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PHYLOGENETIC SYSTEMATICS AND SPECIES REVISITED

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Wheeler and Nixon (1990) belittle our analysis of the species problem (de Queiroz and Donoghue, 1988), implying that it is merely a compilation of ideas without interpretation or synthesis. If this is true, one wonders why they single out our paper for the brunt of their criticisms, rather than dealing with what they suppose to be the original sources. In any case, Wheeler and Nixon object to our view of the relationship between the principle of common descent and phylogenetic systematics and its implications for species concepts. Many of their criticisms are based on a simplistic notion of the relationship between pattern and process that diverts attention from important issues. Others are based on misrepresentations that could have been avoided by a more careful reading of our paper. Wheeler and Nixon's criticisms reveal a shortsightedness that is manifested in their own species concept.

Monophyly

Wheeler and Nixon (p. 77) consider our "use of monophyly, paraphyly, and polyphyly at the infraspecific level" to be "inaccurate", because Hennig (1966) used the terms to apply only to groups of species. It is ironic that they criticize us for not following Hennig's definition of monophyly in that Hennig himself was criticized for redefining the term. In any case, we explicitly rejected Hennig's usage in favor of more general definitions. Our reason for doing so is, to put it briefly, that "species" are not the only kinds of entities related by common descent.

Wheeler and Nixon (p. 77) assert that Hennig's definitions are "based on a clear and concise understanding of the differences between tokogenetic and phylogenetic relationships"; however, the distinction between tokogenetic and phylogenetic relationships is not always clear, notably, as Hennig (1966: 49) himself pointed out, in the case of asexual reproduction. Because asexual organisms do not interbreed and thus do not form populations, relationships of common ancestry among individual organisms form a nested hierarchy. Consequently, phylogenetic relationships among "species" and monophyletic groups of uniparental organisms can be reduced to relationships among individual organisms. This contrasts with the situation in sexual organisms. As a result of biparental reproduction, the relationships of common ancestry among sexual organisms within a single population do not form a simple, nested hierarchy (see Hennig 1966: 18–20). Consequently, phylogenetic relationships among populations and monophyletic groups of populations cannot be reduced to relationships among individual sexual organisms.

Instead of arguing against our generalization of the concept(s) of monophyly (paraphyly and polyphyly), Wheeler and Nixon proclaim that a different terminology

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should be applied to cases involving units less inclusive than species. It certainly is appropriate to distinguish among entities resulting from common descent involving different kinds of units; nevertheless, the concept of an ancestor and its descendants is general in that it applies to all units exhibiting ancestry and descent. Given that the concepts have greater generality than commonly supposed, either the existing terms will have to be given more general definitions or new terms will have to be coined to cover the more general concepts.[1] Wheeler and Nixon's preferences about word usage do not constitute a serious criticism of our analysis.

Individuality

Wheeler and Nixon offer a series of comments on our discussion of continuity and cohesion in relation to individuality. Some of these are absurd. For example, despite our explicit statements that neither current nor historical continuity are necessary properties of individuals, they presume that we concur with Hull's proposition that both continuity and cohesion are necessary for individuality from the mere fact that we have sections devoted to these topics.

Wheeler and Nixon state that our discussion of continuity "reveals a confusion about what is and is not an individual" (p. 77–78), but they never explain what this confusion is. They seem to object to our example of an organism not ceasing to be an individual when it receives an organ transplant, which we used to argue that an unbroken chain of descent from a common ancestor is not necessary for individuality. This objection apparently relates to our supposedly not having given an "adequate explanation of what meaningful historical information is contained among the cells within the life span of one individual" (p. 78). Wheeler and Nixon apparently overlooked our discussion of the propagation of somatic mutations (de Queiroz and Donoghue, 1988: 326). In any case, it is irrelevant whether we provided an adequate explanation of the historical information in cell clones or whether Wheeler and Nixon consider such phenomena as the propagation of somatic mutations to be meaningful. The existence of cell clones and all other entities of common descent is meaningful in itself, and recognizing the existence of such entities may open new avenues of investigation.

