The Limits of Cladism

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Abstract

Hull, David L. (Department of Philosophy, University of Wisconsin, Milwaukee, Wisconsin 53201) 1979. The Limits of Cladism. Syst. Zool. 28:416–440.—The goal of cladistic systematics is to discern sister-group relations (cladistic relations) by the methods of cladistic analysis and to represent them explicitly and unambiguously in cladograms and cladistic classifications. Cladists have selected cladistic relations to represent for two reasons: cladistic relations can be discerned with reasonable certainty by the methods of cladistic analysis and they can be represented with relative ease in cladograms and classifications. Cladists argue that features of phylogeny other than cladistic relations cannot be discerned with sufficient certainty to warrant attempting to represent them in either cladograms or classifications and could not be represented if they could. I argue that a better alternative is to work toward improving methods of cladistic analysis (or else to supplement them with other methods) so that such features of phylogeny can be discerned and to devise methods of representation capable of representing them in both cladograms and classifications. However, cladograms and classifications cannot represent everything about phylogeny. It is better to represent one or two aspects of phylogeny explicitly and unambiguously than nothing at all. [Cladism; classification; evolution; species.]

"Our classifications will come to be, as far as they can be so made, genealogies; and will then truly give what may be called the plan of creation. The rules for classifying will no doubt become simpler when we have a definite object in view" (Darwin, 1859:486).

Charles Naudin's "simile of tree and classification is like mine (and others), but he cannot, I think, have reflected much on the subject, otherwise he would see that genealogy by itself does not give classification" (Darwin, 1899, 2:42).

One possible goal for biological classification is to "represent" phylogeny, to construct classifications so that certain features of phylogeny can be read off unequivocally. However, Darwin was quite correct when he noted that genealogy by itself does not give classification. Different taxonomists may select different aspects of phylogeny to represent. One might choose order of branching, another degree of divergence, another amount of diversity, and so on. Whether or not the rules for classifying become simpler, as Darwin hoped they would, depends on the features of phylogeny which the taxonomist chooses to represent and the particular set of principles which he formulates to represent them. A classification which attempts to represent only one aspect of phylogeny is likely to be simpler than one which attempts to represent two simultaneously. Given any particular goal, the simplicity of the rules capable of accomplishing this goal depends both on the inherent limitations of the mode of representation and the ingenuity of the taxonomist. For example, the traditional Linnaean hierarchy might lend itself to representing certain features of phylogeny more readily than others, but nothing precludes a taxonomist from introducing additional representational devices to remove these limitations. The end result is, of course, more complex rules for classifying. Systematists are thus forced to strike a balance between how much they wish to represent and how complicated they are willing to make their principles of classification and resulting classifications.

In recent years a school of taxonomy has arisen whose members have seriously taken up the challenge of attempting to represent explicitly and unambiguously *something* about phylogeny. The school is cladism, the aspect of phylogeny which the cladists have chosen to represent is order of branching. The cladists have given two reasons for choosing this

particular feature of evolutionary development to represent. First, the Linnaean hierarchy, as a list of indented names, lends itself more naturally to expressing discontinuous than continuous phenomena. Whether or not evolution is gradual or saltative, phylogeny is largely a matter of splitting and divergence. A hierachy of discrete taxa names is well-calculated to represent successive splitting. It is not as well-calculated to represent varying degrees of divergence. Second, the cladists argue that order of branching can be ascertained with sufficient certainty to warrant the inclusion of such information in a classification while other aspects of phylogeny cannot be. The method which cladists have devised to discover order of branching is cladistic analysis.

Cladists argue that, by and large, all a systematist has to go on is the traits of the specimens before him, whether these specimens represent extant or extinct forms. By studying his specimens, he can discover nested sets of characters. Unique derived characters distinguish a monophyletic group from its nearest relatives; shared derived characters combine these monophyletic groups into more inclusive monophyletic groups. In this way the systematist can ascertain nested sets of sister-groups. This method, so cladists argue, cannot be used to discern a variety of other relations—speciation without the appearance of at least one unique derived character, reticulate evolution, multiple speciations, and the ancestor-descendant relation—nor can any other method.

Several questions arise at this juncture. If the Linnaean hierarchy cannot represent certain features of evolutionary development very well, is not that a limitation of the Linnaean hierarchy? Instead of refusing to represent what a particular system of representation has difficulty in representing, a better alternative might be to abandon or improve that system of representation. This is one avenue which the cladists themselves have taken (Griffiths, 1976; Hennig, 1966; Løvtrup, 1973; Nelson, 1972a, 1973c; Patterson and Ro-

sen, 1977; Wiley, 1979). Do the evolutionary phenomena which cladistic analysis cannot discern actually exist? As I understand evolution and evolutionary theory, two of these phenomena clearly occur (ancestors giving rise to descendants and reticulate evolution), one is quite likely (multiple speciation), and the fourth is doubtful (speciation without deviation, although the unique derived character may be all but undetectable). Is not the inability of cladistic analysis to discern the preceding phenomena, assuming they take place, a limitation of the methods of cladistic analysis? Instead of declining to deal with such phenomena because the methods of cladistic analysis cannot discern them, perhaps a better strategy might be to attempt to improve upon the methods of cladistic analysis or to supplement them with other methods. The crucial question with respect to cladism, as I see it, is what is cladistic analysis? What are its limits? Is cladistic analysis *one* way of ascertaining phylogeny, the *only* way of ascertaining phylogeny, the only way of obtaining knowledge of *any* phenomena?

One fact about cladism which complicates attempts to answer the preceding questions is that cladism, like all scientific movements, is neither immutable nor monolithic. At any one time, cladists can be found disagreeing with each other about particular principles and conclusions. In addition, if one traces the development of cladism through time, from its inception in the works of Hennig (1950), through its introduction to English-speaking systematists (Hennig, 1965, 1966; Brundin, 1966; Nelson, 1971a, 1971b, 1972a, 1972b, 1973a, 1973b, 1973c, 1974) to the latest publications of present-day cladists, significant changes can be discerned. The most significant change which has taken place in cladism is a transition from *species* being primary to *characters* being primary. For Hennig (1966, 1975) and Brundin (1972a), the basic units of cladistic analysis are species, characterized by at least one unique derived character. Now,

for a growing number of cladists, any monophyletic group which can be characterized by appropriate traits can function in cladistic analysis, regardless of whether that group is more inclusive or less inclusive than traditionally-defined species. Cladistic classifications do not represent the order of branching of sister-groups, but the order of emergence of unique derived characters, whether or not the development of these characters happens to coincide with speciation events. It is not the emergence of new species which is primary but the emergence of new traits (Tattersall and Eldredge, 1977:207; Rosen, 1978:176). In general, cladists seem to be moving toward the position that the particulars of evolutionary development are not relevant to cladism. It does not matter whether speciation is sympatric or allopatric, saltative or gradual, Darwinian or Lamarckian, just so long as it occurs and is predominantly divergent (Cracraft, 1974; Bonde, 1975; Rosen, 1978; and forthcoming works by Nelson and Platnick, Eldredge and Cracraft, and others).

The writings of most cladists have been concerned with developing methods of ascertaining the cladistic relations between biological taxa, but Platnick and Cameron (1977) have shown that these same techniques can be used to discern the cladistic relations exhibited by languages and texts (see also Kruskal, Dyen, and Black, 1971; Haigh, 1971; and Nita, 1971). In general cladistic analysis can be used to discover the cladistic relations between any entities which change by means of modification through descent (Platnick, 1979). As general as this notion of cladistic analysis is, it still retains a necessary temporal dimension. Transformation series must be established for characters, not just an abstract atemporal transformation series like the cardinal numbers or the periodic table, but a series of actual transformations in time. For example, the vast majority of matter in the universe happens to be hydrogen. In isolated pockets of the universe, more complex molecules have developed, but they have not developed by progressing up the periodic table, from hydrogen to helium, lithium, beryllium, etc.

From the beginning, Gareth Nelson (1973c) seems to have been developing two notions of cladistic analysis simultaneously, one limited to historically developed patterns (cladism with a small 'c'), the other a more general notion applicable to all patterns (Cladism with a big 'C'). His method of component analysis is a general calculus for discerning and representing patterns of all sorts. For example, in a recent discussion, Nelson (1979:28) states that a "cladogram is an atemporal concept . . . a synapomorphy scheme." It remains to be seen whether all of the terms of cladistic analysis from "sister group " to "synapomorphy" can be defined so that none of them necessarily presupposes a temporal dimension. Although I think that the principles of cladistic analysis *can* be extended to any system which genuinely evolves (i.e., changes through time by means of modification through descent), I will limit myself in this paper to phylogeny and biological evolution. I also will not address myself to Nelson's more general notion. Attempting to discuss the principles of cladistic analysis as they apply to phylogeny is a sufficiently difficult task without attempting to present interpretations of these principles which are also consistent with Nelson's more general program.

