FORUM

PHYLOGENETIC SYSTEMATICS OR NELSON'S VERSION OF CLADISTICS?

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In as much as our paper (de Queiroz and Donoghue, 1988) was intended to be a contribution to, rather than a criticism of, phylogenetic systematics, it seems odd that Nelson (1989: 277) views our efforts as being "potentially destructive to the independence of cladistics". On closer inspection, however, Nelson's reaction is understandable as a manifestation of fundamental differences between what he means by "cladistics" and what we mean by "phylogenetic systematics".

Here we argue that (1) contrary to the impression given by Nelson, his version of cladistics is no more independent of a "model", as he terms it, than is phylogenetic systematics; (2) the tenet (model) underlying phylogenetic systematics has greater explanatory power than that underlying what Nelson calls "cladistics"; (3) while Nelson's version of cladistics may "not yet have found a comfortable home within one or another of the ... metatheories of biology" (Nelson, 1989: 275), phylogenetic systematics is secure within the two general disciplines from which it derives its name; and (4) the perspective of phylogenetic systematics clarifies or provides deeper insight into several issues raised by Nelson, including the antagonism over paraphyletic taxa that developed between gradists and cladists, the primacy of common ancestry over characters, and the generality of the concept of monophyly and, consequently, of phylogenetic analysis. The relation between phylogenetic systematics and the principle of common descent not only separates this approach from Nelson's version of cladistics by a fundamental conceptual gap but also enables it to resolve what Nelson sees as incompatibilities between cladistics and theories about evolutionary processes.

Nested Hierarchy and Common Descent

Nelson offers a list of "currently espoused metatheories of biology" (p. 275), which he claims offer "models" of the evolutionary process and are at odds to one degree or another with cladistics. Curiously, Nelson does not include in his list the only "evolutionary metatheory" that we related to phylogenetic systematics, namely the theory of common descent. This theory is "evolutionary" only in the most general sense, for it does not even refer to change. It certainly is not tied to any particular model of the evolutionary process, nor is it at odds with the results of systematic analysis.

As does phylogenetic systematics, Nelson's version of cladistics has an underlying tenet, whether it is called an assumption, a (meta)theory, or a model. The fundamental tenet of phylogenetic systematics is that the entities under consideration are related

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through common descent, and this justifies the search for a nested, hierarchical pattern of relationships (Hennig, 1966). Cladistics, according to Nelson (p. 276), "is ordering homologies into a parsimonious hierarchy, which specifies both taxa and their characters (apomorphies)". Thus, in Nelson's version of cladistics, the principle of nested hierarchy stands by itself. What Nelson presumably means by "the independence of cladistics" (p. 277) is that although his version of cladistics is dependent on the model of nested hierarchy, it is supposedly independent of the principle of common descent.

Judged in terms of explanatory power, independence from the principle of common descent is not necessarily desirable. The explanatory power of this principle is that it accounts for the congruent relationship between the taxonomic hierarchy and the distribution of taxa in space (biogeography; e.g. Rosen, 1978) as well as time (biostratigraphy; e.g. Gauthier et al., 1988), thus unifying the nested, hierarchical patterns of living things in space, in time, and in form under a single general theory. Without this unification, congruence among hierarchical relationships of living things in space, time, and form is not expected, and one wonders why Nelson apparently does expect it (e.g. Nelson and Platnick, 1981).

But even if it were desirable for cladistics to maintain independence from the principle of common descent, it is doubtful that the purported independence exists. Although common descent may not be the only possible cause of nested, hierarchical order, Nelson offers no alternative. If his version of cladistics is truly independent of the theory of descent, one wonders why patterns of relationship other than nested hierarchies (e.g. reticulating networks) are not considered. We will anticipate one response to this question, namely, that the nested, hierarchical pattern is an empirical finding. Nelson and Platnick (1981) went to great lengths to show that taxonomies and taxonomic diagrams throughout the ages could be represented as branching diagrams, from which they concluded that "all, or almost all, systematists seem to be, and seem ever to have been 'cladists.' At least cladistic elements are discernable in the systematic work of whatever age" (p. 327). From this observation, however, it does not necessarily follow that these "cladistic elements" reflect an underlying nested, hierarchical order in nature. The ways that humans represent nature do not necessarily reflect the order inherent in nature, for even artificial classes that do not exhibit nested, hierarchical relationships can be fitted into a hierarchical taxonomy. This is accomplished by granting some class-defining characters primacy over others and repeating the secondary characters within the primary groups (Fig. 1). The observation of nested, hierarchical elements in taxonomies throughout the ages may be attributable to nothing more than the fact that grouping entities into nested sets is a convenient way of ordering knowledge.

