BOOK REVIEWS

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CLADISTS IN WONDERLAND[1]

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''A hill can't be a valley, you know. That would be nonsense,'' said Alice. The Red Queen shook her head. ''You may call it 'nonsense' if you like, but I've heard nonsense, compared with which that would be as sensible as a dictionary.''[2]

I recently returned from a Conservation Genetics symposium at which one of the speakers claimed to have caught a speciation event in the act. Earlier in this century, tiger beetles (*Cicindela dorsalis*) were distributed more or less continuously along the eastern coast of the U.S., but shoreline development extirpated populations in the mid-Atlantic states, causing a range disjunction between still-extant populations in New England and the southern states. By analyzing DNA sequences in living and museum-preserved specimens, small but detectable nucleotide differences were uncovered between these two extant populations, a distinction not formerly possible because mid-Atlantic populations had been polymorphic for the sequences in question. Under one version of the phylogenetic species concept (PSC), a new species had arisen precisely when the polymorphism became a fixed difference (in this case, via the extinction of intermediate demes). If this speaker's PSC-based conclusion about species formation is to be taken seriously, and generalized, conservation biologists might naively rejoice. In the coming decades, as natural populations of many species are extirpated or reduced to small inbred units, intraspecific polymorphisms increasingly will be converted to fixed allelic differences between allopatric demes. Under PSC logic, by definition this will result in a great proliferation of new species. Thus, we may look forward to a twenty-first century in which the rate of species origin (via fixation of genetic variants) may outpace the rate at which currently recognized taxonomic species are driven to extinction. What most biologists had feared as a deepening valley in species numbers may instead soon become a numerical peak in taxonomic species richness!

''It was much pleasanter at home,'' thought poor Alice. ''I almost wish I hadn't gone down that rabbit-hole—and yet—and yet—it's rather curious, you know.''

To scientists raised under the traditional Biological Species Concept (BSC) of Dobzhansky (1937) and Mayr (1963), where the evolution of intrinsic (genetically based) reproductive barriers is the underlying basis of cladogenesis, the speciational world of various cladistic camps can seem as curious as that encountered by Alice in her sojourns down a rabbit's hole or through a looking-glass. To us outsiders, it can be a world of sense and nonsense often turned on its head, of erudite jabberwocky, of impeccably logical illogic, of surreal reality. Now, for the first time, this speciational wonderland is fully explored in a single volume. In *Species Concepts and Phylogenetic Theory*, Wheeler and Meier have assembled a collection of invited articles eloquently portraying a conceptual world that is simultaneously as coherent and incoherent as anything conjured up by Lewis Carroll. I heartily recommend this entertaining treatise to anyone interested in some recent developments (not necessarily advances) in phylogenetic reasoning as applied to species issues.

An opening chapter by Joel Cracraft wisely enjoins readers (p. 6) ''to grab a favorite fetish and conjure up a bit of luck'' in interpreting what will follow. The rest of the book is arranged in an illuminating debate format. In the first section, leading proponents of various phylogenetic, Hennigian, and evolutionary species concepts clearly lay out their respective platforms on the ''species problem.'' This section is followed by counterpoint chapters, written by the same sets of authors, as critical responses to the position statements of their adversaries. The closing chapters are composed of formal rebuttals to these counterpoints. The only unfortunate aspect of this format stems from inevitable delays in the sequential give-and-take of written exchanges: The book was long in production, and little relevant literature (other than that by the authors themselves) is cited post-1993.

''Off with his head!''

Ernst Mayr was the primary traditionalist from Alice's native world to accept an invitation to this phylogenetically oriented tea party. Predictably, he and the BSC are guillotined again for hackneyed reasons such as: The BSC is based on population criteria (intrinsic reproductive isolation [or its converse, potential to interbreed]) that are often difficult or impossible to measure directly in nature, especially among allopatric forms; it can lead to gray areas in species assignment when genetic isolation is incomplete; interbreeding is a plesiomorphic rather than apomorphic condition so it cannot be a valid basis for identifying Hennigian clades; the BSC does not apply to asexual organisms and, thus, is admittedly nonuniversal; BSC guidelines are inexplicit on precisely where to draw species boundaries within a temporal anagenetic sequence of ancestor-descendent populations; and the BSC carries needless baggage because it references a

[1] *Species Concepts and Phylogenetic Theory*. Quentin D. Wheeler and Rudolf Meier, eds. 2000. Columbia Univ. Press, New York. xii plus 230 pp. HB $60.00, ISBN 0-231-10142-2; PB $25.00, ISBN 0-231-10143-0.