Wheeler and Nixon are critical of the idea that populations of interbreeding organisms are individuals. They propose that populations receiving immigrants can be individuals only if they are "defined" extrinsically (e.g. by geographic location). Of course, populations need not receive immigrants, and many probably do not. In any case, the category "population" was defined in our analysis in terms of interbreeding relationships (de Queiroz and Donoghue, 1988: 326) regardless of geographic location (although geographic separation may be evidence of lack of interbreeding). Migration of organisms between populations (and sympatric hybridization) does not imply that individuality is lacking, but only that the boundaries of populations are not always sharply demarcated. Wheeler and Nixon use this absence of sharp spatiotemporal

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[1] The term "clade" has generally been used to refer to entities composed of an ancestral species and its descendants, and the term "clone" to entities of ancestral (asexual) organisms, cells, or less inclusive entities, and their descendants. Synonymizing "monophyletic entity" with "clade", however, leaves unnamed the general category of an ancestor (of any kind) and its descendants. Therefore, a more precise terminology would be gained by using "monophyly" for the general case and elaborating the "clade"/"clone" terminology to cover the different classes of monophyletic entities defined with respect to the units of which they are composed (i.e., "species", organisms, cells, etc.).

boundaries to question the individuality of populations. It should not be supposed, however, that the lack of sharp spatiotemporal boundaries implies the absence of individuality or that it applies only to populations. Even organisms sometimes lack sharp spatiotemporal boundaries. This is most evident in the cases of grafts, organ transplants, and slime molds.

Wheeler and Nixon seem to concede these points when they state that populations have "ephemeral identities as individuals" (p. 78). Ephemerality may characterize some populations, but others may be stable and long-lived. In any case, brief duration does not imply the absence of individuality. Although organisms are considered paradigmatic "individuals", the duration of many organisms is far shorter than that of many populations.

After rejecting interbreeding as a potential source of anything's individuality, on the irrelevant grounds that it varies, Wheeler and Nixon propose that "historical cohesion" results from the inheritance of ancestral characters either in their original or some modified form. According to our definitions (de Queiroz and Donoghue, 1988: 320–322), the sharing of such characters is evidence of historical *continuity*, which results in one kind of "individual" (the monophyletic entity). This should not, however, be confused with *cohesion*, which implies a "sticking together" of parts to form a different kind of "individual". Given that there is a meaningful distinction between what we called "cohesion" on the one hand and "continuity" on the other, Wheeler and Nixon's substitution of one term for the other only confuses the issue.

Classification and Systematization

Wheeler and Nixon believe that our distinction between "classification" and "systematization" is relevant to those adopting an evolutionary taxonomic approach (Mayr, 1974), but not for cladists whose classifications reflect hypotheses about relationships" (p. 78). Here they confuse our use of "classification" with the construction of a taxonomy, evidently failing to realize that we explicitly departed from traditional word usage. We defined "classification" as the ordering of entities into groups whose members belong to those groups because they share some attribute(s), and we contrasted this with "systematization", the discovery of entities that result from some process through which their parts are related (de Queiroz and Donoghue, 1988: 322; see also de Queiroz, 1988). Their failure to understand this distinction leads Wheeler and Nixon to the conclusion, which they attempt to bolster by quoting us out of context, that we equate phylogenetic systematics with traditional evolutionary taxonomy. Nothing could be further from the truth.

We followed de Queiroz (1988; see also Griffiths, 1974), who defined "systematics" as that discipline in which systematization is practiced. We used the adjective "evolutionary" to refer to the process through which the parts of the systems being studied are related, and we used "phylogenetic" to refer to the products of this process, that is, to the systems themselves. Under this concept of evolutionary or phylogenetic systematics, not only is much of traditional evolutionary taxonomy not evolutionary; it is not even systematics. Thus, while the distinction between classification and systematization is certainly *relevant* to those adopting a traditional evolutionary taxonomic approach, its relevance is the opposite of that implied by Wheeler and Nixon. This distinction implies that the recognition of paraphyletic groups as taxa is not based on evolutionary principles. Paraphyletic taxa are holdovers from a period when the distinction between classification and systematization was not made, that is, when classes of organisms defined by the possession of particular characters were not clearly distinguished from systems of common descent. In traditional evolutionary taxonomy, the classes of organisms recognized as taxa are "evolutionary" only in the superficial sense that taxon (class)-defining characters are interpreted as the result of some evolutionary process (de Queiroz, 1988).

Related to the issue of systematization is Wheeler and Nixon's accusation of a self-contradiction on our part. Contrary to their accusation, our rejection of disjunctive species concepts (those based on more than one process) does not contradict our proposition that one can focus on systems resulting from common descent, from interbreeding, or from both. Considering different kinds of systems simultaneously is a means of clarifying their relations to one another. In contrast, disjunctive species concepts obscure these relations by making it appear as though only one kind of entity (the "species") is involved.

Pattern and Process

Wheeler and Nixon object to our consideration of processes before patterns. They associate this practice with "evolutionary taxonomy", which has "favored presumptive knowledge of the evolutionary process over patterns derivable from character analysis" (p. 80), rather than with "cladistics" or "phylogenetics". This attempt to group us with traditional evolutionary taxonomists is very misleading. We considered the processes of common descent and interbreeding and proposed that these were the sources of the relationships among the parts of monophyletic entities and populations, respectively. Far from presuming knowledge of the evolutionary process, this proposition does not even refer to the phenomenon of evolutionary change.

