CHAPTER
SIX

Species Are Not Uniquely Real Biological Entities

Brent D. Mishler

Are species uniquely real biological entities? This question is one of the most controversial topics today in such areas of biology as ecology, systematics, conservation, population genetics, and evolution. "Species" currently play a central role in both theory and practice in these areas, and have a large place in the public's perception of biological diversity as well. This question can be decomposed into two parts: (1) Are species real, and in what sense? (2) If real, is their reality the same as entities smaller or larger than them – i.e., are they real in a sense that genera or subspecies are not? This paper will briefly review historical and current opinions on these questions, but will primarily advocate one particular position that appears to fit biological reality as now understood: that species properly defined *are* real entities, but not *uniquely* real. The longstanding "species problem" can be solved by realizing that there is no such thing as species after all! The so-called "species problem" is really just a special case of the taxon problem. Once a decision is made about what taxa in general are to represent, then those groups currently known as species are simply the least inclusive taxa of that type. As I favor a phylogenetic basis for taxonomy, I want to look at how to include terminal taxa in the PhyloCode, currently a controversial topic even among PhyloCode supporters. In brief, my argument is: (1) life is organized in a hierarchy of nested monophyletic groups – some of them quite fine-scale, well below the level we currently call species; (2) not all known monophyletic groups need be named, just the ones that are important to process or conservation studies and that have good support; (3) those that are named taxonomically should be given unranked (but hierarchically nested) uninomials; and (4) formal ranks, including species, should be abandoned. I will conclude with a brief discussion of the implication of my position on species for academic studies in ecology and evolution as well as for practical applications in biodiversity inventories and conservation biology.

> But be warned, you who thirst for knowledge, be warned about the thicket of opinions and the fight over words.
>
> Hermann Hesse, *Siddhartha*

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1 Historical and Current Views of Species

Over the history of science, people have taken a number of different positions on these issues involving the reality of species. The fundamental view throughout the classical period (basically from the ancient Greeks until Darwin) was that species are indeed the basic, real units of life. The basis for their reality was initially conceived of in a typological or idealistic framework; species were viewed as the basic kinds or types of living things. Later, under the influence of Christian theology, the basis for the fundamental reality of species changed somewhat. They were still viewed as basic kinds, but now as specially created "ideas" in the mind of the creator. Taxonomic groups at more inclusive levels were also manifestations of the creator's ideas, but species were the fundamental kinds, the building blocks of life. This idea continues to the present in the attitudes of the majority of the general public in the United States, under the influence of creationism.

The course of science took a somewhat different path than the public view. The Darwinian revolution did not question the reality of species in scientists' thinking (although see below for Darwin's contribution to a shift in thinking about their uniqueness), but changed the perception of their nature greatly. Instead of representing a natural kind defined by certain necessary and sufficient characteristics, species came to be seen as a natural genealogical unit composed of organisms historically related to each other, with a beginning and an end, *not* defined by any characteristics (i.e., "individuals" in the philosophical sense; Ghiselin, 1974; Hull, 1978; Mishler & Brandon, 1987). They were viewed as a cross-section of a lineage (de Quieroz, 1999). In the Modern Synthesis (called such at the time, but looking rather dated these days!), a view solidified of species being the largest group of interbreeding organisms (the gene pool) and as such the most fundamental unit in which evolutionary change takes place (*the biological species concept*; BSC; Mayr, 1942, 1982). Species came to be regarded as a fundamental level in the hierarchy of biological organization (e.g., molecule, cell, tissue, organism, population, species, community, ecosystem).

This view was nearly unanimous until the 1960s, when, under the influence of highly empirical operationalist philosophies of science then in style, and the seemingly "objective" application of computer algorithms to science, an approach emerged called "numerical taxonomy" or "phenetics." In this view, taxa at all levels, including species, were viewed in a nominalistic manner. A species was just a cluster of similar organisms grouped at some arbitrary numerical level of similarity (*the phenetic species concept*; Levin, 1979; Sokal & Crovello, 1970). It was considered to be unnecessary and wrong-headed to require anything about a deeper basis for reality, whether relatedness or interbreeding ability, to describe species. If named species later turned out to be something useful for inferences about evolutionary or ecological processes, then fine, but their recognition as species was best kept separate from process considerations.