[2] All quotes heading various subsections of this review are from books by Lewis Carroll (see Literature Cited).

causal evolutionary process (when instead a species should be identifiable by an idea-free definitional algorithm).

Mayr articulately responds (yet again) to such charges, with an evident sense of conviction that Alice's home world is the one that is sane, rather than the world of the March Hare and Dormouse. Yet at times he seems thoroughly exasperated by the tea-party repartee (p. 93): ''For someone who has published books and papers on the biological species for more than 50 years, . . . the reading of some recent papers on species has been a rather troubling experience;'' and (p. 163), ''I realize that it is apparently distasteful for a cladist to read anything not written by another cladist.''

> *Tweedledum and Tweedledee agreed to have a battle. . . . ''I know what you're thinking about,'' said Tweedledum, ''but it isn't so, nohow.'' ''Contrariwise,'' continued Tweedledee, ''if it was so, it might be; and if it were so, it would be; but as it isn't, it ain't. That's logic.''*

The more novel aspects of this book are the internecine debates clearly portrayed among various phylogenetically oriented camps. At least four distinct definitions of species exist in this alternative world, and their respective advocates effectively challenge one another's notions as well. Given all the hoopla in the recent literature about the purported demise of the BSC, one might suppose that the revolutionaries had come up with something far better. This volume indicates that they have not. Ironically, this failure to obtain a compelling synthesis on cladistic species notions may be the book's primary (but unintended) contribution. What follows are these four alternative species definitions, and some brief hints at their serious shortcomings (often exposed by the authors themselves).

> *The shop seemed to be full of all manner of curious things—but the oddest part of it all was that, whenever Alice looked hard at any shelf, to make out exactly what it had on it, that particular shelf was always quite empty.*

Wiley and Mayden define a species as ''an entity composed of organisms that maintains its identity from other such entities through time and space and that has its own independent evolutionary fate and historical tendencies.'' In an effort to clarify, the authors add (p. 75): ''To say that an evolutionary species has its own evolutionary fate is simply to say that it is a real entity and not a figment of our imagination.''

The Wiley-Mayden definition of species is an attempt to resurrect George Gaylord Simpson's evolutionary species concept (ESC), which Simpson himself mostly abandoned in 1961 as being rather nebulous for systematic purposes. Although the ESC is certainly compatible with the ''modern evolutionary synthesis'' (and indeed can be interpreted, in effect, as the BSC extended through time), other authors in the current volume likewise see major problems in deriving operational procedures from ESC definitions. Meier and Willmann view the concept as entirely subjective because (p. 178) it ''fails to provide criteria that allow a nonarbitrary delimitation of species in both the temporal and spatial dimensions.'' Mishler and Theriot find the ESC to be (p. 129) ''incoherent to us because it fits everything and nothing.'' Wheeler and Platnick dislike it because (p. 142): ''Saying that lineages exist or that they have histories or tendencies or fates are no more than vague assertions that evolution exists.'' Mayr asks (p. 97) ''What population in nature can ever be classified by its historical fate when this is entirely in the future?''

> *''I think you might do something better with the time,'' Alice said, ''than wasting it in asking riddles that have no answers.''*

Next, Meier and Willmann provide a species definition, which they term the ''Hennigian species concept,'' that at first glance looks much like the BSC: ''Species are reproductively isolated natural populations or groups of natural populations. They originate via the dissolution of the stem species in a speciation event and cease to exist either through extinction or speciation.'' One point of departure from the BSC is the authors' notion that a ''stem species cannot survive speciation,'' an artificial convention necessitated by their operational paradigm that ''a species must comprise the entire branch segment between two speciation events.'' But why, apart from definitional cleanliness, must a stem species instantly dissolve or go extinct? Mayr wonders, for example, why a large ancestral population that budded off a reproductive isolate (e.g., by a founder event at the periphery of its range) must also be viewed suddenly as a new species (p. 94): ''Because the 'new' species is evidently the same genetically as the old species, I do not understand how it can be called new.''

Another point of departure from the traditional BSC is Meier and Willmann's insistence on a *complete* absence of gene flow for the species status of contemporary taxa (p. 40): ''Absolute isolation requires that even if hybrids between species occur, these hybrids are not able to successfully backcross with members of the parental population;'' and (p. 41), ''Only when absolute isolation is used as the sole species criterion are objective and mutually comparable units delimited.'' However, as noted by Wiley and Mayden (p. 157), ''we know of no recently evolved and closely related species of North American freshwater fish that is 100% reproductively isolated from its sister species,'' and (p. 205), ''we are aware of gene introgression among distantly related (nonsister) species'' also.

