

Why the Phylogenetic Species Concept?—Elementary¹

QUENTIN D. WHEELER²

Abstract: Although species play a number of unique and necessary roles in biology, none are more important than as the elements of phylogeny, nomenclature, and biodiversity study. Species are not divisible into any smaller units among which shared derived characters can be recognized with fidelity. Biodiversity inventory, assessment, and conservation are dependent upon a uniformly applicable species concept. Species are the fundamental units in formal Linnaean classification and zoological nomenclature. The Biological Species Concept, long given nominal support by most zoologists, forced an essentially taxonomic problem (what are species?) into a population genetics framework (why are there species?). Early efforts at a phylogenetic species concept focused on correcting problems in the Biological Species Concept associated with ancestral populations, then applying phylogenetic logic to species themselves. Subsequently, Eldredge and Cracraft, and Nelson and Platnick, each proposed essentially identical and truly phylogenetic species concepts that permitted the rigorous recognition of species prior to and for the purposes of phylogenetic analysis, yet maintained the integrity of the Phylogenetic Species Concept outside of cladistic analysis. Such phylogenetic elements have many benefits, including giving to biology a unit species concept applicable across all kinds of living things including sexual and asexual forms. This is possible because the Phylogenetic Species Concept is based on patterns of character distributions and is therefore consistent with the full range of possible evolutionary processes that contribute to species formation, including both biotic and abiotic (even random) factors.

Key words: biodiversity, nomenclature, phylogenetic species concept, phylogeny, species, taxonomy.

For the past 50 years, a single species concept has dominated most disciplines of zoology. Supporters of the biological species concept (BSC) (Mayr, 1942, 1963) were undeterred by the rejection of the concept by most botanists and the obvious inapplicability of the BSC to thousands of asexual organisms. In spite of the proclaimed popularity of the BSC, its requirements were only rarely met and most species decisions were based on indirect inferences about interbreeding at best. For the vast majority of animal species little or no breeding data exist

and available study material is limited to museum collections never designed to answer population biology questions.

Given this disparity between the tenets of the BSC and empirical research methods, how can its broad nominal acceptance among zoologists be explained? Of the many factors that may have contributed to the espousal of the BSC, I attribute the primary influence to a biological analog of “political correctness.” As advances in genetics took biology by storm early in the 20th century, most biologists wanted to be seen as a part of this cutting edge area of the field; certainly no one wished to be painted as a diviner of species ignorant of the latest developments in genetics. Because the BSC was phrased intentionally in genetic (i.e., interbreeding) terms it acquired a certain legitimacy by association with genetic theory and with explicit or implicit endorsement by proponents of the New Synthesis.

One, perhaps unintended, consequence of this emphasis on population genetics was a shift from an essentially taxonomic question (What are species?) to a genetic question (Why are there species?). Why did Darwin choose to title his seminal work *On the Origin of Species* (emphasis on species the author’s)? Simply because taxonomists had

Received for publication 20 November 1998.

¹ Symposium paper presented at the 37th Annual Meeting of the Society of Nematologists, 20–24 July 1998, St. Louis, Missouri.

² Department of Entomology and L. H. Bailey Hortorium, Cornell University, Comstock Hall, Ithaca, New York 14853.

E-mail: qdwl@cornell.edu

I thank the Society of Nematologists for holding this symposium and am especially thankful to Virginia Ferris and James Baldwin for their enthusiastic organization and deployment of the meeting. My views on phylogenetic species expressed here have been shaped by many people, although none of them would likely agree with everything said below. I am especially grateful to Kevin Nixon, Norman Platnick, Rudolf Meier, Joel Cracraft, Eduardo Dominguez, Kefyn Catley, Ranhy Bang, Diana Silva, Xinping Wang, and other participants in laboratory discussions; the contributors to *Species Concepts and Phylogenetic Theory: A Debate* (edited with Rudolf Meier, Columbia University Press, New York, 2000); the National Science Foundation for support of my research on slime-mold beetles that has shaped my concept of species; and Caroline Chaboo for commenting on a penultimate draft of the manuscript.

This paper was edited by E. C. Bernard.

identified, described, and compared already thousands of distinct kinds of organisms getting more of like kind and distinguished one from another by unique combinations of characters. Such taxonomic observations of patterns of characters among “kinds” was the reason that a formal concept of species was required and necessitated also process explanations including Darwin’s evolutionary theory.

