of the evolutionary process is the production of an ever-branching phylogenetic tree, through descent with modification along the branches. This results in life being organized as a hierarchy of nested monophyletic groups. Because the most effective and natural classification systems are those that "capture" the entities resulting from processes that generate the things being classified, the general biological classification system should be used to reflect the tree of life.

The German entomologist Willi Hennig codified the meaning of these evolutionary outcomes for systematics in what has been called the *Hennig Principle* (Hennig 1965, 1966). Hennig's seminal contribution was to note that in a system evolving via descent with modification and splitting of lineages, characters that changed state along a particular lineage can serve to indicate the prior existence of that lineage, even after further splitting occurs. The Hennig Principle follows from that conclusion: homologous similarities[1] among organisms come in two basic kinds, *synapomorphies* due to immediate shared ancestry (i.e., a common ancestor at a specific phylogenetic level) and *symplesiomorphies* due to more distant ancestry. Only the former are useful for reconstructing the relative order of branching events in phylogeny. A corollary of the Hennig Principle is that classification should reflect reconstructed branching order; only *monophyletic groups*[2] should be formally named. Phylogenetic taxa will thus be "natural" in the sense of being the result of the evolutionary process.

This isn't to say that phylogeny is the only important organizing principle in biology. There are many ways of classifying organisms into a hierarchy because of the many biological processes impinging on organisms. Many kinds of nonphylogenetic biological groupings are unquestionably useful for special purposes (e.g., producers, rain forests, hummingbird pollinated plants, bacteria). However, it is generally agreed that there should be one consistent, general reference system, for which the Linnaean hierarchy should be reserved. Phylogeny is the best criterion for the general-purpose classification, both theoretically (the tree of life is the single universal outcome of the evolutionary process) and practically (phylogenetic relationship is the best criterion for summarizing known data about attributes of organisms and predicting unknown attributes). The other possible ways to classify can, of course, be used simultaneously, but should be regarded as special purpose classifications and clearly distinguished from phylogenetic formal taxa.

THE ADVANTAGES OF A RANK-FREE TAXONOMY

A number of calls have been made recently for the reformation of the Linnaean hierarchy (e.g., de Queiroz and Gauthier 1992). These authors have emphasized that the roots of the Linnaean system are to be found in a nonevolutionary worldview—a specially created worldview. Perhaps the idea of fixed ranks made some sense under that view, but not under an evolutionary worldview. Most aspects of the current code, including priority, revolve around the ranks, which leads to instability of usage. For example, when a change in relationships is discovered, several names often need to be changed to adjust, including the names of groups whose circumscription has not changed. Authors often frivolously change the rank of a group even though there is no change in postulated relationships. Although practicing systematists know that groups given the same rank across biology are not comparable in any way (i.e., in age, size, amount of divergence, internal diversity, etc.), many users of the system do not know this. For example, ecologists and macroevolutionists often count numbers of taxa at a particular rank as an erroneous measure of "biodiversity." The nonequivalence of ranks means that at best (to those who are knowledgeable) they are a meaningless formality and perhaps not more than a hindrance. At worst, formal ranks lead to bad science in the hands of a user of classifications who naively assumes that groups at the same rank are comparable in some way.

It is not completely clear at this point how exactly a new code of nomenclature should be written, but the basics are clear. Such a new code should maintain the principle of priority (the first name for a clade should be followed) and other aspects of the current code that promote effective communication of new names to the community. However, the major change would be that the Linnaean ranks (e.g. phylum, family) should be abandoned for more efficient and accurate representation of phylogenetic relationships. Instead, names of clades should be hierarchically nested uninomials regarded as proper names. A clade would retain its name regardless of where new knowledge might change its phylogenetic position, thus increasing nomenclatorial stability. Furthermore, because clade names would be presented to the community without attached ranks, users would be encouraged to look at the actual attributes of the clades they compare, thus improving research in comparative biology.

It is important to emphasize that despite misrepresentations to the contrary, theorists who advocate getting rid of Linnaean ranks do not at all advocate getting rid of the hierarchy in biological classification. Nesting of groups within groups is essential because of the treelike nature of phylogenetic organization. Think of a nonsystematic example: a grocer might classify table salt as a spice, and group spices together under the category *food items.* This simple hierarchy is clear, but requires no named ranks to be understood. In fact, all human thought is organized into hierarchies, and becoming educated in a field essentially means learning the hierarchical arrangement of concepts in that field. Taxonomy is unusual in the assigning of named ranks to its hierarchies; they are superfluous to true understanding.

GETTING RID OF THE SPECIES RANK

Curiously, so far in this debate, even the advocates of rank-free phylogenetic classification have retained the species rank as a special case. All other ranks are to be abandoned, but the species rank is to be kept, probably because the species concept is so ingrained and comfortable in current thinking. However, all the arguments that can be massed against Linnaean ranked classification in general can be brought to bear against the species rank as well. As difficult as it is to overthrow ingrained habits of thinking, logical consistency demands that all levels in the classification should be treated alike.