One trend apparent in the history of thinking about species has to do with organismal specialty; to a large extent, there has been a sociological difference among communities of systematists studying different kinds of organisms. Zoologists tended to favor the biological species concept (Coyne, Orr, & Futuyma, 1988), while botanists and bacteriologists tended to favor the phenetic species concept (e.g., Levin, 1979; Sokal & Crovello, 1970). There have been some exceptions: for example, Grant

(1981), Rieseberg and Burke (2001), and Stebbins (1950) represent a minority BSC tradition viewpoint among botanists, while Wheeler (1999) represents a minority non-BSC viewpoint among zoologists. This striking distinction is probably mostly due to actual differences in reproductive biology among different branches of the tree of life. Specialists on organisms with either very open mating systems or highly clonal reproduction have always had trouble applying the BSC and have looked for alternatives.

The Hennigian phylogenetics revolution that began in the 1970s altered many aspects of theory and practice in systematics, but did not do much to prune the existing variety of species concepts, and in fact added several more. Hennig himself (1966) held to a version of the biological species concept, while other Hennigians preferred the *evolutionary species concept* (basically an interbreeding group viewed through time as a lineage; Wiley, 1978) or various versions of a *phylogenetic species concept*. The latter are a heterogeneous set of concepts as well: some quite similar to the phenetic species concept (i.e., species viewed as a unique set of character states; Cracraft, 1997; Nixon & Wheeler, 1990; Platnick & Wheeler, 2000; Wheeler & Platnick, 2000a, 2000b), others applying Hennigian concepts of apomorphy and monophyly to the species level (Mishler & Donoghue, 1982; Mishler & Theriot, 2000a, 2000b, 2000c; Rosen, 1978).

In comparing different views of species it is important to distinguish two components of any species concept: *grouping* vs. *ranking* (Horvath, 1997). The grouping component of any species concept indicates the criteria for group inclusion, whether ability to interbreed, phenetic similarity, or sharing of apomorphies indicating monophyly. The ranking component of any species concept indicates the criteria for deciding whether a group counts as a species rather than a taxon at some other rank. Both components are necessary because all concepts define groups within groups, and the level of group corresponding to species needs to be specified. Some of the controversy over species concepts has been because people are not clear about this distinction.

The phylogenetic species concept in the sense of my work with Brandon and Theriot (Mishler & Brandon, 1987; Mishler & Theriot, 2000a, 2000b, 2000c) is clear about this distinction, and basically treats species as just another taxon (see also Nelson, 1989), taking the perspective that if we are going to be phylogenetic about taxa in general, we need to be phylogenetic about species. Theriot and I (Mishler & Theriot, 2000a) defined species as follows: “A species is the least inclusive taxon recognized in a formal phylogenetic classification” (p. 46). As with all hierarchical levels of taxa in such a classification, organisms are *grouped* into species because of evidence of monophyly. Taxa are *ranked* as species rather than at some higher level because they are the smallest monophyletic groups deemed worthy of formal recognition, due to the amount of support for their monophyly and/or their importance in biological processes operating on the lineage in question. One obvious question follows from the definition given above: doesn’t the ranking decision sound arbitrary? The short answer is: Yes! If not completely arbitrary, the decision does depend on local context—ranking criteria are pluralistic rather than universal (Mishler & Donoghue, 1982).

The ranking decision in the phylogenetic species concepts discussed above is present because of the way the current codes of nomenclature are written. Monophyletic taxa not only have to be discovered and diagnosed, they must be given a specific rank, including species. But this doesn’t have to be so. We can remove this arbitrary aspect of taxonomy; the best approach is arguably not to designate any ranks at all.

I now advocate an extension of the recent calls for rank-free phylogenetic taxonomy to the species level (e.g., Mishler, 1999; Pleijel, 1999), and will develop this position in the following sections.