In contrast with Nelson's version of cladistics, maintaining independence from the rest of biology is not a primary concern in phylogenetic systematics. Nevertheless, maintaining independence from particular theories about evolutionary processes is desirable if the results of systematics are to be used in testing such theories. Phylogenetic systematics, in being tied only to the principle of common descent, is not dependent on the success of any particular model of the evolutionary process. Furthermore, although part of "evolutionary biology", phylogenetic systematics is not subsumed by the former, because phylogenetic systematics is also part of another general discipline, namely, systematics. What we mean by "systematics", however, is not what is normally understood by this term. We define "systematics" as that discipline concerned with the identification (discovery) of systems, that is, wholes deriving their existence from some process through which their parts are related (Griffiths, 1974; de Queiroz, 1988).
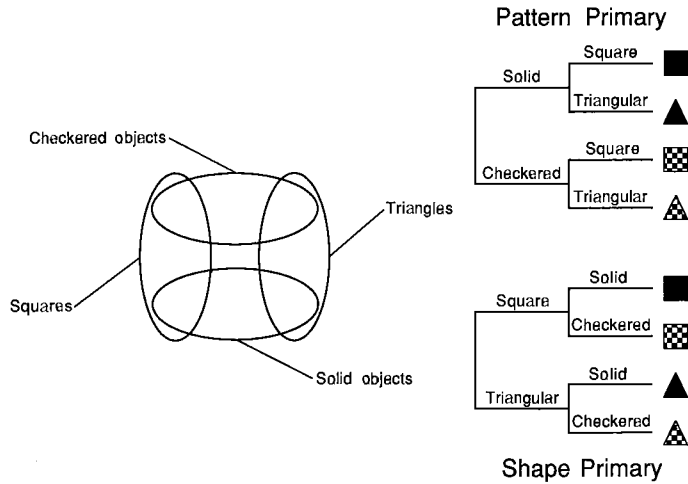
Fig. 1. Nested hierarchical taxonomies do not necessarily imply intrinsic nested hierarchical order. The Venn diagram (left) represents the relationships among four classes: squares and triangles, solid and checkered objects. These classes are not nested within one another. Classes within each pair form non-intersecting sets, while those in different pairs form partially overlapping sets. On the right, entities in the various classes are ordered in two different ways in nested, hierarchical taxonomies.

Phylogenetic systematics is the subdiscipline of systematics that applies to entities related by common descent. In biology, such entities include not only populations and organisms, but also cells, organelles, chromosomes, and genes. Phylogenetic systematics applies even to some non-living things, for example, languages. This is the generality and the independence of phylogenetic systematics.

Cladistics and Phylogenetic Systematics

The preceding implies that among the intellectual descendants of Hennig there are people holding incompatible views about the very nature of their science. The possible consequences of these conceptual differences (whether cladists have "speciated") have drawn attention (e.g. Mishler, 1987; Hull, 1988), but the differences themselves have not been adequately explored (but see Beatty, 1982). Throughout his paper, Nelson uses the terms "phylogenetic systematics" and "cladistics" interchangeably. Equating the two may be appropriate when referring to a sociological entity or to a class of taxonomists defined by the use of certain methods (but see Hull, 1988). The issues involved in this interchange, however, concern underlying tenets and the basic principles of systematics. Here phylogenetic systematics and Nelson's version of cladistics are utterly distinct. Equating the two when discussing such issues obscures important differences concerning the theoretical foundations of the disciplines, while acknowledging these differences clarifies disagreements on other levels.

Those who deny a rift among Hennigians have focused on methods instead of underlying principles, arguing that cladistic methods can be applied without evolutionary considerations (e.g. Nelson and Platnick, 1981; Patterson, 1982; Platnick, 1979, 1982).[1] This focus on practical application ignores the critical issue of how the

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[1] It is not clear that the methods of Nelson's version of cladistics and those of phylogenetic systematics are the same; for example, the ontogenetic method for polarizing characters advocated by Nelson (1978, 1985a) is not a method of phylogenetic systematics (de Queiroz, 1985).

methods and underlying principles were formulated. We argued that Hennig formulated the principles and methods of phylogenetic systematics as deductions from the tenet of common descent (de Queiroz and Donoghue, 1988). Nelson has argued that "cladistic" elements have been present throughout the history of taxonomy (Nelson and Platnick, 1981; Nelson, 1985a). What accounts for the disagreement? The answer lies in what is meant by these statements. By "principles and methods of phylogenetic systematics" we meant such things as the refinement of the definition of monophyly, and the distinction between plesiomorphy and apomorphy and its bearing on the discovery of monophyletic entities. Whether these principles would have been formulated without a concept of common descent is unknown, but surely they have not been present throughout the history of taxonomy. By "cladistic elements" Nelson seems to mean the principle of nested hierarchy. Nested, hierarchical elements may have been present in the taxonomies of whatever age, but as we pointed out above, even artificial classes that do not intrinsically exhibit hierarchical relationships can be arranged in nested hierarchies. Therefore, embracing hierarchical taxonomies does not imply embracing the principles of monophyly and synapomorphy. The conclusion seems inevitable that despite the long history of hierarchical taxonomies, phylogenetic systematics originated relatively recently.

Nelson believes that our view of Hennig's contribution misrepresents history and "fail[s] utterly to explain the antagonism that developed between Mayr and Simpson, on the one hand, and Hennig and other cladists on the other" (p. 276). He proposes that this antagonism relates to the concept of paraphyly and its bearing on views championed by Mayr and Simpson, namely biological species and ancestral higher taxa, respectively. We agree with this assessment, which is not at odds with our view. Nevertheless, our perspective accounts for something that Nelson leaves unexplained; namely, how Mayr and Simpson, as professed evolutionists, were able to maintain their advocacy of paraphyletic "higher" taxa after Hennig had exposed the inappropriateness of such taxa in phylogenetic systematics.