Similarly, Mishler and Theriot note (p. 179) that ''nearly absolute isolation may exist between groups at some extreme levels of divergence, but in many plants that would be at the level currently ranked at about the family level.'' Thus, both sets of critics agree that if Meier and Willmann's requirement of absolute isolation were used as the ranking criterion, orders of magnitude *fewer* species would be recognized than now. This is opposite to the anticipated ballooning in species numbers that would accompany the next two species concepts discussed in this volume.

> *''Curioser and curioser!'' cried Alice.*

The other two species concepts debated in the book are alternative versions of the PSC. Mishler and Theriot define a phylogenetic species as ''the least inclusive taxon recognized in a formal phylogenetic classification. . . . Taxa are ranked as species rather than at some higher level because they are the smallest monophyletic groups deemed worthy of formal recognition. . . ''. To Wheeler and Platnick, a phy-

logenetic species is ''the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states.'' Both versions of the PSC equate ''species'' with monophyletic units, one difference being that the W-P version would name all such units (no matter how small) as taxonomic species, whereas the M-T version would reserve formal taxonomic recognition to those units deemed especially worthy by virtue of the ''amount of support for their monophyly and/or because of their importance in biological processes operating on the lineage in question.'' This too seems remarkably vague.

Both versions of the PSC focus on issues of diagnosability (based directly on character evidence, notably synapomorphies) far more than on any underlying formational evolutionary processes. Wheeler and Platnick are most explicit about this (p. 59): ''Speciation is marked by character transformation. . . . The moment of speciation is, in theory, precise and corresponds to the death of the last individual that maintained polymorphism within a population'' (as, for example, in the tiger beetle case study that opened this review). By equating speciation with character transformation, Wheeler and Platnick (p. 61) believe that they are divorcing the analysis of phylogenetic patterns from unnecessary assumptions about evolutionary process, and are thereby transforming speciation analysis into a rigorous science. Furthermore, in their fanaticism against pheneticism in species concepts, Wheeler and Platnick are forced to disregard altogether any information on the amount of genetic divergence (or even synapomorph numbers) in defining terminal ''clades'' that they wish to call species.

To at least some molecular population geneticists trained in Alice's native world, this myopic focus on species diagnosability by even minute differences may seem utterly nonsensical. In sexual organisms, each individual typically carries a unique combination of genetic variants due to recombinational shuffling of existing Mendelian polymorphisms. Furthermore, thousands of de novo mutations arise and spread relentlessly in populations. Given limited organismal dispersal (and sufficient resolution in the molecular assays), one or more of these synapomorphs often will differentiate regional populations, local demes, extended kin groups, and even nuclear family units (not to mention individuals and sometimes subsets of their constituent somatic cells!). Do we really wish to recognize every such diagnosable unit as a distinct species simply because its members happen to share one or a few derived genetic mutations that we may have detected in our available assays?

Even some of the cladists see a problem here. Willmann and Meier write (p. 105): ''Potential users of Wheeler and Platnick's phylogenetic species concept should be aware that, according to their species definition, the number of character fixations is equal to the number of species, because with every change a new combination of character states is produced.'' Thus, (p. 103) ''even a mutant strain of *Drosophila melanogaster* in a culture vial would constitute a separate phylogenetic species if all members carry the mutation.'' Extending this concern, Meier and Willmann consider a hypothetical herd of deer housed in the basement of the American Museum of Natural History (p. 173): ''Given that the deer . . . are a family group, they probably have some unique genetic markers and would probably constitute a phylogenetic species sensu Wheeler and Platnick.''

Wheeler and Platnick reply (p. 60), ''It has been suggested that our phylogenetic species concept is problematic because it may result in an enormous number of species. . . . Our response is, so what?'' This blithe attitude is inadequate. It may be one thing to advocate (as Wheeler and Platnick do) an epistemological avoidance of underlying concepts in attempting to describe evolutionary processes from observable patterns, but quite another to completely disregard what we do know about underlying ontological reality (in this case regarding such evolutionary processes as mutation, sexual Mendelian inheritance, and genetic recombination) in developing our biological classifications. At least the M-T version of the PSC seems clearer about such issues by reserving species assignments for the somehow more salient of the terminal monophyletic units in the biological world. Still, Mishler and Theriot write (pp. 45 and 46) that ''breeding criteria in particular have no business being used for grouping purposes'' and ''apomorphies [are] considered to be the necessary empirical evidence for unambiguous phylogenetic species.''