Increasing numbers of workers have sought alternatives to the BSC. Many have been no more than variations on the biological species concept itself, such as the recognition concept of Paterson (1985). Others have wandered as far afield as the operational taxonomic units (OTUs) of numerical pheneticists (Sneath and Sokal, 1973) and the individuals-as-terminals-for-cladograms proposed by Vrana and Wheeler (1992). Hennig (1966) recognized a fatal theoretical flaw in the BSC. Reproductive boundaries do not exist between ancestral and descendant populations as one moves vertically through the geologic record; Hennig’s concept provided a conceptual punctuation between ancestor and descendant. Following the general acceptance of Hennigian phylogenetics, however, it became obvious that Hennig’s fix of the biological species concept was inadequate. Even where interbreeding was demonstrable, it was soon recognized as residual shared-primitive genetic compatibility of little relevance (Rosen, 1978). In spite of a plethora of publications on species, there is today no consensus among zoologists regarding species concepts. To the contrary, there are perhaps more species concepts in use today than at any other time in the past century.

The first attempts at a phylogenetic species concept sought to apply cladistic methods themselves to the species problem, e.g., “a geographically constrained group of individuals with some unique apomorphic characters, is the unit of evolutionary significance” (Rosen, 1978: 176). It was reasoned that species should be analogous to monophyletic taxa and therefore be seen as minimal autapomorphic units (e.g., Hill and Crane, 1982), but problems remained. For

one, an ancestral species is predicted by phylogenetic theory to have no autapomorphies relative to its own descendant species; yet an ancestor must have existed and must have been a species in its own time. A modified version of this concept is advocated still by de Queiroz and Donoghue (1988) and Mishler and Theriot (*in* Wheeler and Meier, 2000).

Hennig (1966) recognized the uniqueness of species in the hierarchic pattern of phylogenetic relationships. As a consequence, he defined monophyly and synapomorphy in terms of relations among *species* and their characters, not among populations or individuals, at least in the context of sexually reproducing organisms (Nelson and Platnick, 1981). At best, the application of Hennig’s methods to populations, and of the term monophyly to single species, is explicitly at odds with Hennig’s methods. In practice, cladistic analyses of infraspecific terms result in artifactual patterns that look like, but fail to meet the assumptions of, phylogenies (Davis and Nixon, 1992; Nixon and Wheeler, 1992a).

About 1980, two sets of authors were formulating a new version of the phylogenetic species concept that was fully consistent with phylogenetic theory, yet independent of cladistic analysis. Eldredge and Cracraft (1980) and Nelson and Platnick (1981) proposed remarkably similar species definitions, later amplified by Nixon and Wheeler (1990, 1992a) and Wheeler and Platnick (2000).

THE PHYLOGENETIC SPECIES CONCEPT

The concepts developed independently by Eldredge and Cracraft (1980) and Nelson and Platnick (1981) offered the key to recognition of the elements of phylogenetic analysis, without the misapplication of cladistic theory within panmictic populations. The essential agreement of these definitions is apparent in direct comparison:

- (i) “. . . a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and

descent among units of like kind” (Eldredge and Cracraft, 1980:92), later rephrased by Cracraft (1983) as “. . . the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent” (Cracraft, 1983:170).

(ii) “. . . simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters” (Nelson and Platnick, 1981:12).

The fundamental components of these definitions remain intact, restated in a slightly modified and amplified fashion by Nixon and Wheeler (1990:218): “. . . the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts).” Or, simply, “. . . the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states” (Wheeler and Platnick, 2000).

ALTERNATIVE SPECIES CONCEPTS

A debate of the relative strengths and weaknesses of alternative species concepts is the subject of a new book (Wheeler and Meier, 2000). Rather than critique competing concepts directly, I will simply list some rhetorical questions that illustrate the criteria by which this evaluation would be made. Each of the available alternative species concepts fails, in my estimation, to meet one or more of these criteria.

(i) Is the species concept compatible with phylogenetic theory (its ontological justification)?

(ii) Does the species concept remain independent of cladistic analysis (so that it can provide the elements of such analyses)?

(iii) Is the species concept applicable? That is, does it explicitly provide guidance for making observations leading to species hypotheses?

(iv) Is the species concept based on observable evidence?

(v) Are its hypotheses open to critical testing? That is, can they be falsified by further empirical observations?

(vi) Is the species concept limited by any particular assumption about evolutionary or speciation processes? Alternatively, could this species concept be applied equally well by biologists studying products of very different causal processes (say allopatric vs. sympatric speciation)?