For many evolutionists before Hennig (e.g. 1966), organisms and species were real, but higher taxa were not. Hennig changed that. He deduced from the tenet of common descent that real entities existed above the "species level"—namely, monophyletic entities—and that these might be recognized on the basis of synapomorphy. In short, Hennig changed the role of the theory of descent from that of an after-the-fact interpretation of the order supposedly manifest in existing taxonomies to that of a central tenet from which he deduced the existence of entities (systems) resulting from genealogical relationships among their parts.

Mayr and Simpson were able to maintain antagonism toward Hennig's view because they had not taken this step. Although they accepted common descent, this principle remained for them, at least at the higher taxonomic levels, merely an after-the-fact interpretation of the order manifest in existing taxonomies. Gradists could embrace paraphyletic taxa because they continued to treat taxa at least partly as classes. Specifically, a taxon was viewed as a group whose member organisms belonged to the taxon not because of common ancestry but because they shared some character or characters. This is evident in arguments offered in favor of the continued recognition of paraphyletic (and sometimes even polyphyletic) higher taxa, all of which—even those couched in evolutionary terms such as "anagenesis" and "adaptation"—are ultimately based on shared characters rather than phylogeny (de Queiroz, 1988).

Classes and Systems

Our view of Hennig's contribution derives from a distinction raised in our paper between classes and systems (see also Griffiths, 1974; de Queiroz, 1988; Donoghue and Cantino, 1988) and its bearing on the concept of taxa. We argued that the taxa of phylogenetic systematics are systems of common ancestry rather than classes defined by characters. While this distinction is central to our position, Nelson, at the most, considers it to be of secondary importance (see also Nelson, 1985b). He takes the position that if we can recognize a taxon (by application of the cladistic method), then it must be real. This difference results in a striking contrast between the concept of taxa in phylogenetic systematics and that in Nelson's version of cladistics.

In Nelson's view, characters have primacy over descent. He considers "generality of homology" to be a more fundamental relationship than recency of common descent and recency of common modification; it is supposedly "the most important, of the [three] relationships" (p. 281) from which the others are derived. Thus, Nelson concludes that "descent without modification . . . is insufficient explanation of taxa" (pp. 280–281); "presumably a new taxon comes into being with one or more new homolog" (p. 281); "homology is the part, and the whole, of a taxon and its relationships" (p. 282); and "higher taxa in their entirety belong to lower taxa, which ultimately belong to organisms" (p. 284). These statements imply that a taxon must have an apomorphy to be monophyletic; in effect, that shared characters (apomorphies, homologies) of organisms are the source of a taxon's existence.

Nelson's perspective differs fundamentally from that of phylogenetic systematics, in which common descent is the source of a (monophyletic) taxon's existence, and apomorphies are the evidence by which we recognize it. As Hennig put it:

> In the phylogenetic system the categories [taxa] at all levels are determined by genetic relations that exist among their subcategories. Knowledge of these relations is a prerequisite for constructing the categories, but the relations exist whether they are recognized or not. Consequently here the morphological characters have a completely different significance than in the logical and morphological systems. They are not themselves ingredients of the definition of the higher categories, but aids used to apprehend the genetic criteria that lie behind them (Hennig, 1966: 79–80).

Characters certainly are important in diagnosing taxa; nevertheless, common descent without modification *is* sufficient explanation for monophyletic entities, which exist as systems of common descent even if they have no modifications (apomorphies) by which we can recognize them. Inferences about particular patterns of common descent and modification are based on observations of characters (putative homologies), but this precedence in a sequence of inference does not imply that characters are more basic than the principle of common descent. In phylogenetic systematics, common descent is the fundamental principle in that it provides the rationale for the procedure (e.g. the reason that apomorphies but not plesiomorphies are evidence of relationship) as well as the basis for the definitions of other significant terms, such as homology and monophyly, which are defined with reference to common ancestry.

Despite Nelson's statements about the primacy of characters, he seems to be unable to maintain this position:

> Interesting is the possibility that apomorphies of taxa accumulate in evolutionary time (that evolution is orthogenetic), as if taxa function to constrain or to direct their own evolution. An orthogenetic model is also consistent with cladistics as a discovery procedure. The procedure, however, would be less

> effective in resolving the relationships of early (fossil) representatives of taxa that have a long subsequent history. The fossils would tend to be unrecognizable as representatives of the taxa, because the taxa would have accumulated apomorphies after the death and fossilization of the early representatives. The early fossils would be portrayed as a paraphyletic series of ever earlier and more plesiomorphic sister taxa. (Nelson, 1989: 285).