2 Return to a Darwinian View of Species

Let's consider the two-part question introduced above: (1) *Are species real?* (2) *Are species uniquely real?* All working biologists today think that the answer to the first question is yes: species are real entities in some sense (although the grouping criterion considered to be the basis for their reality varies as described above). The current debate concentrates on the second question: whether or not species are a special level either in biological organization or in the taxonomic hierarchy. In other words, is there a unique ranking criterion for species? The two possible answers to this question can be contrasted as the *Darwinian view* vs. the *Mayrian view*.

One of Darwin's important novel contributions to biology was the explicit recognition that the species level is an arbitrary point in the divergence of two lineages. The *Origin* (Darwin, 1859) is full of passages indicating Darwin's view that the species rank is arbitrary, even though the lineages are quite real. His view was that divergence between two lineages happens, and at some point it is convenient to call the two lineages species according to the judgment of a competent taxonomist, but nothing particularly special or universal occurs at that point.

The Modern Synthesis, in its bringing together of population genetics and taxonomy, emphasized a different point of view on species than Darwin. Species were now viewed as an important and distinct level of biological organization (like "molecule" or "cell"), the largest group within which evolution occurs, held together by sharing a gene pool. Ernst Mayr is particularly responsible for pushing this viewpoint (Mayr, 1982). Following Mayr, many today (scientists and public alike, in a strange convergence between evolutionary biologists and creationists) see species in this special light. Note that I am not calling Mayr or any evolutionary biologist a creationist. I am only pointing out an interesting parallel to their position in this one particular area. I don't think the parallel is an accident, however. I think that the idea of distinct, basic, natural units (i.e., species as the building blocks of biodiversity) is so ingrained in Western thought (coming from before the Christian era so not due to creationists directly) that most evolutionary biologists and ecologists have serious trouble letting go of it. Darwin was a really original and courageous thinker whom many biologists even today have trouble emulating.

There is abundant empirical evidence presented since Darwin's time that shows he had the right view and that the actual "species situation" is much more complex than modeled by the Modern Synthesis adherents (Mishler & Theriot, 2000a, 2000b, 2000c). Gene pools (potential horizontal transfer of genes at some level of probability) usually occur at many nested levels within one lineage, and the most inclusive level is often higher than anyone would want to call species (e.g., corresponding to the current generic and even familiar level in flowering plants). On the other hand, sometimes gene pools don't exist at all in a lineage, in the case of asexual organisms. Alan Templeton (1989) succinctly summarized this spectrum of problems with the Mayrian BSC as ranging from "too much sex" to "too little sex."

It would be conceptually cleaner if Mayr was right that there is a particular, unique level, comparable across the tree of life, at which "species-ness" arises as two lineages diverge. However, empirical reality intrudes on this tidy BSC concept; we need a more flexible concept since such a clean species break rarely if ever appears to be the case. My own view is that Darwin's richer conception is better, and that the supposed advances of the Modern Synthesis were actually retrograde, at least as far as species concepts are concerned. To make progress in this area we need to reject the simplistic Mayrian view and emulate Darwin's view.

My own answer on the twin questions italicized at the beginning of this section is this: entities that are currently called species are indeed real, if grouped correctly as monophyletic groups, but they are not uniquely real, i.e., they are only real in the sense that other levels of monophyletic groups are—there is no special ranking criterion for species. The processes causing divergence of lineages, and keeping them separate afterwards, are many. We must develop a richer view of the tree of life and how best to understand and classify it. Such a view must consider the many nested levels of divergence and reticulation in the tree of life, not just the one we arbitrarily happen to call species.

To develop this view, we need to look closely at several related concepts. One is the nature of *monophyly*. There have been two basically different ways of defining monophyly within the Hennigian tradition of phylogenetic systematics: one is synchronic (i.e., "all and only descendants of a common ancestor"); another is diachronic (i.e., "an ancestor and all of its descendants"). I have argued elsewhere (Mishler, 1999) that the former view (Hennig's own view) is better, because it avoids the time paradoxes inherent in placing the ancestor in a group with its descendants. Just like a zygote is not one of the cells of an adult organism (instead it is *all* the organism at its beginning), the ancestor is not a member of a synchronic monophyletic group when looked at later—it was the whole monophyletic group back in its day.