(vii) Can the concept be applied to all evolving systems of living things, whether sexual or asexual?

(viii) Does the concept apply across geologic time and both geographic and ecological space?

(ix) Does the species concept make unnecessary presumptions not required by phylogenetic theory?

(x) Does the concept provide a clear, testable basis for knowing when we know that species exist? That is, is the concept epistemologically justified?

Based on answers to these questions, there appears to be no viable current alternative to the phylogenetic species concept. It is simple, testable, broadly applicable, and distinguishes the smallest groups of individuals that can logically meet the needs of the elements of phylogeny, nomenclature, and biodiversity study.

ELEMENTAL ROLES OF SPECIES IN BIOLOGY

Elements of phylogeny: I do not agree with Nelson (1989) that species are just another taxon, distinguished only by their arbitrary rank assignment to the Linnaean category “species.” Nor do I believe that theoretical justification exists for using individuals as terms in cladistic analyses as Vrana and Wheeler (1992) suggested. That species exist in nature is one aspect of species about which I can agree with Mayr (1963). The distribution of characters in nature provides unequivocal, explicit, and testable evidence of the existence of species. Unlike monophyletic higher taxa, species cannot be subdivided into smaller entities about which this is also true. They are, in this crucial sense, truly unique and elemental.

Because cladograms express our hypotheses about relationships among terms that

are based on one or more monomorphic properties, phylogenetic theory assumes that those terms are not polymorphic for the attributes in question. This is true for species. It is true for monophyletic clades. It is not true for populations. When species are divided into smaller groups, populations, or other assemblages of individuals, those assemblages no longer manifest constantly distributed characters that can indicate their affinity to other such assemblages. Even if we were able to recognize a single lineage within a species (that is, including all individuals that are genealogical descendants of a common ancestor and not just, for example, a maternal lineage), some of its early members would be genetically more closely related to individuals outside the lineage than they are to distant branches within the lineage. And before characters become transformed and mark the beginning of a new species, there must be one or more polymorphic populations of the common ancestor.

Phylogenetic theory is a powerful tool for retrieving historical patterns of descent with modification above the species level. It is simply irrelevant for population biology questions. What population geneticists have learned during this century about mutations and their dissemination within species is sufficient to convince us that phylogenetic patterns ought not to be anticipated from observations of panmictic situations. Certainly, the occasional history pattern might be retrieved, but it would be indistinguishable from similar-looking but entirely artifactual patterns. The assumptions of cladistic analysis are simply not met by infraspecific patterns in sexually reproductive organisms. Could such branching diagrams occasionally reflect the actual biological history of a lineage *within* a single species? Of course, but we would have no means to distinguish such exceptions from the rule of pseudo-hierarchical patterns for biologically reticulate realities.

Elements of nomenclature: Species also occupy a special and elementary place in zoological nomenclature. Although subspecific names are available as specific epithets, the

species category remains (appropriately) the least-inclusive category in the Linnaean hierarchy. This is yet another reflection of biology's long-standing recognition that species are the scientific equivalent of the common-sense "kinds" of animals. In general, it is appreciated that there is little profit in assigning formal fixed names to populations that are themselves ephemeral in respect to any specific combination of attributes or gene frequency. Species, like monophyletic clades, are characterized by unique combinations of characters and therefore are profitably given formal names. It would be possible to give names to populations, demes, individuals, organs, cells, and so forth, but with millions of undescribed species and little or no function for such names, the reasons for expanding names to less-inclusive classes defined by temporary combinations of features are not compelling. Characters in the strict sense do not occur within phylogenetic species (Nixon and Wheeler, 1992a), providing the logical cut-off point for nomenclature.

In the context of phylogenetic theory, binomial nomenclature seems superbly preadapted to reflect grouping hypotheses. The hypothesized placement of species into genera is reflected formally in such Linnaean binomials and implies why particular species are selected for cladistic analysis. This adds yet another dimension to already noted compatibilities between Linnaean names and phylogenetic theory, primary among which is the hierarchic logical structure of each (e.g., Dominguez and Wheeler, 1997).

Elements of biodiversity: The argument for the elementary role of species in phylogeny and nomenclature is rather straightforward. The justification for viewing species as the elements of biodiversity may be more controversial, primarily because of diverse opinions about what "biodiversity" means. There is great diversity, for example, within species at the population, individual, and molecular levels. Additionally, most of the literature on biological diversity refers to a metaphorical hierarchy progressing from gene to species to ecosystem, rather than the literal hierarchic phylogenetic relationships

that organize biodiversity above the species level into meaningful historical groups (Wheeler, 1995).