Because of the way "apomorphy" is defined in phylogenetic systematics, it is logically impossible for a taxon to acquire apomorphies after its earliest representatives have lived and died. This is not to say that apomorphies cannot arise within a taxon, only that these "orthogenetic" characters are not apomorphies of the taxon in question. If early representatives lacking such characters are unrecognizable as representatives of a taxon, it is not because the taxon has "continue[d] to come into being" by accumulating new apomorphies after the existence its early representatives, as Nelson (p. 285) suggests, but because characters that arose within the taxon have been identified incorrectly as apomorphies at the level of the taxon as a whole rather than as apomorphies of its subtaxa. Nelson's acceptance of these so-called orthogenetic characters as apomorphies of the taxon as a whole contradicts his statements about the primacy of homology. If the early organisms of a taxon lack the apomorphies of that taxon, then what, other than their ancestry, makes them representatives of the taxon?

Monophyly and Taxa

Nelson objects to our generalization of the terms "monophyly", "paraphyly", and "polyphyly". He suggests that under our view, in which monophyletic entities include dead organisms as well as extinct and unknown subgroups, every known taxon would be non-monophyletic. He uses the example (p. 277) that "the known Mammalia [would have to be regarded] as a non-monophyletic taxon in the supposition that...an unknown and anonymous rat is dead" (more accurately, a dead rat is unknown). This conclusion misrepresents our position. That some rat is dead and unknown does not imply that Mammalia is non-monophyletic. As a descendant of the common ancestor of all Mammalia, the unknown, dead rat is a mammal. The point is that the group of *known* entities is not the monophyletic taxon but only its known parts or representatives—*known* Mammalia is not the monophyletic entity Mammalia.

Nelson's misunderstanding results from his reading our statements in light of the view that a taxon is a "group of units" (p. 277). Elsewhere (p. 276), he presents a view that agrees more closely with our concept of taxa, namely, that (monophyletic) taxa are better understood as (phylogenetic) parts of life rather than groups of living units.[2] Nevertheless, units exhibiting common descent exist at various organizational levels. Therefore, a given entity can be viewed from the perspective of the whole or that of the parts. For example, a clade can be viewed as a single, often branched, part of the tree of life. Alternatively, it can be viewed as a monophyletic "group" of the units forming the branches that make up this part of the tree. Biologists commonly restrict their consideration of monophyletic entities to "groups" of organisms, populations, or "species". However, because cells (and chromosomes, and organelles, and genes) reproduce to form lineages, they also form entities whose parts are related through

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[2] We used the term "monophyletic group" as a matter of convention but noted the unfortunate connotations of the term "group" (de Queiroz and Donoghue, 1988: footnote 6).

common descent, and this obtains whether or not we choose to apply the adjective "monophyletic" to such entities.[3]

So long as the properties of common descent and nested, hierarchical relationships at different levels are acknowledged, the level of application of "monophyly" and related terms is a semantic rather than an ontological issue. We prefer the more general usage because it accords with a greater generality of conceptual as well as methodological application. This usage reflects another strength of relating what Nelson calls the "discovery procedure" (i.e. phylogenetic or cladistic analysis) to the principle of descent. The relationship between the procedure and the principle enables us to see the general applicability of the procedure. In other words, it enables us to see that entities other than those we normally consider may exhibit the properties that make their relationships amenable to analysis using the procedure.

Just as monophyletic entities can be viewed from different levels or perspectives, so can other kinds of entities. For example, an organism can be viewed as a single thing or as a group of cells. Nelson asks what is to be gained by regarding an organism as a paraphyletic group of cells. The answer is that it acknowledges that cells can be parts of different kinds of wholes (multicellular organisms and cell clones), and that these more inclusive wholes do not necessarily correspond in terms of their component cells. Put another way, organisms exist as the result of relationships other than common descent among their parts (hence the transplanted organ is considered part of the recipient rather than the donor organism). Like cells, organisms can be parts of different kinds of wholes (such as populations and clades), which likewise do not necessarily correspond in terms of their component organisms. As we tried to emphasize in our paper, looking at the species problem in this way suggests that the difficulty in reaching a single generally accepted definition of the species category exists because several different species concepts describe real biological entities.

According to Nelson, our outlook tolerates imprecision, but his assessment rests on equating precision with considering only one kind of entity (the monophyletic entity) and imprecision with complexity. Recognizing that a given thing can be simultaneously a part of more than one kind of greater whole might be considered imprecise if these systems were not clearly distinguished. For example, it would be imprecise to base a species concept on some combination of properties (e.g. both monophyly and interbreeding); however, we rejected this brand of pluralism. Nevertheless, common descent (monophyly) is not the only kind of biological relationship. Because interbreeding is a kind of relationship, and one that is directly related to descent, the development of phylogenetic systematics will only be hindered by failing to consider it.

Nelson wishes to restrict the concepts of mono-, para-, and polyphyly to particular hierarchical levels—to what he calls "taxa (as taxa are normally understood)" (p. 277). Generalizing these concepts so that they encompass other levels leads to the conclusion that the collections of cells in some organisms and the collections of organisms in some populations are paraphyletic. Perhaps some will interpret this conclusion as legitimizing paraphyly and thus endangering "cladistics", for as Nelson points out, "[elimination of]

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[3] Nelson takes issue with our treatment of organisms as parts of taxa: "Organisms (and their parts) are neither taxa nor parts of taxa . . ." (p. 279), however, his own statements lead to the conclusion that they are. If "taxa . . . have homologies as their parts" (p. 279) and "an entire organism is the homolog of another" (p. 279), then it seems, unless "homologs" are not "homologies", that taxa have organisms as their parts. Similarity, if there is a "taxon (Life or Biota)" (p. 284) and "organisms . . . are ontogenetic parts of life" (p. 279), then unless "Life" is not "life", organisms are parts of taxa.

paraphyly is cladistics' stock in trade" (p. 276). This fear is unfounded. Recognizing the existence of populations (systems of interbreeding) in no way legitimizes recognizing paraphyletic groups as systems of common descent. Because paraphyletic taxa fail to include some descendents of the specified common ancestor, they can never be phylogenetic taxa.