A further consideration is that the word "species" appears in many definitions of monophyly (including Hennig's). This obviously matters if we are discussing the application of monophyly to the species level, because of circularity concerns. We need a definition that is both synchronic and neutral about taxonomic ranks, like this: a monophyletic group is all and only descendants of a common ancestor, where "ancestor" is interpreted broadly to mean an individual in the philosophical sense of Ghiselin (1974) and Hull (1978), e.g., an organism, or breeding groups of various sizes.

Another distinction that is needed is between *clades* and *lineages*. While sometimes treated loosely as synonyms, they are not exactly the same thing—some refinement of terminology is needed. Figure 6.1 shows the difference. A "clade" is a synchronic entity, a monophyletic group as discussed above (a group composed of all descendants of a common ancestor). A "lineage," by contrast, is a diachronic concept, a series of ancestors and descendants (replicators in the abstract sense of Hull, 1978) through time. They are related terms, of course: a clade could best be viewed as an instantaneous snapshot of a lineage.

This distinction helps us clarify some of the murky debates over phylogenetic species concepts. Some phylogeneticists have focused their species concepts on clades (e.g., Baum & Shaw, 1995; Mishler & Brandon, 1987; Mishler & Theriot, 2000a, 2000b, 2000c), and some on lineages (e.g., de Quieroz, 1999; Wiley, 1978), but it is important to note that both clades and lineages form hierarchies. Clades are obviously nested inside

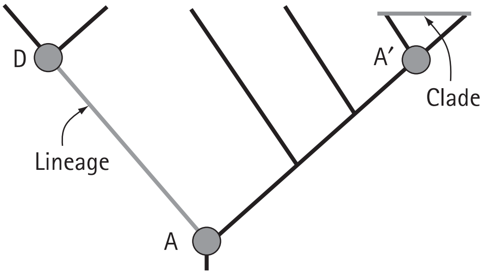

Figure 6.1: The distinction between clades and lineages. A clade is a synchronic, monophyletic set of lineage-representatives, where monophyly is defined synchronically as "all and only descendants of a common ancestor" (represented by A′ in this case). A lineage is a diachronic ancestor–descendant connection (between A and D in this case): "species" in the de Queiroz sense.

of other clades, but less widely understood is that the same is true of lineages. A smaller-scale lineage (say of cells) is nested inside of larger-scale lineages (such as organisms or larger groupings acting as individuals in a philosophical sense). There is no privileged level that can be recognized in either of these nested hierarchies; there is no unique species rank in either clades or lineages.

I prefer applying our formal classification system to name clades (i.e., monophyletic groups) for the following reasons: (1) clades are more nicely nested hierarchically than lineages; (2) we have a well-thought-out code of nomenclature available for naming clades (the PhyloCode); and (3) there are many more kinds of lineages, biologically speaking, due to the multiple kinds of replication which can occur in nature. Some recent workers have thought about providing a code to name lineages, i.e., a "Species Code" (see discussion in the PhyloCode preface at: http://www.ohiou.edu/PhyloCode/preface.html), perhaps to complement the PhyloCode (which is based on clades), but this will prove to be very challenging.

The generalized view presented above, abandoning species in favor of describing clades at several nested levels, has many advantages in theory. Yet it requires considerable further explication before being applied in practice, since so many other areas of biology are accustomed to using species as a unit. I will go through several of these areas below, beginning with systematics, where it all starts.

3 Practical Implications

3.1 Truly rank-free classification, all the way down

As covered in many previous papers (summarized by Mishler, 2009), it has become clear that the ranks in the Linnaean system are problematic for classification, both theoretically and practically. Let me just summarize these general arguments briefly here. Rapid advances in phylogenetic research have made it obvious that there are not nearly enough ranks to suffice in classifying the tree of life, with its thousands of nested levels of clades. The need to maintain the hierarchy of the ranks leads to instability, with names being changed without good reason, as, for example, when one currently recognized genus is found to be nested inside another (a common occurrence). Ranked classifications can lead to bad science in such fields as ecology or macroevolution, if a user of a classification naïvely (but understandably) assumes that taxa placed at the same rank must be comparable in some way.