One of the first questions asked about biodiversity, or any taxon, is "How many species (of nematodes, or mites, or beetles, or fungi, . . .) are there?" Our response is usually received as useful information. Because biologists recognized diagnosable species in nature, there was a natural inquisitiveness about where they came from. As Nelson and Platnick (1981) explained it, it was the recognition of this and phylogenetic patterns that made a theory of evolution necessary. Without such patterns, there would be nothing for evolution to explain.

However, naturalists do generally agree that discrete numbers of "kinds" of living things exist. Whether native peoples knowledgeable about the local fauna or taxonomists studying related species worldwide, there emerge opinions about how many kinds exist in a particular taxon, in a particular place, or during a specified time.

Existing literature about the distribution of biodiversity on Earth illustrates why elements of biodiversity are needed. How can we determine conservation priorities if we cannot agree on some way to measure and compare biodiversity across ecosystems, geographic places, or taxa? With a range of species concepts in use today, many comparative statements about biodiversity are misleading, at best. What does it mean to say that there are 800,000 species of insects, 170,000 species of dicots, 12,000 species of nematodes, or 500 species of slime-molds unless we can agree that species are comparable among such taxa? It is boldly stated that there are more species at certain tropical sites than in any similar-sized area on Earth, but again the significance of this proclamation is no better than the species concepts used to arrive at such counts. Similarly, exciting new indices capable of guiding conservation prioritization depend on both phylogenetic hypotheses and a credible uniform species concept (Nixon and Wheeler, 1992b).

Some biologists have looked at the incredible diversity of speciation modes and biolo-

gies of the lineages involved and arrived at the conclusion that no single species concept could possibly address so many varied processes (Mishler and Donoghue, 1982). This diversity is real, but does it justify giving up on our long search for a unit or elementary species concept? Such pluralists make the same mistake as do the proponents of the biological species concept—that of confounding process and pattern and assuming that we must know modes of speciation in order to recognize or count species.

We need not know or understand the processes driving speciation in order to recognize species. Indeed, despite the great differences in our interpretation of the origins of species from Creation to evolution, most biologists given the same specimens and information could largely agree on how many species there were before them. That species can be recognized outside the context of particular process assumptions is historical fact. Just as we can reconstruct patterns of phylogeny prior to, and independent of, any assumptions about causal evolutionary processes (Nelson and Platnick, 1981), we can recognize species *based on patterns of character distributions*. This is the sense in which Cracraft (1983) described species as the products of evolution. Evolution, in this context, encompasses a vast array of processes, both biotic and abiotic.

Among the many benefits of an evidential (i.e., character-based) species concept is that it describes the outcome of a unique sequence of unspecified historical events. By divorcing the "why" of species from the "what," it is possible to empirically arrive at hypotheses regarding how many species exist in such biologically disparate groups as algae and birds. It is then instructive to ask what processes might have been involved in each example and to compare the relative impact of this or that process to the history of evolution. In other words, by distinguishing species aside from any process assumption about speciation, it is possible to ask whether an asexual lineage of algae will result in more or fewer species than a sexually reproducing bird over the same span of geologic time. Unless the notion of species is

the same, how could we ever hope to study, compare, or understand modes of speciation or the tempo of microevolutionary change?

IS THE PSC THE UNIT SPECIES CONCEPT?

I suggest that the phylogenetic species concept is the long-sought-after unit species concept, applicable across the vast diversity of living things. Some have suggested a pluralistic approach out of the overwhelming frustration of such diversity among different kinds of living things. We may never know with certainty the factor or factors operative in the formation of any particular species, but as a minimum we can restrict our process ideas to those consistent with the pattern inherent in phylogenetic species. Accepting a pluralistic view amounts to giving up the long search for a single sufficient species concept. Unless we continue to critically test the alternatives, we can always think up *ad hoc* justifications for various species concepts. We can only discover the unit species concept—I suggest the phylogenetic species concept—by continuing to apply single concepts. Were we to attempt to base a species concept on a biological process, for instance, interbreeding, then no single concept could conceivably prove representative of protists, fungi, angiosperms, and nematodes. This is but one good reason to refrain from process assumptions built into species concepts or their logical tests.