METHODOLOGICAL PRINCIPLES AND OBJECTIONS

In spite of certain observations which cladists have made periodically about the evolutionary process, the principles of cladistic analysis do not concern evolution but the goals of biological classification and the means by which they can be realized. These principles are primarily methodological. As I see it, the goal of cladism is to represent cladistic relations in both cladograms and classifications as explicitly and unambiguously as possible. Thus, cladistic methodology has two parts: rules for discerning cladis-

tic relations and rules for representing them in cladograms and classifications. For example, Nelson raises two objections to the ancestor-descendant relation: first, "ancestral species cannot be identified as such in the fossil record" (Nelson, 1973b:311), and second, "they are also inexpressible in classifications" (Nelson, 1972a:227).

One source of the confusion which has accompanied the controversy over cladism is the interpretation of their methodological principles as empirical beliefs about evolution. The claim that dichotomous speciation never occurs is an empirical claim to be tested by empirical means. The claim that we can never distinguish between dichotomous speciation events and more complex sorts of speciation is a methodological claim about the limits of our methods of scientific investigation. Finally, the claim that multiple speciation, if it occurs and if it can be discerned, cannot be represented unambiguously in cladograms and/or classifications is a comment about the limitations of these modes of representation. Once the principles of cladism are recognized for what they are, *methodological principles*, the logic of the cladistic position on a variety of issues becomes much clearer.

Scientists are interested in truth, not Absolute Truth, but truth nevertheless. Although philosophers have yet to produce a totally unproblematic analysis of science as the pursuit of truth (see, for example, Laudan, 1977), I think that scientists are correct in the focus of their attention. Scientists also present arguments to buttress their empirical claims and try to make their arguments as good as possible. Unfortunately, scientists are rarely able to present their arguments in the unproblematic forms thus far analyzed successfully by mathematicians and logicians. The reasoning which goes into the formulation and testing of scientific theories is a good deal more complex and informal than any explicit rational reconstruction has yet been able to capture. Scientists are interested in both

truth and cogency of argument, but they are a good deal more interested in truth than in cogency of argument. If a line of reasoning which led to a particular conclusion turns out to be somewhat less than perfect, it really does not matter all that much, just so long as the conclusion depicts reality with greater fidelity than previous attempts.

Scientists have limited patience when it comes to discussing arguments. That patience is even more limited when the arguments are methodological. As strange as it may sound coming from a philosopher, I am highly sceptical of methodological principles and prescriptions, especially when they are presented in the midst of scientific disputes. They tend to be suspiciously self-serving, designed to put one's opponents at a disadvantage while shoring up one's own position. Invariably the advocates of a particular methodology can know what they need to know while their opponents can never hope to know what they need to know. For example, the pheneticists claim that we can analyze traits into unit characters, but we can never hope to establish genuine, evolutionary transformation series among characters. None too surprisingly, the pheneticists need to know the former but not the latter. Only the cladists and evolutionists need to know the unknowable. Similarly, the cladists claim that we can establish transformation series with sufficient certainty to warrant the role which they play in cladistic systematics but that ancestor-descendant relations are unknowable. As luck would have it, cladists need to know the former but not the latter. Only the evolutionists need to know the unknowable.

As cynical as the preceding remarks may sound, I think they have some validity. It is no accident that all four of the phenomena which the cladists claim cannot be known, cannot be discerned by the traditional means of cladistic analysis and cause problems for the explicit and unambiguous representation of sister-group relations in both cladograms and classifications. It is also no accident that

one of the phenomena which cladists claim cannot be known (the ancestor-descendant relation) plays a central role in the research program of their chief rivals—the evolutionists. I do not mean to imply that the preceding remarks apply uniquely to the cladists. They apply to scientists in general. If I were investigating the pheneticists or the evolutionists, comparable observations would apply as readily to them. These are the sorts of games which scientists (not to mention philosophers) play with each other.

In general, I think it is very bad strategy for proponents of a particular scientific research program to stake their future on epistemological considerations, especially on our inability to know something. Phenomena which scientists in one age claim can never be known often become common knowledge at a later date. The history of science is littered with the bodies of scientists who staked the success of their movements on what we can never know. I agree with Einstein (1949:684), who, in response to philosophical criticisms of his work, stated:

> Science without epistemology is—insofar as it is thinkable at all—primitive and muddled. However, no sooner has the epistemologist, who is seeking a clear system, fought his way through to such a system, than he is inclined to interpret the thought-content of science in the sense of his system and to reject whatever does not fit into his system. The scientist, however, cannot afford to carry his striving for epistemological systematic that far.

I hardly want to argue against methodological rigor in science, but I also do not want to see scientific progress sacrificed to it. Invariably methodological rigor is a retrospective exercise, carried on long after all the Nobel prizes have been won. From the point of view of current methodologies, scientists will, as Einstein (1949:684) noted, appear to the "systematic epistemologist as a type of unscrupulous opportunist." Instead of cladists insisting that certain aspects of phylogeny can never be known and could not be represented cladistically if

they could be known, a wiser strategy would be to attempt to devise methods of analysis capable of discerning these features of evolutionary development and representational techniques sufficient to represent them. In this paper, I have attempted to produce an internal criticism of cladism; that is, I have accepted the goals of cladism and have set myself the task of deciding which methodological principles are central to the undertaking, which peripheral, and which could be modified or abandoned without loss and possibly with some gain.

CLADOGRAMS, PHYLOGENETIC TREES, AND EVOLUTIONARY SCENARIOS

A curious feature of scientific development is the frequency with which a new movement is named by its opponents. Social Darwinists no more wanted to be called Social Darwinists than cladists have wanted to be called cladists. Twenty years ago, Julian Huxley (1958) coined the terms "clade" and "grade" to distinguish between groups of organisms with a common genetic origin and groups distinguished by different levels of organization. Later Mayr (1965:81) and Camin and Sokal (1965:312) introduced the term "cladogram" to refer to a diagram "depicting the branching of the phylogenetic tree without respect to rates of divergence" (Mayr, 1978:85). Finally, Mayr (1969:70) invented the term "cladism" as a substitute for "phylogenetic systematics," the name preferred by Hennig and his followers. Gradually the cladists themselves have come to use the term to refer to themselves, albeit grudgingly.

Whether the Hennigian school of systematics is called "phylogenetic" or "cladistic" is not very important, but the precise nature of cladograms as they function in cladistic analysis is. In fact, uncertainty over what it is that cladograms are supposed to depict and how they are supposed to depict it has been the chief source of confusion in the controversy over cladism. Like all terms, the meaning of "cladogram" has changed through the

years. It no longer means to cladists what Mayr, Camin and Sokal proposed. The meanings of "cladism" and "cladistic analysis" have changed accordingly. In an attempt to reduce the confusion over the meaning of "cladogram," cladists have introduced the distinction between cladograms, phylogenetic trees, and evolutionary scenarios.[1] Once again, the particular terms used to mark these distinctions are not important; the distinctions themselves are. It is also true that the cladists have devised these distinctions for their own purposes. Others might want to draw other distinctions or to draw these distinctions differently. In any case, all three appellations refer to representations, not to the phenomena being represented. "Cladogram" and "tree" refer to two sorts of diagrams, while "scenario" refers to a historical narrative couched in ordinary biological language.

Phylogenetic trees are designed to depict phylogenetic development, indicating which taxa are extinct, which extant, which gave rise to which, degrees of divergence, and so on. As diagrams they do not include discussions of the methods used to construct them, the natural processes which produced the phenomena they depict, and a variety of other considerations of equal importance. A tree is a diagram, not an entire taxonomic monograph. All sorts of conventions have been devised to represent phylogeny in a diagrammatic form; for example, lines usually represent lineages, forks represent speciation events, the slant and length of a line reflect the rapidity with which divergence took place, and the termination of a line indicates extinction. Other techniques of representation have also been used on occasion; for example, dots indicating questionable connections, lines of varying thicknesses reflecting relative

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[1] The distinction between cladograms, trees, and scenarios discussed in Tattersall and Eldredge (1977) was taken from a manuscript by Gareth Nelson. See Mayr (1978) for early definitions of such terms as "cladogram," "phenogram," and "phylogram."

numbers of organisms, and so on. However, as a diagram in two-dimensional space, a tree can include only so much information before a point of diminishing returns sets in. Eventually attempts to include additional sorts of information result in the loss of information. If trees are supposed to be systems of information storage and retrieval, the information must be retrievable.