The current codes of nomenclature can be tweaked to name monophyletic groups, but they are far from ideal for that purpose. The current codes are used to name *all* kind of groups; thus a user has no way of easily knowing if a given taxon is thought to be monophyletic. Only a search into the literature can uncover the basis for a particular taxon name under the current codes, while under the PhyloCode one knows that the author of the name hypothesized it to be a monophyletic group. A name that can be used to convey anything really conveys nothing.

It has become clear that the current codes don't lend themselves well to naming monophyletic groups unequivocally, primarily because there is only one type specimen. It is possible to patch the current codes of nomenclature to name phylogenetic taxa, as suggested by (Barkley et al., 2004). But, for many reasons it would be better to develop a new code of nomenclature specifically designed for phylogenetics. It really is time to bite the bullet and complete a synthesis between the Darwinian revolution and the Hennigian revolution (de Queiroz, 1988). Ranked classifications are a hold-over from the pre-Darwinian creationist mindset (Ereshefsky, 2002). They are not just a quaint anachronism; they are resulting in miscommunication at many levels. Completely rank-free phylogenetic classifications are far better for teaching, research, communicating with other scientists, and interfacing with the larger society.

What about the fundamental taxonomic level, species? Most published discussions about rank-free taxonomy are based on considerations of higher taxa alone, yet all the criticisms of taxonomic ranks summarized above can be extended to species—it is clear that all the arguments about the inadequacy of the current codes for naming phylogenetic taxa apply to the species level also.

The developing PhyloCode may be accessed online (http://www.ohiou.edu/PhyloCode/). This code maintains many of the features of current rank-based codes, but removes all ranks from clade names, and also uses multiple types (called "specifiers") to precisely fix the name of a clade. Important to this discussion, the current draft of the PhyloCode unfortunately does not deal well with providing names for what have been called species. Many uncomfortable special conventions are currently suggested for dealing with this particular rank. Thus even the community of supporters of the PhyloCode is conflicted about what to do about species! More work is needed to make the PhyloCode work seamlessly at all taxonomic levels.

How could rank-free classification be applied to terminal taxa? Exactly as at other levels: names of all clades (including the terminal level) should be hierarchically nested uninomials regarded as proper names (current usage should be followed as much as possible to retain links to the literature and collections). As at all taxonomic levels, we could use either node-based or stem-based names with multiple internal specifiers (I personally think the use of apomorphy-based names is incoherent at any level, but that is another argument!). Specifiers should be actual specimens (this should be true at all levels).

In my opinion, species names should be converted from the current epithets (despite the current prohibition of this is the PhyloCode draft; see example of this in Fisher, 2006). The overriding principle is to achieve maximum continuity with previous literature for the sake of preserving connections to databases, literature, museum specimens, etc. There are two additional important principles, in my opinion: the naming system should be consistent for clades at all levels, and the PhyloCode should be distinct from the existing codes in terms of rules. In this approach, then, each clade named under the PhyloCode, including the terminal-most clade, has a uninomial given name, but also has associated with it a set of more and more inclusive "family names" (its clade address). In a database at least, all the higher clades to which a taxon belongs would be regarded as part of its complete name; this would help computers (and users) keep track of information in the database. Homonyms, which would result when converting species epithets to uninomials, can thus be told apart by higher-level clade names if their context is unclear, just as a teacher uses last names to distinguish among several children in class having the same first name.

3.2 Phylogenetic monography

How can monographs be done under this view of species? In a rank-free framework, they can be done as well as or better under the current codes, as exemplified through the pathbreaking approach by Fisher (2006). Her approach was as follows: (1) use earlier taxonomies as a criterion for stratified-random selection of specimens to study (Hennig's semaphoronts); (2) after that, ignore taxonomic designation during character analysis and character scoring; (3) once operational taxonomic units are established (based on scored characters), conduct phylogenetic analysis; (4) use the resulting phylogenetic tree to inform taxonomic decisions, including naming of terminal clades consistent with the PhyloCode's treatment of more inclusive monophyletic groups. Specifiers used are specimens on deposit in an herbarium or museum, and the formal specifiers as well as other specimens studied are cited much as in traditional monographs.