The PSC avoids such confusion at the population and species level in precisely the same way that cladistics avoids parallel confusion among the vast diversity of causal forces contributing to evolution, from sexual selection to asteroid: by focusing instead on patterns of character distributions. In the case of monophyletic clades, it is the sharing of apomorphies. In the case of species, it is the unique combination of characters that consistently distinguishes one kind from the others.

As a measure of character distributions independent of any particular process, phylogenetic species are at once compatible with any and all conceivable processes one may

wish to investigate and are applied with equal facility to all life forms—from the asexual to the sexually reproductive. Such a unit species concept has clear implications for studies of biodiversity as described above but offer also major benefits to evolutionary biologists who are concerned with processes.

PHILOSOPHICAL SOPHISTRY

For decades, two arguments have persisted in the taxonomic literature that, from my perspective, add little substance to the species debate and serve to distract from actual fundamental concerns. The first asks “Are species individuals?” Species, the argument goes, are individuated through history because they have unique beginnings, periods of existence, and ends. Stated another way, species are spatiotemporally isolated from one another. Philosophers of science differ as to whether there is even a difference between “groups” and “individuals” in this context. In practice, the only observable evidence that species differ comes in the form of unique combinations of characters. Species are groups of individuals, the groups defined by these sets of characters. Because the boundaries between species are marked by the death of individuals (Nixon and Wheeler, 1992a), arguments that species-as-individuals are cohered by interbreeding are without force. Indeed, immediately following speciation there may well exist individuals within one daughter species more closely related to individuals in a sister species than some individuals in its own (new) one. Genetic cohesion is of far more value in visualizing the maintenance of boundaries between contemporary species than describing events at the beginning and end of species.

The contention that species are individuals rather than groups—and a related argument that characters “point to” species rather than “define” them—amounts in my view to philosophical sophistry. It is argued that an ontological belief that species exist is necessary prior to and in justification of any discovery process designed to distinguish among species. As a historical fact, species

were recognized prior to evolutionary theory or the ontology of either phylogenetic or biological species, and it was the observation of unique “kinds” (diagnosed by unique combinations of characters) that necessitated development of an explanatory ontology. Historically and procedurally, characters are observed, species are hypothesized, and more characters observed to test such hypotheses of species. Background hypotheses exist at this level too, of course, in the form of homology assertions, for example.

Stated in extreme terms, ontology divorced from epistemology is a better description of religion than science. It is overly simplistic to accuse the phylogenetic species concept of being entirely operational—that is, to lack an ontological basis. For the phylogenetic species concept, as for cladistic theory, the assumption is made that there is descent with modification. This minimal background hypothesis is sufficient to justify an expectation of hierarchic patterns of synapomorphy distributions among species and higher taxa *and* hypotheses of character transformation as a punctuated event distinct from shifting gene frequencies (“traits” *sensu* Nixon and Wheeler, 1992a). Linnaeus’ ontology involved a belief in God and the causal process “Creation” following a Divine plan; yet, his observations of character distributions led him to accurately define many species recognized to this day. Nothing in the intervening centuries has modified this fundamental tenet of taxonomy: Character distribution patterns suggest the existence of species and (in the case of synapomorphies) hierarchically related higher taxa for which causal explanations are required. In the words of Nelson and Platnick (1981), “no pattern, nothing to explain.”

CONCLUSIONS

Species were visible to humans, at least in a common sense and provincial way, long before any effort to formalize a species concept was undertaken. It is unquestionably the case that the question “What is a spe-

cies?” occurred to biologists and philosophers precisely because they could see and agree upon their existence. Being naturally intrigued by the possibility of learning how species come to be, and bolstered by a rapidly growing modern science of genetics, the emphasis shifted early in this century largely toward mechanisms of speciation. This would have been an entirely positive development had these emerging ideas about speciation not been applied to the refinement of species concepts and supplanted the study of phylogeny. Once species patterns and speciation processes were confounded, the search for a single adequate definition of species applicable to all life forms became unattainable and experts on various taxa developed their own ideas about species. The fact that the biological species concept was inapplicable to the many clonal, asexual forms of life was simply accepted as a biological reality, as was its dismissal by most botanists.