Scenarios, as cladists use the term, are not diagrams. They are historical narratives which attempt to describe not only which groups gave rise to which (the sort of information contained in trees) but also the ecological changes and evolutionary forces which actually produced the adaptations which characterize the organisms discussed. Romer's (1955:57) story of the role which the drying up of ponds and streams played in the transition from the crossopterygians to early amphibians is by now a classic example of an evolutionary scenario. Because scenarios are presented in ordinary language—supplemented with a host of technical biological terms—the phenomena which scenarios can describe are limited only by the limitations of language.

Hennig's early cladograms (Hennig, 1950:103; 1966:59, 71) give every appearance of being highly stylized trees. The circles arrayed along the top of the diagram apparently represent extant species, while those at the nodes represent extinct, common ancestors (see Fig. 1a). At one stage in the development of the cladogram, Nelson (1972b, 1973b) argued that the circles at the nodes did not represent real common ancestors but "hypothetical ancestors." The term is problematic. All taxa that ever existed are equally real. Only our ability to discern them varies. We can usually discern extant species with greater certainty than extinct forms, but the postulation of any taxon, whether extant or extinct, involves highly complex inferences and requires evidence which is frequently quite difficult to obtain. (Recall the objections which pheneticists raised to the biologi-
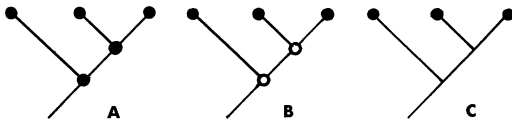
FIG. 1.—The evolution of the cladogram. (a) A cladogram in which the darkened circles at the termini represent extant species, while those at the nodes represent common ancestors. (b) A cladogram in which the darkened circles at the termini represent species, both extant and extinct, while the circles at the nodes represent "hypothetical common ancestors," i.e., morphotypes. (c) A cladogram in which the darkened circles at the termini represent species, both extant and extinct, while the nodes represent speciation events and/or the emergence of unique derived characters.

cal species concept even when it is applied to extant forms.) If extinct forms are "hypothetical" because of their inferential basis, then so are extant forms. The difference between extant and extinct species is not between observation and inference, but between inferences of varying degrees of certainty.

Another interpretation of "hypothetical ancestor" is that the circles which appear at the nodes of cladograms are not supposed to be taxa at all but "morphotypes," rational constructs characterized by the defining traits of the taxa listed at the termini of the cladogram and no others. As Platnick (1977c:356) observes, the "nodes of cladograms represent only inferred species (or, more accurately, only minimum sets of synapomorphic characters)." In this sense, hypothetical ancestors are "hypothetical," but they are not "ancestors." They are not even taxa (see Fig. 1b). In present-day cladograms, all taxa, whether extinct or extant, appear along the top of the cladogram. Cladograms would be much less misleading if they included *nothing* at the nodes (see Fig. 1c).

If the nodes in a cladogram do not represent real taxa (ancestral or otherwise), what do the lines and forks in cladograms represent? Two answers have been given to this question, which may or may not be reducible to the same answer. A fork in a cladogram can represent either a spe-

ciation event (the splitting of one species into two), or the emergence of an evolutionary novelty (a unique derived character), or both. If the emergence of a unique derived character occurs always and only at speciation, then the two answers always coincide. If not, not. Similar observations hold for the term "cladistic relation." It can refer to order of splitting of taxa, or to order of appearance of evolutionary novelties, or both. The decision hinges on how "operational" one wishes to make cladistic analysis. Since speciation events are inferred by means of the appearance of evolutionary novelties, one inferential step can be eliminated by talking only about the emergence of evolutionary novelties and not speciation events.

CERTAINTY AND LEGITIMATE DOUBT

One reason for the cladists' introducing the distinction between cladograms, trees, and scenarios was to clarify the technical sense in which they were using the term "cladogram." Too many people were misinterpreting cladograms as bizarre, highly stylized trees. A second reason was to establish the logical and epistemological priority of cladograms over trees and of trees over scenarios. As cladists define these terms, an inclusion relation exists between them. Scenarios include all the information contained in trees, and more besides. Trees include all the information contained cladograms, and more besides. Thus, any knowledge required for a cladogram is required for a tree, and any knowledge required for a tree is required for a scenario, but not vice versa. Thus, cladograms are more certain than trees, and trees more certain than scenarios. As harmless as the distinction between cladograms, trees, and scenarios may seem on the surface, it results in cladistic analysis being in some sense basic to all evolutionary studies.

The relations set out above *do* obtain between cladograms, trees, and scenarios—as the cladists define these terms. That is one reason why non-cladists might prefer other definitions. But even

if one were to accept the cladists' defi-
nitions, certain conclusions which clad-
ists have claimed follow from the preced-
ing line of reasoning do not. For example,
in claiming that "trees should always be
based on cladograms and that scenarios
should follow from trees," Tattersall and
Eldredge (1977:205) are confusing logi-
cal and epistemological order with tem-
poral order. The conclusion to an argu-
ment follows logically from its premises.
That does not mean that people must
think of the premises first and only then
think of the conclusion. Sense data are
epistemologically prior to all knowledge,
but that does not mean that scientists
should begin every scientific study with
an extensive investigation of their own
sense data. If scientists had actually pro-
ceeded in this fashion, we would still be
awaiting Ptolemaic astronomy, not to
mention relativity theory. The inferences
which take place in the actual course of
scientific investigations are very intricate
and frequently "feed back upon each oth-
er," as Tattersall and Eldredge (1977:205)
note. In retrospect, there is considerable
point to unraveling these inferences and
setting them out in some logically coher-
ent fashion, but the insistence that sci-
entists must always begin at the begin-
ning and proceed step by step according
to some sort of logical or epistemological
order would stop science dead in its
tracks.[2]

Cladists also make much of the differ-
ences in certainty between cladograms,
trees, and scenarios. In actual practice,
scientists wander from one level of anal-
ysis to another in the course of their in-
vestigations. As a result knowledge ac-

quisition is a process of both "reciprocal
illumination" (Hennig, 1950; Ross, 1974)
and "reciprocal blundering." Getting one
element right helps improve our under-
standing of the other elements, but errors
feed through the system just as readily.
Although cladists might well admit that
knowledge acquisition in general is a
process of reciprocal illumination, they
also tend to be so sceptical of trees and
scenarios that they see all the illumina-
tion going in a single direction—from
cladograms to trees and scenarios. At
times cladists seem to argue that not only
should evolutionary studies *begin* with
cladograms but also they should *end*
there as well. Cladistic relations are
knowable; everything else about phylog-
eny is unknowable.

For example, Platnick (1977d:439) ar-
gues that the *only* way that phylogenetic
trees can be tested is by the same means
used to test cladograms, "by evaluation
in the light of newly discovered charac-
ters." Any three taxa can be ordered into
22 different trees. Some of these trees can
be rejected by discovering appropriate
characters, i.e., the appropriate autapo-
morphies and synapomorphies. Other
trees can be rejected only by claiming
that no autapomorphies exist for the rel-
evant taxa. Since the most that a system-
atist can legitimately claim is that he has
yet to detect such autapomorphies, he is
not justified in rejecting these trees. Plat-
nick (1977d:440) concludes that "phylo-
genetic trees are not testable by character
distributions and thus that scientific phy-
logeny reconstruction is *not* possible at
the level of phylogenetic trees and must
be restricted to the level of cladograms."
But the same sort of argument can be pre-
sented against the cladists. They do not
need to know ancestor-descendant rela-
tions, but they do need to establish trans-
formation series and to determine the po-
larity of these series. They do need to
individuate characters and decide which
are autapomorphic, synapomorphic, etc.
For instance, synapomorphies can be
used to test cladograms *if* they are syn-
apomorphies, but no one has yet to sug-

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[2] The pheneticists presented similar arguments
for the epistemological priority of phenetic classi-
fications. According to the pheneticists, the only
place at which systematists can legitimately begin
is phenetic characters and the construction of pure-
ly phenetic classifications. Once such a phenetic
classification is erected, then a systematist could
put various "interpretations" on his classifications
and possibly produce one or more "special pur-
pose" classifications; see e.g., Sneath and Sokal
(1973).

gest any infallible means for deciding whether or not a trait is actually a synapomorphy. The same can be said for such relations as the polarity of transformation series. In fact, Tattersall and Eldredge (1977:206) state, "In practice it is hard, even impossible, to marshal a strong, logical argument for a given polarity for many characters in a given group." The sort of argument from negative evidence which the cladists use against others at the level of taxa can be used against them at the level of traits. Of course, their opponents also must individuate and categorize traits. Thus, the cladists' position is refuted at only one level of analysis, while the position of their opponents is refuted at two. Put more directly, such arguments refute no positions whatsoever.