3.3 DNA barcoding

This discussion touches upon the current debates over DNA barcoding, another recently proposed system for characterizing species, which uses a short stretch of DNA sequence from a standard gene. Similarity above a certain percentage, say 2%, equals species status. This approach has gained popular appeal, but suffers from obvious philosophical problems. Contrary to their posturing as cutting-edge, DNA barcoders are actually returning to an ancient, typological, single-character approach, and are maintaining a pre-Darwinian view of species. There are two aspects to DNA barcoding, one good (but not new), the other new (but not good): DNA-based identification (i.e., using sequence data from a standard gene) and DNA taxonomy (i.e., using sequence data from a short stretch of a standard gene to recognize and name taxa). All critics (including me) are strongly in favor of the good idea of using DNA for identification of already well-characterized taxa, but that is old hat—the important use of DNA for identification goes back to the beginning of molecular systematics. The DNA barcoders can't take any credit for that—the most that they can claim is that they will scale-up, standardize, and database. But, there is really no need to set up a new bureaucracy or new databases (wasting the money of naïve funding agencies, who could be directing their attention toward real phylogenetic systematics)—current efforts elsewhere (such as GenBank) are more than sufficient. The new idea that DNA barcoding can replace normal taxonomy for naming new species and studying their relationships is not only bad philosophically, it is destructive in a practical sense. We should use all available resources to build real capacity to do systematics right (Will, Mishler, & Wheeler, 2005).

3.4 Implications for ecology, population genetics, and evolution

The species level is highly embedded in current ecological theory and practice. It is widely accepted that within- and between-species interactions are different in kind. Niche theory is usually conjoined with a view that the species level provides a fundamental break. Gause's (1934) theory of competitive exclusion talks about the ability of species needing to differentiate in order to live in the same environment. The species level is likewise highly embedded in studies of population genetics. The species is thought to be the largest unit in which gene flow is possible, thus the largest group that can actually evolve as a unit.

It is beyond the scope of this paper to elaborate on the ways to modify ecological theory to fit with a rank-free view of phylogenetic diversity (i.e., no species or other ranks). It needs to be done, however—based on the arguments presented above it is clear that the world is more complex than the current BSC allows for. If the systematic community moves to a rank-free view of biodiversity, then basic ecological and evolutionary research must be modified to account for this view. Fortunately, phylogenetic comparative methods are under active development in many areas (beginning with seminal studies such as Burt, 1989; Cheverud & Dow, 1985; Felsenstein, 1985; Harvey & Pagel, 1991; Huey & Bennett, 1987; and Martins, 1996). Studies can go forward on niche differentiation, competition, coexistence, species-area curves, community assembly, gene flow, macroevolutionary diversification, etc., but in a more rational manner taking into account nested hierarchical levels in these phenomena, without using ranks.

3.5 Implications for conservation biology

As argued in detail above, biodiversity isn't species—biodiversity is the whole tree of life, not just the arbitrary place at which species are named. There are clades smaller and larger than the traditional species level. Species are not comparable between lineages in any manner, just an arbitrary cut-off somewhere along a branch in the tree of life. Thus only someone sharing the BSC view that species are fundamental (a view interestingly shared by creationists, as discussed above) should think that species are the basic units of biodiversity, or that a list of currently named species in some way provides an inventory of biodiversity. Biodiversity is a much richer tapestry of lineages and clades.

So how can we inventory biodiversity without species? Since counting species or measuring their ranges and abundances is a poor measure of biodiversity, what should be done? New quantitative measures for phylogenetic biodiversity need to be applied which take into account the number of branch points (and possibly branch lengths) that separate two lineages. Phylogenetic measures of biodiversity have been developed that could be used as a basis for rank-free measures of biodiversity (Faith, 1992a, 1992b; Mishler, 1995; Vane-Wright, Humphries, & Williams, 1991). There are two possible approaches: counting of number of nodes separating two terminal clades, or summing the branch lengths separating two or more terminal clades. Advantages and disadvantages of each exist, and more work needs to be done, but the direction to move is clear.