Three recent events have forced a critical reevaluation of this situation. First, Hennig’s (1966) phylogenetic systematics demanded that species, the elements of cladistic analysis, be distinguished before phylogenetic patterns were hypothesized, much less correlated with possible causal evolutionary processes. Second, this new phylogenetic paradigm brought experts together who had for decades or centuries communicated in detail about taxonomy only with others studying related species. In other words, phylogenetics has blurred the former boundaries between microbiology, botany, zoology, etc., encouraging systematists to ask the same fundamental questions about patterns in evolutionary history regardless of their favorite organisms. And finally, the realization that there is an imminent biodiversity crisis adds an urgency to our need to inventory Earth’s species. This, in turn, demands access to a uniform species concept that can allow comparisons of the species diversity of clades, ecosystems, geographic areas, and geologic horizons.

What has emerged is an approach to species that mirrors the divorce of pattern and process in regard to higher taxa (Eldredge

and Cracraft, 1980) and the recognition that species based on observable, testable characters simply avoid the confusion imparted by considerations of modes of speciation. From the perspective of science, it is important that this now centuries old debate about species continues to its logical and acceptable conclusion. With the menace of the biodiversity crisis at our doorstep, however, we had best accelerate the process and work as diligently as possible toward a single uniform species concept.

LITERATURE CITED

- Cracraft, J. 1983. Species concepts and speciation analysis. *Current Ornithology* 1:159–187.
- Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life. London: J. Murray.
- Davis, J. I., and K. C. Nixon. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. *Systematic Biology* 41:421–435.
- de Queiroz, K., and M. J. Donoghue. 1988. Phylogenetic systematics and the species problem. *Cladistics* 4:317–338.
- Dominguez, E., and Q. D. Wheeler. 1997. Taxonomic stability is ignorance. *Cladistics* 13:367–372.
- Eldredge, N., and J. Cracraft. 1980. *Phylogenetic patterns and the evolutionary process*. New York: Columbia University Press.
- Hennig, W. 1966. *Phylogenetic systematics*. Urbana, IL: University of Illinois Press.
- Hill, C. R., and P. R. Crane. 1982. Evolutionary cladistics and the origin of angiosperms. Pp. 269–361 in K. A. Joysey and A. E. Friday, eds. *Problems of phylogenetic reconstruction*. New York: Academic Press.
- Mayr, E. 1942. *Systematics and the origin of species*. New York: Columbia University Press.
- Mayr, E. 1963. *Animal species and evolution*. Cambridge, MA: Belknap Press.
- Mishler, B. D., and M. J. Donoghue. 1982. Species concepts: A case for pluralism. *Systematic Zoology* 31:491–503.
- Nelson, G. 1989. Species and taxa: Systematics and evolution. Pp. 60–81 in D. Otte and J. A. Endler, eds. *Speciation and its consequences*. Sunderland: Sinauer Associates.
- Nelson, G., and N. I. Platnick. 1981. *Systematics and biogeography: Cladistics and vicariance*. New York: Columbia University Press.
- Nixon, K. C., and Q. D. Wheeler. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6:211–223.
- Nixon, K. C., and Q. D. Wheeler. 1992a. Extinction and the origin of species. Pp. 119–143 in M. J. Novacek and Q. D. Wheeler, eds. *Extinction and phylogeny*. New York: Columbia University Press.
- Nixon, K. C., and Q. D. Wheeler. 1992b. Measures of phylogenetic diversity. Pp. 216–234 in M. J. Novacek and Q. D. Wheeler, eds. *Extinction and phylogeny*. New York: Columbia University Press.
- Paterson, H. E. H. 1985. The recognition concept of species. Pp. 21–29 in E. S. Vrba, ed. *Species and speciation*. Monograph No. 4. Pretoria: Transvaal Museum.
- Rosen, D. E. 1978. Vicariant patterns and historical explanation in biogeography. *Systematic Zoology* 27:159–188.
- Sneath, P. H. A., and R. R. Sokal. 1973. *Numerical taxonomy*. San Francisco: W. H. Freeman.
- Vrana, P., and W. Wheeler. 1992. Individual organisms as terminal entities: Laying the species problem to rest. *Cladistics* 8:67–72.
- Wheeler, Q. D. 1995. Systematics and biodiversity: Policies at higher levels. *Bioscience, Science and Biodiversity Policy Supplement*, pp. s21–s28.
- Wheeler, Q. D., and R. Meier, eds. 2000. *Species concepts and phylogenetic theory: A debate*. New York: Columbia University Press.
- Wheeler, Q. D., and N. I. Platnick. 2000. The phylogenetic species concept (sensu Wheeler and Platnick). In Q. D. Wheeler and R. Meier, eds. *Species concepts and phylogenetic theory: A debate*. New York: Columbia University Press (in press).