These considerations suggest that a primary factor in the tension surrounding the term "species" is disagreement about whether species are to be considered the same kind of entities as other taxa. In other words, given that we accept a distinction between (monophyletic) taxa on the one hand and things like populations and organisms on the other, should we apply the term "species" to the least inclusive things in the former category or the most inclusive things in the latter? There are precedents either way. In fact, there is disagreement on this issue even among cladists. Nelson considers all taxa, including species, to be monophyletic, while others (e.g. Hennig, 1966; Platnick, 1977; Willmann, 1983; Ax, 1987) have argued that the concept of monophyly does not apply to species but only to groups of species.

An important consequence of generalizing the concept of monophyly is that it reveals an inconsistency in the views of some cladists concerning species. Although they insist that all taxa are monophyletic, this requirement is relaxed for species. Species are said to be monophyletic, but in reality they are only "diagnosable"; they are not necessarily diagnosed by synapomorphies, but only by "unique sets of characters" (e.g. Nelson and Platnick, 1981: 11–12; Wheeler and Nixon, 1990). Such "taxa" may be adequate as terminal "units" in cladistic analysis in that they permit application of the method, but this does not justify recognizing them as (monophyletic) taxa (de Queiroz and Donoghue, 1990).

Why aren't species held to the same standard as other taxa? The answer is probably that holding species to a strict criterion of monophyly would result in some organisms and populations, in particular, ancestral ones, not being assignable to species level taxa (de Queiroz and Donoghue, 1988). Nelson asks how the truth of this claim might result from a discovery procedure such as cladistics, and he asserts that in fact the claim runs counter to the results of cladistics. That ancestors will not be assignable to monophyletic species taxa is a conclusion reached by deduction from the principle of descent and the properties of cladistic analysis. Any apomorphies of an ancestor must also be present in its descendents. Therefore, ancestral organisms or populations will appear on cladograms as single branches lacking (aut)apomorphies or as unresolved polytomies of branches lacking (aut)apomorphies.[4] Nelson's assertion that these claims are contradicted by the results of cladistics presumably refers to the difficulty of identifying ancestors. But as we pointed out, the inability to assign ancestors to monophyletic species taxa does not depend on their actually being recognized as ancestors. The problem exists regardless of considerations of ancestry. Minimally diagnosable samples are not the same thing as monophyletic taxa.

"Species" and Evolutionary Models

The perspective of phylogenetic systematics resolves what Nelson sees as conflicts between certain evolutionary models and his version of cladistics. For example, Nelson

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[4] Character reversal does not result in an ancestor having an apomorphy that is absent in its descendant(s), because in such a case the character (as a synapomorphy) is not truly absent in the descendant, that is, the absence is not plesiomorphic but apomorphic. Of course, the ancestor will appear to be apomorphic relative to its descendants, and if the reversal is not detected, the ancestor might be identified incorrectly as monophyletic and thus not ancestral.
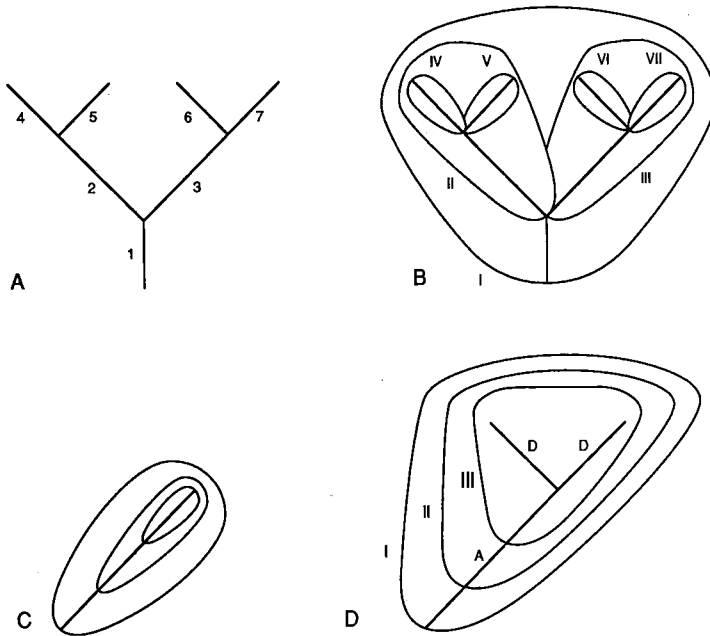
Fig. 2. Monophyly in relation to time-extended populations. (A) The naming of species as time-extended populations; "species" 2 is a population lineage prior to splitting and consequently does not include the descendants 4 and 5. (B) The naming of monophyletic groups of such species; taxon II is a monophyletic entity that includes the "species" 2, 4, and 5 of A. (C) Monophyletic entities within a time-extended population ("species"); less inclusive groups represent later parts of the "species". (D) Splitting in the later part of the lineage shown in C results in one (Eldredge and Gould, 1972) or two (Hennig, 1966) daughter "species" (D), the organisms of which are parts of some monophyletic entities (e.g. III) that include organisms from the later part of the ancestral "species" (A) but not earlier ones. (A and B modified from Griffiths, 1974, Fig. 3).