Given the background developed in the previous three sections, the conclusion seems inescapable: *the species rank must go the way of all others.* We must end the bickering over how this rank should be applied and instead get rid of the rank itself. This solution is truly the "radical solution to the species problem" sought unsuccessfully by Ghiselin (1974). Biological classification should be a set of nested, named groups for internested clades. Not all clades need be named, but those that are should be named on the basis of evidence for monophyly (see further discussion of the meaning of monophyly in Mishler and Brandon 1987). We stop naming groups at some point approaching the tips of the phylogeny because we don't have solid evidence for monophyly at the present stage of knowledge. This may be due to rampant reticulation going on below some point or simply to a lack of good markers for distinguishing finer clades. We shouldn't pretend, however, that the smallest clades named at a particular time are ontologically different from other, more inclusive named clades. Further research could easily result in subdividing these groups or lumping several of them into one if the original evidence that supported them is discovered to be faulty.

Given the redundancy now present in species epithets (e.g., *californica* is used in many genera), there needs to be a way to uniquely place each smallest named clade in the classification. My recommendation for nomenclature at the least inclusive level under a totally rank-free classification would be to regard names in a similar way as personal names are regarded in an Arabic culture. Each clade, including the least inclusive one named, has its own uninomial name; however, the genealogical relationships of a clade are preserved in a polynomial giving the lineage of that clade in higher and higher groups. Therefore, the familiar binomial, which does after all present some grouping information to the user, could be retained, but should be inverted. Our own short clade name thus should be *Sapiens Homo*. The full name for our terminal clade should be regarded as a polynominal that gives the names of the more and more inclusive clades all the way back. To use the human example, this full name would be something like: *Sapiens Homo Homidae Primate Mammalia Vertebrata Metazoa Eucaryota Life.*[3] Again, as in a traditional Arabic name, this formal and complete name would be used only rarely and for the most formal purposes (although it would be very useful behind the scenes for data-basing purposes); the everyday name of the clade would be *Sapiens Homo*.

PRACTICAL IMPLICATIONS

"Getting rid of species" has another, all too ominous meaning in today's world. Named species are being driven to (and over) the brink of extinction at a rapid rate. What will be the implications of the view of taxa advocated in this paper? If we get rid of the species rank, with all its problems, will we hamstring conservation efforts? I tend to think not; scientific honesty seems the best policy here as elsewhere. The rather mindless approach followed in conservation—that if a lineage is ranked as a species, it is worth saving, but if it is not considered a species, it is not worth considering—is misguided in many ways. It is wrong scientifically; the species rank is a human judgment rather than any objective point along the trajectory of diverging lineages. It is also wrong ethically; any recognizable lineage is worth conservation consideration. Not all lineages need be conserved, or at least be given the same conservation priority, but such judgments should be made on a case by case basis.

All biologists are concerned about defining biodiversity and about its current plight; thus, the radical move suggested here (i.e., getting rid of the species rank) will no doubt worry many. People who want to characterize and conserve biodiversity commonly complain that "without species we will have no way of quantifying biodiversity or of convincing people to preserve it." This viewpoint, although expressing a commendable and important concern, is ultimately misguided, both in theoretical and practical terms. There may a comfortable self-deception going on to the contrary, but only a moment of thoughtful reflection is enough to remind us that species are not comparable in any important sense and cannot be made so.

However, the recognition that a count of species is not a good measure of biodiversity does not mean that biodiversity cannot be quantified. All named species are unique, with their own properties and features, and they represent only the tip of the underlying iceberg of biodiversity. We must face these facts and move to develop valid measures of the diversity of lineages, taking into account their actual properties and phylogenetic significance. A number of workers have suggested quantitative measures for phylogenetic biodiversity, which take into account the number of branch points and possibly branch lengths separating the tips of the tree (Vane-Wright, Humphries, and Williams 1991; Faith 1992a, 1992b).

Many macroevolutionary studies are framed in terms of comparing diversity patterns at some particular rank (e.g., families of marine invertebrates, phyla of animals). The adoption of rank-free classification would (fortunately) make such studies impossible, but would it make all studies of macroevolution impossible? Of course not: comparisons among clades would still be quite feasible, but it would be up to the investigator to establish that the clades being compared were the same with respect to the necessary properties (i.e., equivalent age or disparity, and so on). Similar arguments could be made with respect to the many ecological studies that compare numbers of species in different regions or communities. The bottom line is that rank-free classification would lead to much more accurate research in ecology and evolution because, investigators would be encouraged to use cladograms directly in their comparative studies instead of relying on equivalence in taxonomic rank as a (very) crude proxy for comparability of lineages. Given the rapid progress in development of quantitative comparative methods (Funk and Brooks 1990, Brooks and McLennan 1991, Harvey and Pagel

1991, Martins 1996) and the rapid proliferation of ever-improving cladograms for most groups of organisms, this change can only be for the best.

Species, RIP.

NOTES

1. In Hennigian phylogenetic systematics, *homology* is defined historically as a feature shared by two organisms because of descent from a common ancestor that had that same feature.

2. A strictly monophyletic group (a clade) is one that contains all and only descendants of a common ancestor. A paraphyletic group is one the excludes some of the descendants of the common ancestor.

3. Note that some of the nested clades will have formal suffixes indicating their previous rank (e.g., *-idae* for family). Although these endings would be retained for existing clade names in order to avoid confusion, there would be no meaning attached to them, and newly proposed clade names would have no particular suffix requirement.

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