What does "rarity" mean without ranks? This relatively new phylogenetic worldview can clarify greatly this term (Mishler, 2004). Rarity fundamentally means having few living close relatives, and these days "few" and "close" can be defined quantitatively on cladograms. Conservation priorities can actually be better guided by phylogenies rather than by taxonomy *per se*. Phylogenies provide a richer view of our knowledge of nested clades, and are directly associated with the evidence used to build them. Just like in the more theoretical areas discussed above, the most practical application of systematics in the modern world, conservation, needs to drop its reliance on species.

Postscript: Counterpoint

I agree with the quote at the beginning of Dr. Claridge's paper (about mountains in Switzerland) and with his statement that "species taxa represent attempts to recognize real biological entities." I believe mountains and taxa are real; as I explained in detail above, the issue for me is not whether taxa are real (they are, if monophyletic), but whether entities given the rank of species are real in a unique and special way that entities larger and smaller than them are not. Claridge and I agree that the entities we call species are real biological units. Our main difference is in what that reality is due to: for me it is monophyly, for Claridge it is sharing reproductive bonds. In either case, my point is that there are such real entities deeply nested inside each other, with no one level fundamental or unique. Species are real, but not in a unique and special way.

Claridge understates the fundamental differences between interbreeding groups and monophyletic groups; they are not the same thing theoretically or practically. In fact they are diametrically opposed, by definition. As was first pointed out by Rosen (1978), the ability to interbreed is certainly a plesiomorphy and thus not a good guide to monophyly. It is the derived *inability* to interbreed, say the origin of a new mate recognition system, that can be an apomorphic feature useful to diagnose a monophyletic group. Any empirical test for reproductive compatibility is certain to be measuring plesiomorphic similarity. The BSC is (and should be) anathema to a cladist, which makes it puzzling how someone could be a solid cladist at all levels but species.

I agree with Claridge that breeding relationships are very complex and diverse—but would point out that this observation actually strengthens my point. There are smaller inbreeding groups (sometimes actual, sometimes potential) nested inside of larger interbreeding groups: local populations, clusters of populations, geographic regions, even up to the intergeneric level in flowering plants like orchids. The potential to successfully interbreed gradually trails off as one looks at more and more distantly related populations (as Darwin pointed out). Claridge acknowledges this when he says that "the process of speciation is a continuous one, so that drawing real lines between species as they evolve will be very difficult and intermediate stages must be expected," but then he contradicts himself in the same paragraph by saying: "species are of unique and real biological significance." In most organisms there is no magical level at which the probability of successfully interbreeding suddenly drops from near 100% to near 0%. Thus even under the biological species concept there is no unique and special level. Again, keep in mind the important distinction between grouping and ranking: breeding *groups* are very real—no one is denying that—it is the *ranking* decision about which level among many levels of nested breeding groups is to be called species that is arbitrary. Darwin was very aware of this distinction; we should still take his views seriously.

Evolutionary biology will be richer and much more accurate in its models of the world if this Darwinian hierarchical perspective is accepted. Evolutionary and ecological processes are occurring at many nested levels. "Speciation" is a major field of study, with many books and papers to its credit, which my point of view would seem to denigrate. But while I do think that "speciation" is an oversimplified concept, like the biological species concept on which it is based, I believe that there are important processes being studied by these researchers. I call it "diversification," the splitting of lineages influenced by a variety of interesting processes (ecological, reproductive, genetic, developmental, etc.). The important distinction I make is that diversification happens at many nested levels, not a single magical one, and full accounting of these is needed for a complete understanding of evolution. Focusing at the level of the entities taxonomists happen to call species in a particular case, as in standard studies of "speciation," is a one-dimensional look at a multidimensional, hierarchically nested process.

We can do better with a completely rank-free view of taxonomy. Claridge thinks that my discussion of rank-free classification is peripheral to our argument over species, but if course it is central to my position. The arguments against comparability of entities at a particular rank apply to "species" as much as "families" or "orders." Evolutionary processes are not just operating to produce what we happen to call species; they operate at many nested levels in producing the tree of life, "which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications" (Darwin, 1859, pp. 170–171).

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