considers Hennig's "model" of phylogeny to be paradoxical in cases where an ancestral species accumulates several apomorphies before splitting. Although the early organisms of the ancestral species are considered to be members of the monophyletic taxon including the ancestral species and its daughter species, these organisms supposedly lack some or all of the apomorphies of the higher taxon. Consequently, for Nelson (p. 286), Hennig's position implies that evolution is "orthogenetic at the species level" (i.e. that at least some apomorphies of the higher taxon came into being within its ancestral species *after* the origin of the higher taxon).

This supposed paradox results from restricting considerations of monophyly to the "species" level and above, that is, failing to recognize that monophyletic entities can exist within time-extended populations. Griffiths (1974) pointed out that names can be applied to a phylogeny in at least two different ways: they can be applied to each "species" (time-extended population) delimited by successive processes of splitting (Fig. 2A), or they can be applied to the monophyletic groups of such species (Fig. 2B). Monophyletic groups of "species", however, are not the only monophyletic entities. Within a time-extended population, later organisms may be parts of monophyletic entities that do not include earlier organisms of the same "species" (Fig. 2C). Furthermore, if splitting takes place in the later part of the lineage, then later organisms of the ancestral species will be parts of monophyletic entities that include organisms of other species but not earlier organisms of the same species (Fig. 2D).

Application of the concept of monophyly to organisms within populations reveals two aspects of the concept that generally have not been distinguished. On the one hand,

there is the property of exclusivity of relationships; a monophyletic entity is an entity in which no included unit is more closely related to a unit that is not part of the entity than to any unit that is part of it. Related to (but not the same as) this property is the property of common ancestry. Thus, an alternative concept of monophyly is simply that a monophyletic entity is an ancestor and all of its descendants. Under this concept of monophyly, anything that has descendants, including a single organism in a population of sexually reproducing organisms, is the originator of a monophyletic entity. In the case of "higher" taxa, the properties of exclusivity and common ancestry coincide, and the monophyletic entities are internested and non-overlapping. This coincidence applies not only to "higher" taxa but also to any monophyletic entities the units of which do not form reticulating ancestor–descendant lineages. In contrast, in the case of reticulation resulting from sexual reproduction, the two aspects of monophyly are uncoupled. Within populations of biparental organisms, the relationships among entities consisting of ancestral organisms and their descendants form a fundamentally different pattern from that seen among clones of uniparental organisms or clades of reproductively isolated populations. As a result of having two parents (ancestors), these entities are partially overlapping rather than forming nested hierarchies (Fig. 3). Entities of exclusive common ancestry do not exist where reticulating relationships are prevalent, which may explain why some authors propose that the concept of monophyly does not apply to species and populations.[5]

Nevertheless, there may be no reticulation between the parts of a population existing at different times. Therefore, monophyletic entities can exist within time-extended populations even under the concept of exclusive common ancestry, and sometimes these entities will be diagnosable. This can be seen by first considering monophyletic entities as ancestors and their descendants. Over short time spans, monophyletic entities of organisms within populations often will not be diagnosable using organismal characters. Allelic segregation during the formation of gametes implies that a novel character will be present in some, but not all, descendants of the organism in which the character originated (Fig. 3). Nevertheless, certain inferences about ancestry can be made on the basis of such a character. Although not all organisms of the monophyletic entity bear the novel character, the organisms possessing the character are descendants of the ancestor in which the character originated, and they are a subset of the organisms making up the monophyletic entity stemming from that ancestor.

Considered over a sufficiently long span of time, some entities of exclusive common ancestry are recognizable within the population, although their boundaries are not sharp. If the character reaches fixation, then *all* organisms in the part of the time-extended population subsequent to the fixation event are recognizable, by their possession of the character, as descendants of the organism in which the character originated. Of course, all those organisms lacking the character that were conceived before the organism in which the character originated are not part of this monophyletic