The rise of phylogenetic systematics involved a critique of using presumptive knowledge about tempos, modes, and mechanisms of evolutionary change in analyzing phylogenetic relationships. In that knowledge of such evolutionary processes is often dependent on knowledge of phylogenetic relationships, phylogeneticists were justly skeptical of granting theories about evolutionary processes primacy over patterns of character distribution. Nevertheless, to think that pattern is somehow more fundamental than process is an oversimplification, as is Wheeler and Nixon's view that "if we continue to bow to the study of process over pattern, then our endeavors to elucidate pattern become irrelevant" (p. 79).

In scientific theories, processes and their resultant patterns exist at various levels. Process theories at one level (e.g. particular mechanisms of evolutionary change) are tied to patterns (e.g. phylogenetic relationships) that result from more general processes (e.g. common descent). Failing to distinguish among the hierarchical levels of different processes and their associated patterns can lead to serious errors. Wheeler and Nixon's false characterization of our work provides a good example.

Populations

Wheeler and Nixon also accuse us of a contradiction concerning the role of populations in phylogenetic systematics, but they never explain what this is. Perhaps they think our argument that it is inappropriate to inquire about phylogenetic relationships among actually interbreeding organisms contradicts our statement that populations are basal units in the phylogenetic systematics of organisms. If so, their accusation is based on a misunderstanding of what we meant by "the phylogenetic systematics of organisms". Within a population of interbreeding organisms, entities composed of ancestral organisms and their descendants do not form a simple nested hierarchy. Therefore, the basal units in the phylogenetic systematics of sexual organisms, that is, the least inclusive units at or above the organismal level that potentially exhibit nested, hierarchical relationships of common ancestry, are populations of interbreeding organisms.

Alternatively, Wheeler and Nixon may think that our view that populations can serve as units in phylogenetic analysis is flawed because populations do not necessarily form diverging lineages. In this case, their misunderstanding results from failing to consider different time scales. Over long time scales, populations might diverge and later merge and consequently might not form trees (nested hierarchies). Nevertheless, over shorter time scales populations may exhibit a strictly divergent (tree-like) pattern of relationships, and these relationships are potentially recoverable through the analysis of shared, derived characters. While it may not be practical to formally name such relatively short-lived monophyletic entities, they are nonetheless relevant to theories about biogeography and evolutionary processes.

Metataxa, Metaspecies, and Species

The term "metataxon" was proposed to distinguish taxa based on symplesiomorphies but not "known" to be paraphyletic from paraphyletic taxa, that is, taxa for which some descendants of the most recent common ancestor of the included entities are not included in the taxon (Gauthier et al., 1988). The distinction is between absence versus presence of knowledge, for some metataxa doubtless will subsequently be found to be paraphyletic; however, some also may be found to be monophyletic. The metaspecies convention was proposed by Donoghue (1985) in order to allow unresolved groups of organisms, which currently are distinguished from their closest relatives only by plesiomorphies, to be formally recognized as species. Flagging the names of such groups with an asterisk would draw attention to the fact that they may or may not be monophyletic.

Wheeler and Nixon's criticisms of these concepts fail to distinguish between paraphyly and unresolved relationships. They state that "metaspecies is an attempt to apply a name to 'paraphyletic', unresolved situations at a level where this concept does not apply, while 'metataxa' is a redundant name for paraphyletic taxa" (p. 79). This is simply incorrect. Paraphyly differs from unresolved relationships in that it specifies that some members of the group judged to be paraphyletic are more closely related to entities not included in that group. In other words, in contrast with the case of metataxa (unresolved relationships), the conclusion that a taxon is paraphyletic requires resolution of relationships.

Wheeler and Nixon also criticize the metaspecies concept on the grounds that it supposedly asks for phylogenetic resolution within species and that the ideas of monophyly and paraphyly do not apply infraspecifically. This criticism is incorrect even under Wheeler and Nixon's definitions of "monophyly" and "paraphyly", for the metaspecies convention does not imply that phylogenetic resolution is possible. If such resolution is impossible, a "species" distinguished from its "sister species" only by the plesiomorphic state of a character is still a metaspecies.

In the case of Wheeler and Nixon's concept of species, phylogenetic resolution within species is precluded by the very nature of the concept. For them, "species are the smallest terms analyzed by cladistic methods", and "in cases where cladistic analysis is possible... we are dealing with distinct species and not with infraspecific units" (p. 77). One wonders how Wheeler and Nixon deal with the type of resolution made possible using organellar DNA. The nucleotide sequences of mitochondrial DNA, for example, vary within populations (Avise et al., 1987), and characters derived from base sequences of this maternally inherited molecule can be used to reconstruct relationships among maternal lineages within interbreeding groups of organisms (e.g. Avise, 1989), including *Homo sapiens* (Cann et al., 1987). Thus, even adopting Wheeler and Nixon's usage of the term "monophyly" does not imply that resolution of relationships of common ancestry is necessarily impossible within what others, and possibly even they, would call species.