The cladists have weakened the force of their arguments by presenting them in a needlessly dichotomous fashion. The only thing that they need to know to produce cladograms are cladistic relations, and they are knowable. Others who wish to produce trees need to know much more; e.g., ancestor-descendant relations, the existence of multiple speciation and reticulate evolution, etc. These phenomena are totally unknowable. The cladists need not present such an extreme (and suspiciously self-serving) position. Estimations of cladistic relations are inferences and as such carry with them the possibility of error. However, it is certainly true that everything which the cladists need to know the evolutionists also need to know, while the evolutionists need to know more besides. These additional phenomena also carry with them a certain degree of uncertainty. Hence, evolutionary classifications are bound to be more uncertain than cladistic classifications. The question remains whether all evolutionary phenomena other than cladistic relations are so uncertain that no attempt should be made to include information about them in a classification. In the succeeding sections of this paper, I will investigate various phenomena which cladists argue cannot

be known (or at least cannot be known with sufficient certainty) to see why they are so difficult to discern. Is it that they cannot be known, or that they cannot be known by means of cladistic analysis? Is there no way to acquire knowledge of the world other than by cladistic analysis? The point of this section is, however, that the difference in our ability to ascertain cladistic relations and other evolutionary phenomena is one of degree, not kind. Differences in degree of certainty are neither very neat nor aesthetically pleasing, but they are the most that cladists can justifiably claim. What they lose in elegance and simplicity, they gain in plausibility.

Certain cladists, in more recent publications, seem to be moving in precisely this direction. For example, Eldredge (1979:169) states that, contrary to his earlier opinions:

I no longer oppose the construction of phylogenetic trees outright, or for that matter, scenarios (which are, after all, the most fun), but merely point out that, in moving through the more complex levels, we inevitably become further removed from the original data base in adding assumptions and *ad hoc* (and largely untestable) hypotheses. As long as we understand precisely what we are doing at each step in the analysis, which includes having an adequate grasp of the probability that we are wrong and of what the assumptions are what we have added along the way, there no longer seems to me any reason for anyone to tell anyone else what *not* to do.

Although those workers engaged in the production of trees and scenarios might differ with Eldredge on the situation being as extreme as he makes it out to be, they too are aware of the difficulties. For example, Lucchese (1978:716) concludes a paper on the evolution of sex chromosomes with the following remarks:

. . . for an individual to profess an insight into the biological changes that have occurred through time remains an act of faith of considerable magnitude. [Yet, within] the limitations just set forth, the purpose of this article has been to spin a relatively reasonable evolutionary tale in the hope of expanding the current perception of a highly significant example of genetic regulation in eukaryotes.

THE PRINCIPLE OF DICHOTOMY

Few principles attributed to cladistic taxonomists have caused more consternation and confusion than the claim that all cladograms and classifications must be strictly dichotomous. When cladism was first introduced to English-speaking systematists, cladists and anti-cladists alike agreed that the principle of dichotomy was "essential to the philosophy of Hennig and Brundin " (Nelson, 1971a:373; see also Darlington, 1970:3; Mayr, 1974:100; Bonde, 1975:302; Platnick, 1977d:438). Although Cracraft (1974:79) agrees that "phylogenetic classification *sensu* Hennig and Brundin would appear to require the assumption of dichotomous branching," cladistic classification in a more general sense "does not necessitate dichotomous branching, and the exact pattern of branching is determined by the manner in which shared derived character-states cluster taxonomic units." The question remains why the principle of dichotomy has seemed so central to most cladists and continues to seem so to some.

Although no cladist has ever maintained that the principle of dichotomy is an empirical claim about the speciation process, few cladists have been able to resist the temptation to justify it by reference to empirical considerations. For example, Hennig (1966:210, 211) begins by stating that dichotomy is "primarily no more than a methodological principle" and then goes on to add, "A priori it is very improbable that a stem species actually disintegrates into several daughter species at once." Cracraft (1974:79) interrupts the discussion quoted above with the remark that the principle of dichotomy "can be justified on theoretical grounds not associated with classification." Bonde (1975:302) agrees. Although dichotomy is a methodological principle, in nature "speciations are probably nearly always dichotomous."

Whether multiple speciation seems possible or impossible depends on the unit of time one selects to define "simul-

taneous." As Hennig (1966:211) notes, the issue of dichotomous speciation can be trivialized by defining "simultaneous" too narrowly. If it is defined in terms of split seconds, then multiple speciation is impossible. Conversely, if "simultaneous" is defined too broadly, everything can be made to occur "at the same time." The question of dichotomous speciation can be made significant only by the specification of a unit of time which makes sense in the context of the evolutionary process. In the absence of such a unit, the notion of simultaneity can be expanded or contracted at will and the issue decided by fiat (see Cracraft, 1974:74).

Whether multiple speciation as an empirical phenomenon seems plausible or implausible depends on the model (or models) of speciation which one holds. If speciation is viewed as the gradual splitting and divergence of large segments of a species, as Hennig (1966:210) maintains, then multiple speciation looks less likely than if it is viewed as a process in which small, peripheral populations become isolated and develop into separate species, as Wiley (1978:22) supposes. But, as the cladists have reminded us often enough, dichotomy is a methodological principle. If speciation were always dichotomous, this fact about evolution would certainly lend support to dichotomy as a methodological principle, but good reasons might exist for producing exclusively dichotomous cladograms and classifications even if speciation is not always dichotomous.

Cladists have presented two sorts of justification for their preference for the principle of dichotomy: our inability to *distinguish* dichotomous speciation from more complex sorts of speciation and our inability to *represent* unequivocally more complex sorts of speciation in cladograms and classifications. If one limits oneself just to traditionally-defined traits (e.g., presence of various sorts of appendages, dentitions, etc.) and if one assumes that these traits have been appropriately individuated and identified,

then the argument which the cladists put forth is reasonably straightforward. If a cladist starts with any two species chosen at random and compares a third species to them, two of these species will be cladistically more closely related to each other than either is to the remaining species. If the cladist continues to add species to his study one at a time, he will produce a consistently dichotomous cladogram until one of two things occurs: either he happens upon a genuine instance of multiple speciation or else he is unable to resolve this complex situation into the appropriate sequence of successive dichotomies. Because dichotomy is the simplest hypothesis, it should always be preferred, evidence permitting. But as the cladists see it, given the sort of data available to the systematist and the resolving power of his methods of analysis, he will always end up where he begins—with doubt or with dichotomy. Never is a systematist justified in concluding that a speciation event is genuinely trichotomous because he is never justified in dismissing the possibility that an apparent trichotomy is really a pair of unresolved dichotomies.

If the preceding is a fair characterization of the cladists' argument, it has two weaknesses. First, the cladists are selective in acknowledging possible sources of error. After all, a systematist cannot guarantee that a trait which he considers to be unique and derived actually is. There is always the possibility that he is dividing a single group into two or lumping two groups into one. If a trichotomy represents either a genuine trichotomy or two unresolved dichotomies, then a dichotomy could just as well represent either a genuine dichotomy, a lumped trichotomy, or a single lineage divided mistakenly into two. When a systematist claims that a particular speciation event is trichotomous, he may be mistaken, but he may also be mistaken in claiming that it is dichotomous. During the early stages of investigation, doubts about the actual cladistic relations which characterize the

groups under study are legitimate. Many trichotomies are very likely to be resolvable into dichotomies after further study, many of the groups treated as single may have to be split into two or more groups, and vice versa. However, as the groups are studied more exhaustively, the legitimacy of continued doubt decreases. If after exhaustive study, three species continue to appear to be related trichotomously, the claim that they might actually be related by a pair of dichotomies begins to ring rather hollow. Descartes has shown where that sort of mindless scepticism leads. If a systematist can become reasonably certain that he has correctly discerned a genuine dichotomy, I see no reason why he cannot also attain that same level of certainty in the identification of trichotomies—even using just the traditional methods of cladistic analysis. But systematists are not limited just to the study of ordinary taxonomic traits. There is no reason for not using the methods of cladistic analysis on other sorts of evidence, e.g., the data of historical biogeography. As Platnick and Nelson (1978:10) remark:

> Trichotomous cladograms are of no significance as tests (or as initial hypotheses) unless the cladograms for all available test groups are trichotomous, in which case we may suspect that an event disconnected an area into three smaller areas simultaneously. Testing this hypothesis by biotic relationships seems impossible (because we have no way of distinguishing those cladograms reflecting actual trichotomies from those reflecting only our failure to find the relevant synapomorphies that would resolve a dichotomous cladogram), but it should be subject to independent testing by data from historical geology, which can either be in accordance with such a synchronous tripartite disconnection of the total area or not.