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[5] Correspondence or the lack of correspondence between the two components of monophyly depends on the form of descent, that is, whether it is reticulate or diverging. If the terms "phylogenetic" and "tokogenetic" refer to this difference, then phylogenetic relationships do not give way to tokogenetic relationships at one particular hierarchical level (e.g. the "species" level). The relationships among uniparental organisms or among organellar genes are analogous to those between reproductively isolated populations of biparental organisms, and consequently it is meaningful to talk about phylogenies and monophyletic entities in each of these cases. In order to emphasize the uncoupling of exclusivity from common ancestry that occurs within populations, it might be preferable to call entities of common ancestry within populations something other than clades or clones.
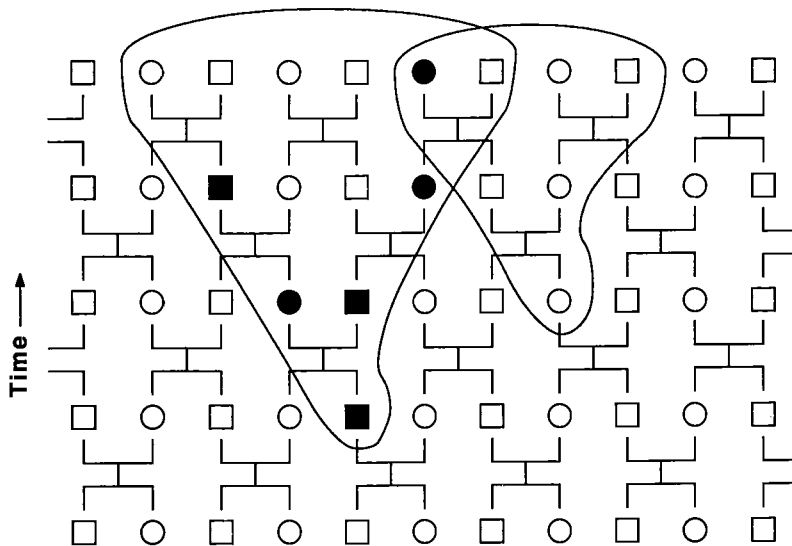
Fig. 3. Ancestors and their descendants (entities of common ancestry) within a population of interbreeding organisms. Because of biparental reproduction, these entities partially overlap with others, as illustrated by the two bubbles, rather than forming a simple, nested hierarchy. In diploid, biparental organisms, a novel allele (represented by black) often will not be present in all descendants of an ancestor possessing it as a result of allelic segregation during gamete formation. This example is simple so that the entities are easily visualized; phenomena such as dominance, sex-linkage, random mating, overlapping generations, variation in numbers of offspring, polygamy, etc. complicate the pattern.

entity. Therefore, although there will be a "grey zone" between the origin and the fixation of the character within which absence of the character is uninformative about ancestry, the organisms on the later side of this zone are part of a diagnosable entity of exclusive common ancestry relative to the organisms on the earlier side of the zone (Fig. 4).

These conclusions resolve what Nelson supposes to be a paradox in Hennig's model of phylogeny (see above). The reason that some organisms of the ancestral species appear to lack the apomorphies of the "higher taxon" in question is that what was treated as a single "higher taxon" is really several internested monophyletic taxa (Fig. 2C, D). The early organisms of the ancestral "species" lack the apomorphies of the less inclusive of these taxa (e.g. III in Fig. 2D) because they are not parts of it. In other words, the
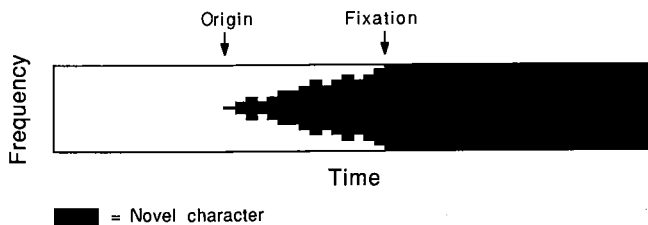

Fig. 4. Diagnosable monophyletic entities of exclusive common ancestry within a time-extended population. In the case of normal biparental reproduction, all organisms possessing a novel character are part of the monophyletic entity stemming from the organism in which the character originated. During the interval in which the character exists as one variant of a polymorphism, its absence is uninformative about ancestry (Fig. 3). After fixation of the character, all organisms in the population share a common ancestor (the organism in which the character originated) not shared by those organisms that lived before the origin of the character.

apomorphies that originated within the ancestral "species" are not apomorphies of the monophyletic taxon that includes the entire ancestral "species" (e.g. I in Fig. 2D); they are apomorphies of one of its subgroups. What appears to Nelson to be the result of "orthogenesis" is simply the result of a mistake about the level at which apomorphies diagnose monophyletic taxa.

Another proposition about species that appears paradoxical to Nelson is that an ancestral species, which lacks apomorphies of its own, is an individual. That Nelson considers this paradoxical is not surprising if he considers monophyly to be the only kind of individuality. Individuality, however, can be viewed as a more general concept in which as many kinds of individuals (systems) exist as processes through which their parts are related (de Queiroz, 1988; de Queiroz and Donoghue, 1988). Under this concept of individuality, monophyletic entities are one kind of individual, and populations are another. If the term "species" is used to refer to a subcategory of the category "monophyletic entities", then it is nonsensical to talk about ancestral species, let alone to discuss their individuality. Alternatively, if the term "species" is used to refer to a subcategory of the category "population", then not only do ancestral species exist, but apomorphies are irrelevant to their individuality. A consistent position is possible under either definition.[6]

Nelson supposes that the issue of whether species are the same kind of entities as other taxa is to be decided by evidence, as if such claims are theories rather than logical consequences of adopting particular definitions of words. He concludes that available evidence does not support the view that species and (higher) taxa are different kinds of things, because some species, just like some presently recognized higher taxa, have apomorphies (appear to be monophyletic) and others do not. The claim that species are different kinds of things than monophyletic entities, however, is a logical consequence of using "species" for a kind of population; it is not a theory about what is presently named or recognized. Presumably, Nelson would not argue that populations and monophyletic entities are the same kinds of things. Therefore, the disagreement is not over what different kinds of entities exist, but over which kind of entity is to be associated with the term "species".