Wheeler and Nixon propose to define species as "the smallest non-arbitrary units supported by unique combinations of character states" (p. 78). A serious limitation of this species concept is that although it may be sufficient to apply the methods of cladistic analysis, this does not justify the claim that it delimits "real" and "significant" units. Their species concept may allow the discovery of higher level monophyletic entities (which are real and significant entities), but the "species" themselves are only groups of convenience that allow application of a method. There is no reason to think that Wheeler and Nixon's "species" exist as wholes (systems). These "species" are not necessarily populations, but neither are they necessarily monophyletic entities, for they are not diagnosed by synapomorphies but only by unique combinations of characters. Many of Wheeler and Nixon's species are likely to be metaspecies.

Given the lack of justification for Wheeler and Nixon's "species", their desire to restrict the concept of monophyly to entities above the species level is understandable as an attempt to protect their own species concept. Such a restriction would effectively preclude calling into question the status of these "species" as phylogenetic entities. Similarly, Wheeler and Nixon's antagonism toward the metaspecies convention is predictable, for this convention would call attention to the questionable phylogenetic status of many of their "species".

Conclusion

An underlying theme in Wheeler and Nixon's paper is that phylogenetic systematists need not consider such phenomena as interbreeding in devising a species concept that is sufficient for their purposes. Their definition of species refers to "the smallest non-arbitrary units" (p. 78), but what qualifies as a non-arbitrary unit? An apomorphy may arise in a single organism within a population. It may persist in that population as one variant of a polymorphic character, or it may vanish or eventually become fixed. A derived, sex-linked character may be expressed only in the males of a population. Wheeler and Nixon presumably would consider the group composed of the organisms bearing one of the variants of a polymorphic character and the group composed of the males but not the females to be arbitrary, for they wish to distinguish between inconstant "traits" of populations and constant "character states" of "species". According to Wheeler and Nixon, this distinction depends on whether the attribute in question is present "in all individuals of a terminal taxon" (p. 77). But how is one to distinguish between variable traits and constant character states unless one recognizes beforehand the unit ("terminal taxon") within which the organisms bearing these attributes, whether variable or constant, occur? One possibility is that the unit is recognized on the basis of inferences about interbreeding.

Considering more inclusive collections, suppose there is a group of reproductively separated populations, the individual populations of which cannot be distinguished consistently from one another on the basis of the characters of their component organisms. Such a group does not qualify as a "unit" just because its member populations are undifferentiated in terms of organismal characters. Treating the collection of populations as if it were a unit may suffice for cladistic analysis above a certain level, but if two such "units" are distinguished from one another by the presence or absence of a single apomorphy, then the collection lacking the apomorphy does not qualify as a non-arbitrary unit any more than does any other collection whose members are "united" by symplesiomorphy. In contrast, the individual populations making up the collection do qualify as units, that is, systems deriving their unity from interbreeding among organisms. That we cannot always distinguish different populations on the basis of organismal characters is irrelevant to the individuality of such populations, for existence as a whole does not imply the possession of one or more unique and constant organismal character states. It seems, then, that populations of interbreeding organisms are better candidates for "nonarbitrary units" than are some collections of organisms bearing unique combinations of character states.

Wheeler and Nixon imply that although populations and interbreeding are significant to population biologists studying such things as gene flow, these phenomena are not critical to cladists studying phylogeny. They apparently overlook the fact that in biparental organisms, reproduction and common descent are intimately tied to interbreeding. Patterns of common descent among biparental organisms within a population are fundamentally different from those among uniparental organisms, which do not form populations in this sense. Consequently, interbreeding sets a lower limit on the application of "cladistic" analysis (i.e. using shared, derived characters) for reconstructing nested patterns of common ancestry among entities composed of biparental organisms. Interbreeding is relevant not only to population biologists, but also to phylogenetic systematists.

Because Wheeler and Nixon think that they have developed a species concept that is preferable to others, at least for "cladists", they "were puzzled" (p. 77) that we did not advocate a particular species concept. The purpose of our paper was not to choose among alternative species concepts, but to offer an explanation for a conflict among them. It was intended to explain why species concepts such as Wheeler and Nixon's, although sufficient for cladistic analysis above certain levels, designate groups of convenience rather than systems of common ancestry and as such are inadequate for phylogenetic systematics. It was also intended to explain why, even if Wheeler and Nixon had advocated a truly phylogenetic species concept, that is, one based on monophyly, there still would be a conflict.

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