When all is said and done, much of the brouhaha between the PSC and the BSC often boils down to what taxonomists might wish to do with what now are considered geographic populations. After all, if two or more groups of sexual organisms coexist sympatrically without interbreeding, by definition they are good biological species. *For this same reason* (and only for this reason, although many cladists seem loath to admit it), they would also be valid phylogenetic species. The remaining practical question is what to do with allopatric populations. Wheeler and Platnick would formally recognize a phylogenetic species as any current population distinguishable from others by so little as one derived mutation. By contrast, most followers of the BSC would wish to rank as subspecies (using a Latin trinomial) only the better-marked of the geographic populations within a ''polytypic'' species. As stated by Mayr (p. 26), ''the use of trinomials conveys two important pieces of information: closest relationship and allopatry. Such information is valuable, particularly in large genera.''

Granted, we humans can choose to make words mean what we will, and in this sense, there can be no ultimate right or wrong in species definitions. Those with entrenched views (on any side of the debate) can always survive by digging in their definitional heels. But to remove (as would many cladists) all reference to evolutionary-genetic processes (including reproductive relationships) in species concepts seems to me (and Mayr) a big step backward to the old days of typological thought.

> *''When I use a word,'' Humpty Dumpty said in a rather scornful tone, ''it means just what I choose it to mean—neither more nor less.'' ''The question is,'' said Alice, ''whether you can make words mean so many different things.'' ''The question is,'' said Humpty Dumpty, ''which is to be master—that's all.''*

At the outset, Cracraft warns the reader: ''The literature on species concepts is riddled with confusion and obfuscation'' (p. 7); ''arguments and conclusions using the same

words might not mean the same thing'' (p. 5); and ''definitions do not necessarily make things real'' (p. 11). Indeed, the speciational wonderland revealed in this volume is rife with subterfuge and shifting meanings. For example, in their zeal to remove all explicit mention of interbreeding and reproductive relationships in species definitions, the cladists have fully adopted Hennig's (1966) term ''tokogeny,'' which Meier, Willmann, Wheeler, and Platnick nonetheless use virtually synonymously with interbreeding. However, according to Mishler and Theriot, tokogeny is (p. 127) ''the diachronic relationship through time between a parent and an offspring'' (and, thus, applies to asexual as well as sexual taxa). Overall, much of the species debate in the cladistic world hangs on such (re)inventional word games.

In another such example, Wheeler and Platnick redefine ''character'' and ''trait'' in an unconventional, stricter sense (p. 196): ''A trait is an attribute that varies among individuals or populations within a single species. . . A character is an attribute that varies between but not within species.'' This definitional sleight of hand may be a useful device for escaping some of the pitfalls of equating every change in a (conventional) trait with a speciation event, but it also introduces considerable lexical confusion (not to mention circular reasoning) to the broader debate.

> *Said the Cat: ''we're all mad here. I'm mad. You're mad.'' ''How do you know I'm mad?'' said Alice. ''You must be,'' said the Cat, ''or you wouldn't have come here.''*

In various passages throughout Wheeler and Meier's volume, readers from Alice's original realm may well begin to question the very notion of sanity itself in the cladistic world. So too do some of this book's authors themselves, as for example when the cladistic ''fear of paraphyly'' (Harrison, 1998) is parodied by Wiley and Mayden (p. 82):

> ''We have a hard time accepting a 'thing' as paraphyletic unless lots of other 'things' are paraphyletic. Consider Ed Wiley. From one point of view, he is an individual. From another point of view, he is a group of cells. Why not apply these terms to Ed Wiley? He is, after all, a kind of a group. Ed Wiley has three children. They do not reside in his body, nor are they all named 'Ed Wiley.' Obviously, following [such] reasoning, Ed Wiley is paraphyletic. He might even be considered polyphyletic if one followed Nelson (1971). If Gary Nelson wished to apply the term *paraphyly* to individual organisms, he might assert that Ed Wiley does not exist. . . . This leaves Aaron Wiley in a fix. . . . Yet Aaron exists. De Queiroz and Donoghue (1990) would accept the paraphyletic Ed Wiley; they would just claim that his primary spermatocytes are actually more closely related to Aaron than to Ed's own brain cells. Mishler and Brandon (1987) would deny that Ed and Karen exist or would assert that they are only collections of cells. Aaron exists only until such time as he has children.''

> *So Alice sat on, with closed eyes, and half believed herself in wonderland, though she knew she had but to open them again and all would change to dull reality.*

After reading *Species Concepts and Phylogenetic Theory,* readers may fairly ask, ''Is this all there is to the PSC revolution? Is this the crowning legacy of nearly 20 years of cladistic hyperbole on species concepts? Is this really the stuff to which the BSC must be abandoned? Was the conventional reality on biological species really so dull, so grotesquely inadequate, so positively misleading that an entirely new wonderland of species concepts was necessitated?''