If multiple speciation can occur in nature and if in certain circumstances it can be discerned, then cladists would be wise to devise methods of representing multiple speciation in their cladograms and classifications. One theme which the cladists repeatedly voice is that anything represented in a cladogram and classifi-

cation should be represented explicitly and unambiguously. If cladists were willing to argue that trichotomous speciation never took place, then trichotomies in cladograms would not be ambiguous. They would always represent a pair of unresolved dichotomies. As things stand now, they are ambiguous, representing either a genuine trichotomy or else a pair of unresolved dichotomies. Whether or not cladists think that instances of multiple speciation can be discerned, the adoption of such an ambiguous mode of representation seems counter-productive. A better alternative would be to reserve trichotomies for representing trichotomous speciation events the way that dichotomies are used to represent dichotomous speciation events, epistemological doubts to one side, and to devise another way of indicating incomplete knowledge. For example, if a systematist is reasonably sure that two species are each other's closest relatives, he can indicate this by a dichotomy. If he thinks they might be but is not sure, he can connect them by dots. Similar remarks apply to trichotomies (see Fig. 2). No system of representation can represent everything, but if doubt is important enough to represent in a cladogram, it is important enough to represent unequivocally.

Similar remarks are equally applicable to classifications. For example, Nelson (1973c) distinguishes between the two sorts of representation commonly used in the Linnaean hierarchy—subordination and sequencing—and shows how combinations of these two conventions can represent a variety of evolutionary phenomena including trichotomous speciation. More recently, Wiley (1979) has suggested using *sedis mutabilis* whenever the order of listing taxa in a classification means nothing. In addition to the difficulties which the recognition of multiple speciation raises for cladograms and classifications, it also poses problems for the proper definition of monophyly and related terms (Wiley, 1977; Platnick, 1977c).
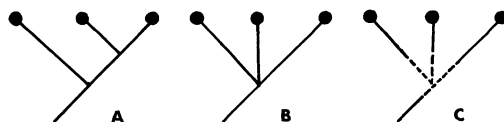

FIG. 2.—The ambiguity between genuine trichotomies and unresolved dichotomies. (a) A cladogram which represents unambiguously a pair of successive dichotomies; epistemological doubts, if any, are not indicated. (b) A cladogram which is commonly used to represent a pair of unresolved dichotomies, a genuine trichotomy, common ancestry and reticulate evolution. (c) A cladogram which indicates doubt about the actual relations between the species indicated. Such cladograms might in time resolve to (a) a pair of dichotomies or (b) a genuine trichotomy. Common ancestry and reticulate evolution must be represented in some other but equally unambiguous fashion.

ANCESTOR-DESCENDANT RELATIONS

Although some disagreement exists over the occurrence of multiple speciation, everyone agrees that certain species which once existed no longer exist and that some of these species gave rise to Recent species. The cladists' complaints about the ancestor-descendant relation cannot possibly be interpreted as empirical. They are clearly methodological. Once again the distinction must be made between difficulties in discerning ancestor-descendant relations and difficulties in representing them. Farris (1976:272) acknowledges this distinction when he presents two reasons for not treating fossil species as ancestral to later species:

> First, there is no obvious way of using a classification to represent ancestor-descendant relationships. A taxonomic hierarchy with its well-nested taxa is naturally suited only to the representation of sister-group relationships. Second while sister-group relationships may more or less readily be established through the detection of apomorphous similarities, ancestor-descendant relationships may not be so established.

A second distinction of equal importance is between the recognition of extinct species as species and deciding which species gave rise to which. Those cladists who are willing to recognize extinct species as species while maintain-

ing that the ancestor-descendant relation is unknowable are put in the position of explaining how we can know the former but not the latter (Engelmann and Wiley, 1977). Those cladists who argue that neither is knowable are spared this dilemma but are faced with the problem of what to do with fossils. Løvtrup (1973) argues that extinct species are so poorly known that they should be totally excluded from classifications. Crowson (1970) sees the differences in our ability to recognize extinct and extant forms to be sufficiently great that they should be included in separate classifications. Nelson (1972a:230) reasons that fossil groups should be fitted into classifications which also contain recent groups but distinguished by some convention. Finally, Rosen (1978:176) agrees that extant and extinct forms should be distinguished but that they should be treated as the same sorts of entities—groups distinguished by unique derived characters. In this section I will deal first with difficulties in discerning species and ancestor-descendant relations and then with problems of representation.

Hennig (1966, 1975) and Brundin (1972b) maintain that the biological species concept is central to phylogenetic systematics. From the beginning, critics of the biological species concept have argued that it is not sufficiently "operational" even for extant species. Perhaps it is possible to ascertain which organisms actually have mated with one another to produce fertile offspring and which organisms cannot mate with each other and/or produce fertile offspring, but it is impossible to discover which could have done so but did not. When the species under investigation are extinct, so the critics argue, nothing can be discovered directly about their breeding relations. It is certainly true that the biological species concept is not very operational, but as I have argued elsewhere, no theoretically significant concept in science is (Hull, 1968, 1970). The interesting question is whether biological species can be discerned often

enough and with sufficient certainty to justify systematists' attempting to represent them in their classifications. An even more fundamental question is whether biological species are sufficiently important to the evolutionary process to warrant the attention they are given. But in any case, the existence and extent of biological species are almost always inferred indirectly from character distributions. Hence, mistakes will be made. When these species are extinct, mistakes are even more likely and our ability to correct them even more limited. No one could possibly claim that all pterodactyls belonged to a single species, but finer distinctions are highly problematic.

Thus, those cladists who continue to maintain that biological species are the ultimate units in their investigations are forced to admit that their cladograms and classifications might be mistaken. They might have lumped several species into one or divided a single species into two or more species. For extinct forms, these mistakes are difficult, if not impossible, to remedy. Cladists who have abandoned the biological species concept are spared this problem. They are not classifying species but are grouping organisms according to the possession of particular traits. The only doubt associated with such an exercise is whether the organisms actually have the trait attributed to them, whether or not it is actually a trait and not several, and whether it has the distribution attributed to it. The question remains whether it is any easier to individuate traits than it is to individuate theoretically significant taxa. The two seem both conceptually and inferentially very closely connected.

If extinct species cannot be recognized as genuine groups of some sort, they cannot be recognized as sister groups. But assuming that extinct forms can be recognized as extinct species or as extinct groups delimited by a particular trait, can ancestor-descendant relations between extinct and extant forms also be discerned? Cladists are all but unanimous in claiming that they cannot. As Nelson

(1973b:311) states, "Indeed, I have assumed that ancestral species cannot be identified as such in the fossil record, and I have pointed out that this assumption is fundamental to Hennig's phylogenetic systematics." Two considerations seem central to the cladists' claim that ancestor-descendant relations are unknowable. First, any distribution of characters which would imply that one taxon was ancestral to another would equally imply that one was the sister group of the other, and no other way exists for deciding ancestor relations. Second, given the vast number of species which must have existed from the beginning of time and the relatively few which have left records, it seems very unlikely that very many actual common ancestors have been discovered.

I find the second argument more persuasive than the first. It is always *possible* that what appears to be a genuine ancestor is really a sister group and that the two share an unknown common ancestor. Of course, it is always *possible* that a trait which has been recognized as a single trait is actually two, that a trait which is considered to be derived really is not, that a derived character which is thought to be unique really is not, etc., etc. The *possibility* of error pervades all of science. What is needed is some reason to believe that not only is it possible for the two groups to be sister groups instead of one being ancestral to the other, but that one hypothesis is more probable than the other. Reference to the vast number of species which have existed and the few which have left any traces of their existence does just that. If paleontologists claim that they have identified an extinct species which is in a direct line of descent to some earlier or later species, then such claims are on the face of it extremely unlikely.

For example, when Romer claims that amphibians arose from ancient crossopterygians, he surely could not have meant that one of the fossils already collected represented the actual stem species from which all amphibians arose and that he knew precisely which fossils these were. Perhaps paleontologists have been overly enthusiastic in identifying missing links and common ancestors, but I find it hard to believe that they have been this foolhardy. As Harper (1976) and others have pointed out, paleontologists rarely specify a particular species as a common ancestor. Almost always a genus or higher taxon is specified. When paleontologists claim that one genus or other higher taxon arose from another, they do not mean that higher taxa "evolve," although at one time macroevolution was more popular than it is now. All they mean is that the species which is ancestral to this higher taxon, if it were ever discovered, would be placed in the taxon which has been specified as being ancestral. For example, whether or not specimens of the actual species which gave rise to amphibians have been discovered, whether or not they could be recognized as such if they were, Romer is committed to the view that they would be placed among the crossopterygians. Nor are paleontologists necessarily committed to Simpson's definition of monophyly. Even though they may be willing to specify only a genus or other higher taxon as a common ancestor, they may still have the goal of making all higher taxa monophyletic at the species level and would redraw the boundaries of their higher taxa if they became convinced that a higher taxon was descended from two or more species, even though these species were all included in a higher taxon of equal or lower rank. But it must also be admitted that claiming a higher taxon as a common ancestor is not as empirical as claiming that a particular species is. Higher taxa, as they are usually constructed, are largely a function of the principles of classification adopted (Engelmann and Wiley, 1977).