This conclusion runs counter to Nelson's belief that the tension we identified is not between the choice of interbreeding versus common ancestry in the definition of the species category, but "between a model (of biological species, of 'population thinking' with orthogenetic overtones, and ultimately of neodarwinism) and the results of a discovery procedure (cladistics)", which he equates with "empirical findings" (p. 288).

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[6] There are, however, inconsistencies in Nelson's position. For example, according to Nelson, "Cladistics as a discovery procedure is blind, perhaps rightly so, to the dicta of the models: that species are not taxa, and that new homologs (of species) do not form apomorphies (of taxa). For cladistics, discovery of apomorphies and discovery of taxa are one and the same. A species is only a taxon" (p. 287). But if cladistics is truly blind to the dicta of the "models", then it specifies neither that species are, nor that they are not, (monophyletic) taxa. Nelson's statement is further complicated by his ambiguous use of the term "taxon", which he defines as "a species or a monophyletic group of species; or more generally, a terminal taxon or monophyletic group of terminal taxa" (p. 276); or "monophyletic (or phylogenetic) parts of life" (p. 276). By equating "taxon" with "monophyletic entity", Nelson obscures a distinction between named groups or entities (taxa in the usual sense) and monophyletic entities. Moreover, Nelson's statement that "with further study a taxon ... might be found complex—to be in reality a monophyletic, polyphyletic, or paraphyletic assemblage ..." (p. 275) contradicts his own definition. If taxa are defined as monophyletic, then a taxon can never be found to be para- or polyphyletic, for if it is, then it is not a taxon. In any case, the "models" being criticized by Nelson never claim that species are not taxa (in the sense of named entities), only that species are not necessarily monophyletic.

This attempt to tie our discussion of interbreeding to orthogenesis and neodarwinism is misleading. Although the biological species concept figured prominently in the development of neodarwinism, the existence of interbreeding in no way depends on the validity of this theory. Some organisms reproduce sexually. Interbreeding is no less an "empirical finding" than is the hierarchy of taxa found by cladistic analysis.

Conclusions

Nelson sees incompatibilities between his concept of cladistics and various evolutionary "models", and he proclaims, "If cladistics delivers empirical findings that conflict with the [evolutionary] model . . . then surely the model must, if possible, adapt to the findings or go extinct" (p. 288). Just what are these empirical findings of cladistics that supposedly conflict with current models of the evolutionary process, let alone the principle of common descent?

In Nelson's (p. 277) view, the results of cladistics not only fail to demonstrate ancestor–descendant lineages but also undermine all demonstrations previously proposed. Cladistic analysis identifies monophyletic entities. Because ancestors are not monophyletic, it is hardly surprising that cladistic analysis fails to demonstrate them. Phylogenetic systematics exposed a logical problem with demonstrating direct ancestry that is analogous to that of supporting a null hypothesis: although both can be refuted, they are "supported" only by the failure to refute. That character evidence can only fail to refute hypotheses of direct ancestry, however, should not be taken as evidence against such hypotheses.

Other conflicts offered by Nelson illustrate the tension we identified between interbreeding and monophyly concerning the definition of the species category. But the conflicts are not between patterns revealed by cladistic analysis and theories about evolutionary processes, they are disagreements about the definitions of words. Nelson's conclusions appear to contradict widely held views because he has interpreted statements made within one conceptual framework according to definitions of another. For example, Nelson's disagreement with Hennig is not about whether apomorphies can accumulate in a population over time, but about whether such time-extended populations are to be called species. Likewise, there is no disagreement about whether population lineages split, only about whether this splitting, instead of the origin of apomorphies, is to be called speciation. The definitions preferred by Nelson are not theory-neutral; they are part of his version of the cladistic model, and they lead him to particular interpretations of "empirical findings". These same findings can also be interpreted in the context of phylogenetic systematics, where they form parts of a consistent world view.

The contrast between Nelson's view and ours makes it clear that different "cladists" hold fundamentally incompatible ideas about the nature of systematics. The existence of these conceptual differences explains many of the disagreements that have surfaced in the present interchange. Nelson obscures these distinctions by using the terms "phylogenetic systematics" and "cladistics" interchangeably, and then criticizing our statements about phylogenetic systematics as if they were statements about his version of cladistics. Nevertheless, Nelson has also helped clarify the differences by elaborating his version of cladistics, and he implicitly acknowledges their existence in his different "ways of seeing" (p. 285). At the heart of these differences is the principle of common descent. Nelson considers it important for his version of cladistics to maintain independence from

this principle. In contrast, such independence is antithetical to phylogenetic systematics. Indeed, it is the foundation of phylogenetic systematics in the general theories of systematics and of common descent that gives it the power to explain what appear to be paradoxes from Nelson's perspective. It is precisely this connection to the principle of common descent that insures phylogenetic systematics a central role in systematic and evolutionary biology and accounts for its ever-increasing success.

Acknowledgments

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