This book is indeed an illuminating and valid compilation of thought about speciation from the realms of Hennigian as well as transformed cladistics. Thus, it succeeds as a historical treatment and as an extended case study in the sociology of science. It also reveals more clearly than any BSC proponent ever could that most of the recent cladistic pillars really have an insecure foundation when it comes to species concepts.

Yet, there are bona fide advances in phylogenetic aspects of speciation theory, spurred at least in part by a response to this cladistic revolution, that are totally missing from this book. I'm referring to a large and growing body of relevant phylogenetic thought and literature coming not from the cladistic world per se, but rather from the more Aliceian realms of molecular biology, population genetics, and coalescent theory (Tajima 1983; Avise 1989, 2000; Hudson 1990; Hey 1994; Baum and Shaw 1995; Doyle 1997; Maddison 1997).

> *''Why, it's got branches, I declare! How very odd to find trees growing here!'' said Alice.*

When studies of maternally inherited mitochondrial (mt) DNA were introduced to population biology in the late 1970s, they soon led to the revolutionary concept that asexual, nonanastomose, hierarchical gene genealogies exist even within what are otherwise sexually reproducing populations. This motivated the now conventional distinction between gene trees (of which great numbers occur within any extended population pedigree) and population trees or species phylogenies. This perspective carries a host of ramifications for species concepts, not the least of which is the recognition that it makes little biological sense to focus unduly on single diagnostic genetic characters, including synapomorphies, as a basis for distinguishing sexual species (in part because, from first principles of population genetics, the historical transmission pathways of alleles vary from gene to unlinked gene, and often will be inconsistent in the molecular clades they describe). It also helped spawn the rise of modern coalescent theory, which addresses how the historical demographies of populations impact (indeed, are virtually inseparable from) genealogical patterns.

Nowadays, *phylogenetic aspects* of biological speciation processes should center on the following sorts of questions: Exactly how do various nonequilibrium population dynamics (and natural selection) influence gene-tree structures? What are the ramifications of appreciating that a traditional stick-like cladogram for sexually reproducing taxa is really a statistical ''cloudogram'' of gene trees with a variance (Maddison 1997)? How many genealogical pathways are needed to estimate major disjunctions in an organismal phylogeny that we might wish to formally name, or perhaps taxonomically earmark for special conservation efforts? How do various kinds of genealogical concordances and discordances arise among multiple gene trees within an extended organ-

ismal pedigree, and what are their relevances to salient biological discontinuities at the population or ''species'' level? If speciation is to be viewed properly as an extended temporal process (rather than a point event as in the oft black-and-white cladistic world), then what are the means and variances in the temporal durations of this biological phenomenon?

Under modern phylogeographic perspectives on species, there is no inherent conflict between the criterion of historical reproductive isolation and *properly formulated* phylogenetic criteria in accounting for salient biological discontinuities in nature that we might wish to call species. In this phylogeographic approach, scientists begin with basic Mendelian, population-demographic, and population-genetic principles, toss in a large dose of historical geographic considerations, and thereby produce a synthetic conceptual framework for species recognition that attempts to fully integrate the better elements of the traditional BSC and PSC.

> *Alice laughed. ''There's no use trying,'' she said: ''one can't believe impossible things.'' ''I daresay you haven't had much practice,'' said the Queen.*

In this attempted synthesis based on phylogeographic and coalescent principles, both reproductive and phylogenetic criteria are seen as intimately related concepts, and as mutually informative aspects of what is usually a temporally extended speciation process for sexual organisms: ''Reproductive barriers are important for species concepts (even within a strict phylogenetic framework) because they generate and promote through time increased genealogical depth and concordance across composite DNA transmission pathways. . . . Conversely, phylogenetic considerations are important (even within the philosophical framework of the BSC) because they force explicit attention on historical and demographic aspects of the speciation process'' (Avise, 2000). Furthermore, an explicit focus on population demographic aspects of historical lineage sorting may go a long way toward explaining how and why biological discontinuities often appear to exist among asexually reproducing organisms as well.

Perhaps the ongoing phylogeographic synthesis that tries to wed (rather than divorce) phylogenetic and reproductive concepts in species recognition will yet prove to be only another fantasy. But I doubt it. Instead, I have great hope that the peculiar tea-party banter between the Aliceians and the Mad Hatters over species concepts will eventually clarify, and that a more intelligent dialogue and eventual synthesis will emerge. If so, the 20-year quarrel between proponents of the BSC and the PSC, so cogently encapsulated in the Wheeler and Meier volume, will someday be remembered as little more than a ''tempest in a teapot.''

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