Harper (1976) also presents eight principles which he thinks can help distinguish sister-group relations from ancestor-descendant relations. All of Harper's principles cannot be discussed here, but one is sufficiently important to warrant

mentioning—the role of fossils. Does not the existence of fossils in certain strata and their absence in others, especially when a fairly extensive fossil record is available, imply something about possible ancestor-descendant relations? Hennig thinks it does. For example, he (Hennig, 1966:169) argues that the "sequence in which the characters in question evolved" is "sometimes clarified by fossils." He also thinks that fossils can help determine the minimum age of the monophyletic groups to which they belong (Hennig, 1975:112). Nelson (1969:245) is a good deal more sceptical: "If a given fossil could be demonstrated to have been a representative of a population ancestral to a Recent species," it might be of some significance, but such an "ancestor-descendant relationship strictly speaking cannot be demonstrated." Even though Nelson (1972b:367–370) admits that data concerning "relative stratigraphic position" might narrow the "range of possible relationships held by the taxa in question," he recommends divorcing "problems of relationships from data concerning stratigraphic distribution of fossils." He concludes that ancestor-descendant relations are both unknown and unknowable in an "empirical sense," that is, "by way of inference from observation of study material" (Nelson, 1973b:311).

Following Popper (1959, 1972), several cladists have argued that hypotheses about ancestor-descendant relations are unscientific because they are unfalsifiable (Wiley, 1975; Engelmann and Wiley, 1977; Platnick and Gaffney, 1977, 1978; Cracraft, 1978; Nelson, 1978a; Patterson, 1978). Because these hypotheses are unscientific, they should play no role in science. At one time Bonde (1975) agreed with this line of reasoning, but in the meantime he (Bonde 1977:772) has noticed something else about ancestor-descendant hypotheses: they are bolder than sister-group hypotheses. Because cladograms claim less than trees and trees claim less than scenarios, scenarios are bolder than trees and trees are bolder

than cladograms. And, according to Popper, bolder hypotheses are preferable to less bold hypotheses. Thus, two of Popper's desiderata come into conflict. If all the relevant data were available, bolder hypotheses would be easier to falsify because they imply more. The problem is that in this case, the evidence necessary to test the bolder hypotheses is much harder to obtain than the evidence necessary to test the less bold hypotheses. And what is worse, mistakes in ascertaining ancestor-descendant relations introduce much more serious errors into a study than mistakes in ascertaining sister groups (Engelmann and Wiley, 1977).

As I mentioned earlier, I am highly suspicious of scientists claiming that something cannot be known, especially when they do not need to know it and their opponents do. In this case, I think that the cladists have exaggerated the difficulties in making reasonable inferences about probable ancestors for a second reason as well—difficulties in representation which common ancestors pose for both cladograms and classifications. If common ancestors cannot be recognized with reasonable certainty, then the evolutionists are in trouble. If they can be, then cladists are in trouble. As Tuomikoski (1967:144) remarks, "Hennig and Brundin are aware of the fact that such a linear classification of monophyletic groups is capable of expressing only horizontal sister relationships, not vertical mother-daughter relationships." If ancestor-descendant relations can never be known with sufficient certainty to warrant postulating them, then the inability of cladograms and classifications to represent them is no great drawback, but Wiley (1977) has suggested that a better strategy would be to devise representational devices capable of representing them just in case. So far, several systems of representation have been suggested for distinguishing extinct from extant groups, and the difficulties which attempts to distinguish between sister-group relations and ancestor-descendant relations in cladograms and classifica-

tions have been pursued at great length (Nelson, 1973c; Cracraft, 1974; Patterson, 1976; Patterson and Rosen, 1977; Wiley, 1979). For example trichotomies in cladograms are already ambiguous, representing either trichotomous speciation events or a pair of unresolved dichotomies. Attempting to represent common ancestry in this same way would introduce yet another dimension of ambiguity. But I see no reason why some system of representation cannot be developed to distinguish these three possible situations in both cladograms and classifications.
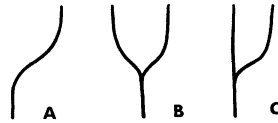

FIG. 3.—Three possible patterns of evolution. (a) A phylogenetic tree in which a single lineage changes in time without splitting. (b) A phylogenetic tree in which a single ancestral lineage splits into two descendant lineages and both descendant lineages diverge from the ancestral lineage. (c) A phylogenetic tree in which splitting occurs but only one of the descendant lineages diverges from the ancestral lineage.

PHYLETIC EVOLUTION AND SPECIATION

Cladists are frequently interpreted as claiming that phyletic evolution does not occur. Once again, the actual thrust of their discussion of phyletic evolution is methodological, not empirical. Figure 3 represents three possible patterns of evolution: gradual change in a lineage without the lineage splitting, splitting followed by both descendant lineages diverging, and splitting followed by only one of the descendant lineages diverging. Simpson (1961) has argued that sometimes lineages change sufficiently through the course of their development so that later stages should be considered distinct species even though no splitting has taken place. The inevitable operationalist objections have been raised against Simpson's suggestion: that no non-arbitrary way exists for dividing a continuously evolving lineage into distinct species and that lineages cannot be established in the first place because there is no way of knowing which organisms are ancestral to which. I have already discussed these topics at sufficient length both in this paper and elsewhere (Hull, 1965, 1967, 1970). If the continuity of phyletic evolution were sufficient to preclude "objective" subdivision, then all our measurements of physical space would be equally suspect because space is even more continuous. Perhaps the establishment of lineages is a risky business, but it is also an extremely important undertaking, not for the purposes of classification but for the purposes of formulating and testing hypotheses about the evolutionary process. As important as scientific classifications are, scientific theories are even more important.

Eldredge and Gould (1972) have argued that phyletic evolution rarely, if ever, occurs and that the evidence for it is largely illusory. However, regardless of whether or not phyletic evolution occurs, the cladists maintain that a single lineage should not be divided into species no matter how much it might change. New species are to be recognized only when splitting occurs. According to Hennig (1966, 1975), species are not classes of similar organisms but well-integrated gene pools. In phyletic evolution, the lineage changes through time but retains its integration. Hence, it should be considered a single species. As Platnick (1977a:97) argues:

> To attempt to divide a species between speciation events would indeed be arbitrary: we would not call an individual person by one name at age 10 and a different name at age 30. Dividing species at their branching points, however, becomes not only non-arbitrary but necessary: we would not call a son by the same name as his father.

In this instance, I think Hennig is right, not because of any epistemological or methodological reasons, but because his decision is consistent with the most theoretically appropriate definition of "species." Species are integrated lineages developing continuously through

time (Simpson, 1961; Mayr, 1963; Ghi-selin, 1974; Hull, 1976, 1978; Wiley, 1978). Cohesiveness at any one time and continuity through time are what matter, not phenotypic or even genotypic simi-larity. Some lineages may diverge exten-sively through time without splitting; some not. It does not matter. A continu-ously evolving lineage should no more be divided into distinct species than an organism undergoing ontogenetic devel-opment should be divided into distinct organisms. These same considerations apply to the other situations shown in Fig. 3.

Cladists argue that new species should be recognized *only* when splitting oc-curs. In non-saltative speciation, tempo-ral continuity is maintained, but the co-hesiveness of the lineage is disrupted. They also argue that *whenever* splitting takes place, the ancestral species must be considered extinct. Bonde (1975:295) characterizes Hennig's position as fol-lows:

> By the process of speciation the ancestral species is split into *two new species* called *sisterspecies* (or daughterspecies) . . . . That the two sisterspe-cies are *new* and the ancestral species becomes extinct at the speciation is most practical for a consistent terminology, and it also follows from Hennig's species concept, and from the defini-tion of phylogenetic relationship below (cf. Brundin, 1972a:118).

According to Hennig, the two sorts of splitting depicted in Figs. 3b and 3c are to be treated in exactly the same way; i.e., as a mother species becoming extinct as it divides into two daughter species. It does not matter that in one instance both daughter species diverge from the moth-er species, while in the second only one does. As much trouble as it may cause the systematist attempting to distinguish ancestors from descendants, it simply does not matter that the mother species is indistinguishable from one of its daughter species. I agree with Hennig's reasoning but not his conclusion. If in-tegration is what matters, then the differ-ences indicated in Figs. 3b and 3c are irrelevant for the individuation of species.

If divergence is irrelevant *without* split-ting, it should be just as irrelevant *with* splitting. On Hennig's view, what should really matter is the integration of the gene pool. At speciation, so Hennig claims, the ancestral gene pool totally disintegrates, resulting in the extinction of the ancestral species. According to Bonde (1977:754), Hennig's species con-cept is the "only logical extension in time of the concept of the integrated gene pool. At speciation this gene pool is dis-integrated and two (or more) new sister species originate, while the original species becomes extinct." Wiley (1978: 21–22) agrees that "in most cases the methodological necessity of postulating extinction of ancestral species in phylog-eny reconstruction as advocated by Hen-nig (1966) is biologically (as well as methodologically) sound," but not al-ways. According to his own evolutionary species concept, an ancestral species can survive a split, if it can "lose one or more constituent populations without losing its historical identity or tendencies."

If speciation can occur only by the mas-sive disintegration of the parental gene pool, then Hennig's decision always to treat ancestral species as extinct is well-founded biologically. However, if Mayr (1963), Carson (1970), and Eldredge and Gould (1972) are right and speciation al-ways (or usually) takes place by the iso-lation of small, peripheral populations, then it seems very unlikely that such an event will totally disrupt the organization of the parental gene pool, and Hennig's convention of treating ancestral species as always going extinct upon speciation loses its empirical support.[3] As interest-ing as these empirical considerations are, as I have mentioned several times pre-viously, cladists are currently disasso-ciating themselves from any particular

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[3] The arguments presented by Eldredge and Gould (1972) support Hennig's contention that new species should be recognized only when splitting occurs. These same arguments, however, count against Hennig's contention that ancestral species always disintegrate upon speciating.

views about the evolutionary process. For example, Bonde (1977:793) states that "contrary to my earlier beliefs, the details of the process of speciation are not important for the phylogenetic systematic theory because the patterns resulting from allo-, para- and sympatric speciations can be analyzed in the same way in terms of degrees of phylogenetic relationship." If so, then facts about the evolutionary process cannot be used to cast doubt on the cladists' research program. Such considerations cannot thereby be used to support it either, and Hennig's arguments must be abandoned.

The only remaining consideration is "consistency of terminology." Hennig seems to think that calling a species by the same name before and after speciation would cause all sorts of terminological confusion. However, comparable terminological difficulties are easily surmounted at the level of organisms. When a single *Paramecium* splits down the middle to form two new organisms, each is considered a distinct organism. If we were prone to name such entities, we would give each a separate name. However, *Hydra* can continue to exist while budding off other *Hydra*. Once again, if we were inclined to, we could give each of these organisms its own name. The parent *Hydra* would retain its name even though it budded off other descendant *Hydra*. Finally, in sexual reproduction, two parental organisms produce gametes which come together to form a third. Organisms need not cease to exist when they mate. Queen Victoria and Prince Albert remained the same organisms as they produced child after child. Occasionally, we do call a son by the same name as his father. Usually we have the good sense to add "Jr.," but whether we do or not, they remain distinct organisms. If such practices occasion so little confusion at the level of organisms, there seems no reason for them to introduce insurmountable terminological difficulties at the level of species.

In this section I have argued that if one accepts Hennig's conception of species as integrated gene pools, then species changing gradually through time should be considered single species and not divided successively into distinct species. New species should be recognized *only* at splitting, but at splitting the ancestral species does not *always* go extinct. How many species are to be recognized at splitting depends on what happens to the integration of the parental gene pool. If it remains largely unaffected, then the ancestral species continues to exist as it buds off descendant species. If not, it becomes extinct. Whether or not the daughter species diverge after splitting is irrelevant for the individuation of species as integrated gene pools. Divergence may matter for a host of other reasons, but not for the individuation of species. Of course, none of the preceding is relevant to those cladists who think that the recognition of species as some sort of significant evolutionary unit plays no role in cladistic systematics. It is also true that in the absence of some sort of divergence, the systematist is unlikely to notice that speciation has occurred (see later discussion of the Rule of Deviation).

MONOPHYLY AND RETICULATE EVOLUTION

The term "monophyly" has had an extremely varied history. According to Mayr (1942:280) all taxa should be monophyletic. By this he means that all organisms included in a taxon should be "descendants of a single species." He does not say, however, whether *all* the descendants of a single species should be included in a single higher taxon, nor whether this stem species itself should be included in this higher taxon or excluded from it. In later discussions, Mayr (1969) states that he intended no such implications. He also states explicitly that, as far as animals are concerned, reticulate evolution may be disregarded. He justifies his position by reference to how rare genuine hybrid species are among animals. Botanists might choose to make another decision. Hennig (1966:73) defines "monophyly" somewhat different-

ly: "A monophyletic group is a group of species descended from a single ("stem") species, and which includes all species descended from this stem species." On Hennig's definition, all and only those species (both extant and extinct) which are descended from a single species must be included in a single higher taxon (see also Bonde, 1975:293; 1977:757). Hennig (1966:207–208) also recognizes that the hybrid origin of species would produce "special complications" for the principle of monophyly and echoes Mayr in his response that luckily hybridization is rare in animals. Among plants he is willing to countenance polyphyletic species but not polyphyletic higher taxa (Hennig 1966:208). Hennig (1966:64, 70–72, 207) is not clear about the recognition and placement of "stem species" in his classifications.

As much as Mayr and Hennig differ with respect to the principle of monophyly, they agree that all species included in a single higher taxon must be descended from a single stem *species*. Simpson (1961:124) presents a much broader definition: "*Monophyly is the derivation of a taxon through one or more lineages* (temporal successions of ancestral-descendant populations) *from one immediately ancestral taxon of the same or lower rank*." According to Simpson, a taxon is strictly monophyletic if it arises from a single immediately ancestral species; it is minimally monophyletic if it arises from a single immediately ancestral taxon of its own or lower rank. Thus, a genus is *strictly* monophyletic if it arises from a single immediately ancestral species. It is only *minimally* monophyletic if it arises from two or more species which are included in the same genus. It is polyphyletic if it arises from two or more species not included in the same genus. As broad as Simpson's definition is, it too is confronted by the difficulty of accommodating hybrid species (Hull, 1964).[4] His response is the

same as that of Mayr and Hennig: hybrid species may occur in plants, but they are rare in animals. Simpson also does not specify any uniform way in which stem species are to be treated.

Several points are at issue in the preceding discussion: (1) should all taxa be monophyletic at the level of species, (2) if so, how are hybrid species to be treated, (3) should all the descendants of a single stem species be included in the same higher taxon, and (4) if so, what should be done with the stem species itself? The cladists find themselves in agreement with respect to (1) and (3). All species in any higher taxon must be descended from a single ancestral species. Conversely, all the descendants of any one stem species must be included in a single higher taxon. Some disagreement exists over the proper treatment of (2) and (4), hybrid species and stem species. For those cladists who maintain that the only kind of event in the past which can be reconstructed with reasonable certainty is speciation (or at least the production of unique derived characters), common ancestry, whether single or multiple, cannot be ascertained. The distribution of characters resulting from hybridization is indistinguishable from that resulting from a trichotomy, which in turn is indistinguishable from a pair of unresolved dichotomies, which in turn is indistinguishable from common ancestry. Since all three phenomena can produce the same distribution of traits, all such distributions of traits should be interpreted as unresolved dichotomies—other things being equal.

The claim that we can never distinguish between a genuine common ancestor and a closely related sister group has some plausibility. The claim that we can-

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[4] Although the main purpose of Hull (1964) was to argue that allowing taxa to be only minimally

monophyletic further weakens the already loose relationship between phylogeny and biological classifications which Simpson proposes, Bonde (1975, 1977) interprets me to be defending Simpson's definition of "monophyly." There is a point to making one's polemics as polite as possible, but when an attack is interpreted as a defense, that point has been passed.

not discern hybrid species does not. We know with as much certainty as we know any empirical phenomenon that certain species are of hybrid origin. We did not observe the hybridization event in the past, but we can infer its occurrence with a high degree of certainty. For example, if a species were discovered at the boundary between two species with the combined chromosomes of these two species, the likelihood is very high that this species is a hybrid of the other two. Perhaps the outcome of a cladistic analysis of these three species would be a pair of unresolved dichotomies, but that is a problem for cladistic analysis.

Another reason which cladists have for rejecting both stem species and hybrid species as unknowable is the difficulties which both relations pose for unequivocal representation in both cladograms and classifications. For example, Nelson (1979:8) observes:

> An instance of hybridization would be represented in fundamental cladograms by non-combinable components that exhibit non-random replication, and in the general cladogram by tri- or polytomies that present conflicting, but non-random, possibilities for dichotomous resolution (as exemplified in fundamental cladograms).

Instead of introducing yet another dimension of ambiguity into polytomous cladograms, a better alternative would be to devise distinct methods of representation for each of these distinct phenomena. Perhaps we will never know which species are actually stem species, perhaps we will never know which speciation events are trichotomous, perhaps we will never know which species are of hybrid origin, but just in case someday we can, why not devise methods of representing these phenomena in cladograms and classifications? Wiley (1978, 1979) proposes to do just this.

In the previous sections I have argued that certain methodological principles attributed to the cladists really do not contribute all that much to the long-term goal of cladism—the representation of cladistic relations explicitly and unambiguous-

ly. If speciation is on occasion trichotomous and such events can be discerned, why not represent them? If common ancestors and reticulate evolution can be discerned, why not represent them? However, the principle of monophyly *is* important to cladism. In recent years a large literature has grown up over the "proper" definition of "monophyly" and related terms (Ashlock, 1971, 1972; Nelson, 1971b, 1973b; Farris, 1974; Platnick, 1976, 1977b, 1977c; Wiley, 1977). Scientific terms change their meanings as science develops. "Gene" did not mean the same thing at the turn of the century as it does today. One important function of the history of science is to trace such semantic changes. However, the results of such inquiries cannot be used to designate certain meanings as "proper" and others as "improper." I'm not sure what Darwin meant by the term "monophyly." I'm not even sure he ever used the term. Changing the definitions of terms in science haphazardly introduces needless confusion. From the point of view of making assertions about classifications, the term "holophyly" will do as well as "monophyly." The desire on both sides to retain the term "monophyly" for their concept stems from the need to establish continuity in scientific development. Just as continuity matters in individuating lineages in biological evolution, it matters in individuating scientific lineages in conceptual evolution. The sort of fighting over words which is so common in science is not an idle exercise.

Terminological squabbles to one side, the dispute between Ashlock (1971, 1972) on the one hand and Nelson (1971b, 1973b) and Farris (1974) on the other hand has some substantive points. Cladists want to represent cladistic relations by nested sets of derived traits. To do so, they must exclude what they term "paraphyletic" taxa. As far as assertive content is concerned, which definition of "monophyly" wins out is irrelevant; the structure of the resulting classifications is not. Whether one claims that all taxa must be holophyletic (sensu Ashlock) or monophyletic (sensu the cladists) is important

sociologically. What matters substantively is that the taxa themselves be grouped appropriately.

However much cladists and evolutionists disagree about the proper definition of "monophyly," they agree on one point: hybrid species pose a problem. Although I hate to destroy this rare instance of unanimity, I think they are mistaken. The goals of neither school of taxonomy require that all species arise from single ancestral species. All that is needed is that all species have a single origin. In most cases, species do have their origins in the speciation of single ancestral species. It follows that these species also have single origins. But sometimes a new species arises from two immediately ancestral species. They nevertheless have their origins in a single speciation event, and that is all that is necessary. Both schools need to require that all taxa be monophyletic, but only as monophyletic as nature allows.

THE DEVIATION RULE

According to Hennig (1966:207), "When a species splits, one of the two daughter species tends to deviate more strongly from the other from the common stem species" (see also Hennig, 1950:111). Brundin (1972b:71) claims that the deviation rule is "one of the most fundmental aspects of the principle of life" and essential to cladism. Bonde (1975:296) views deviation as a common (though not universal) pattern of evolution, which is important (though not necessary) to cladism. Schlee (1971:5) finds it "unessential" to the Hennigian approach, while Nelson (1971a:373) concludes that it is both unessential and a methodological principle. If the rule of deviation is supposed to be an empirical claim about evolution, it has some plausibility. As Bonde (1975:296) notes, if speciation takes place only when an "atypical" population becomes isolated in an "atypical" environment, one might reasonably expect this new daughter species to diverge more from the ancestral species than its sister does.

The rule of deviation also has a methodological form. Whether or not speciation is always accompanied by the production of at least one unique derived character in one of the groups,[5] if no such character is discernible, the groups will not be discernible by the methods of cladistic analysis. Of course, they will not be discernible by any other methods either. It is unlikely (probably impossible) for speciation to occur without at least one new character developing, but if "character" is used in its traditional sense to refer to such things as tooth structure, feather color, type of blood proteins, peculiarities in mating dance, etc., it may be the case that speciation can occur without the production of a distinguishing feature of the sort that a systematist is likely to notice. He can know that the two groups are *two* groups because they do not mate. He may even be able to tell which group is which because they inhabit different ranges. But he will not be able to decide which species a specimen belongs to merely by examining it. (Of course, one might redefine the term "character" to include spatial location or some such.)

For those cladists who see their task as the recognition of species and the grouping of these species into more and more inclusive taxa, the discovery of the appropriate unique derived characters and shared derived characters is crucial. It is very likely that the relevant characters exist. The task is to discover and categorize them appropriately. The cladists

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[5] The number of characters necessary to distinguish a new taxon depends on a variety of decisions. For example, if one assumes that the ancestral species has already been delineated and can bud off new species without itself going extinct, a single unique derived character will do. If the ancestral species also must be delineated, a second unique derived character is necessary. If ancestral species are always considered to be extinct upon speciation and speciation is always dichotomous, still another character is required, and so on. Of course, in traditional cladistic classifications, all these "ancestral" species will be treated as sister groups.

share this task with all systematists. For those cladists who see their task as the recognition of sequences of unique derived characters and shared derived characters, regardless of the coincidence of the emergence of these characters with speciation events, the rule of deviation becomes a tautology. It reduces to the claim that when a unique derived character is recognized a new group is recognized; otherwise not. By terming the rule of deviation, interpreted in this way, a tautology, I do not mean to denigrate it.

CONCLUSION

In this paper I have examined some of the principles which cladists have suggested to facilitate the representation of sister-group relations in cladograms and classifications. Currently some disagreement exists among the cladists themselves over the precise makeup of these principles, but eventually a single, generally accepted, reasonably simple system of conventions is likely to materialize. The consistent application of these principles will result in classifications which allow anyone who wishes to read off from them the sister-group relations which went into their construction. I have also raised questions concerning some of the prescriptions which cladists have enunciated about what cannot be known about phylogeny or represented if it were known. All scientific knowledge is fallible, including the recognition of sister groups. Perhaps ancestors, hybrid species and multiple speciation events cannot be discerned with the same degree of confidence as sister-group relations, but the contrast is not between fact and fantasy. Cladists have selected sister-group relations because they are relatively easy to discern using the methods of cladistic analysis and just as easy to represent in cladograms and classifications. Opponents have complained that the price is too high. Being able to infer sister-group relations from biological classifications is not worth the increase in complexity and asymmetry of the resulting classifications. They argue

that the cladists' rules for classifying are simple enough, but that the resulting classifications are not.

Another avenue of attack, employed by some taxonomists, is to agree that genealogy is worth representing in classifications but object to the aspect selected by the cladists. Divergence is also an important feature of evolutionary development. Instead of constructing classifications solely on the basis of cladistic relations, varying degrees of divergence should also be reflected. One problem with this response is that no methods have been set out thus far which permit the inclusion of both sorts of information in a single classification in such a way that both are retrievable. It is one thing to let a variety of considerations influence how one constructs a classification. It is quite another to formulate a set of principles so that others can retrieve this information from the classifications. If classifications are to be systems of information storage and retrieval, information must actually be *retrievable*. So far, only Ashlock and Brothers (1979) have taken up the challenge. A second problem with this alternative is that it is likely to increase the complexity of both the rules of classification and the resulting classifications. If classifications which represent only sister-group relations are too complicated, classifications which represent sister-group relations, ancestor-descendant relations *and* degrees of divergence are likely to be even more complicated.

Another possible response is that cladists have taken Darwin's suggestion too literally. Classification should be in some vague sense "phylogenetic," but biological classifications cannot be made to reflect very much about phylogeny without frustrating other functions of scientific classification. The most that systematists can hope to do is to weigh a variety of conflicting goals and produce the best possible compromise. Clear decisions between these various alternative goals are not easy, but if the cladists have done nothing else, they have shown the sorts of rules which are necessary if biological

classifications are to represent explicitly and unambiguously a particular feature of phylogenetic development. They have also posed clearly and forcefully a challenge to their fellow systematists: if the goal of biological classification is *not* to represent one or more aspects of phylogenetic development, what *is* the goal of biological classification?

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