

PHILOSOPHY AND THE TRANSFORMATION OF CLADISTICS

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Abstract

Platnick, N. I. (Department of Entomology, The American Museum of Natural History, New York, New York 10024) 1979. *Philosophy and the transformation of cladistics*. *Syst. Zool.* 28:537–546.—Although Hennig presented cladistic methods by referring to a model of the evolutionary process, neither the value nor the success of the methods is limited by the value or success of that evolutionary model. Dichotomous cladograms can be preferred simply on the basis of their maximal information content, without reference to speciation mechanisms. Because only the interrelationships of diagnosable taxa (those with unique sets of apomorphic characters) can be investigated, questions about whether speciation can occur without branching, or whether species become extinct at branching points, are irrelevant to cladistic practice. The distinction between plesiomorphic and apomorphic character states depends not on the reconstruction of actual evolutionary history, but on the discrimination of more general from less general characters; groups based on plesiomorphy are defined by the absence of characters and are therefore artificial. Hence cladistic methods are not the methods of phylogenetics *per se*, but the methods of natural classification in general; phylogenetic conclusions are an extrapolation from hypotheses about natural order. [Cladistics; phylogenetics; characters; natural classification.]

At least two students of current systematic theory have suggested that there has been in recent years a transformation within phylogenetic systematics or cladistics. David Hull, in a paper delivered at the 1977 Toronto meeting of the Society of Systematic Zoology (Hull, 1979), distinguished between early views of cladistics as a means of reconstructing evolutionary history and later, more general views of cladistics as a means of discerning natural order in any system that involves some sort of descent with modification. A somewhat different division within the ranks of cladists was subsequently postulated by George Simpson (1978a) in a review of the recent NATO symposium on vertebrate evolution. Simpson distinguished between what he called canonical and non-canonical versions of cladistics on the basis of whether their proponents do or do not regard cladograms as being equivalent to phylogenetic trees.

The first question that comes to mind, of course, is a historical one: has such a transformation actually occurred? In this regard, it's interesting that even though Hull and Simpson distinguished their respective groups of cladists at least partly

on different grounds (or characters); both classifications do cluster many of the same workers together. On the basis of this congruence, the two groups of cladists might be regarded as natural ones, and hence as real reflections of history.

At any rate, the possible extent of the differences between classical and modern cladistics is highlighted in another statement made by Simpson in his recently published autobiography (1978b: 271):

The main principles of the Hennigian system are: first, that the basic process of organic evolution (phylogeny) is the splitting (dichotomy) of an ancestral species into two descendant species; second, that each dichotomy should be taken as marking the origin of two new units (taxa) of classification; and third, that the hierarchic level of such units (whether species, genera, families, etc.) should be determined by the geological time when the dichotomy occurred, the earlier the time, the higher the level.

Having thus discovered what *the* main principles of the Hennigian system are, Simpson goes on, of course, to demolish them:

I will just say that the first principle, as given above, an apparent statement of fact, is not true and that the second and third principles, statements of opinion, are inane.

Simpson's criticisms are certainly open to question themselves, particularly with regard to his implicit claim to know just how the evolutionary process works, but even more dubious is his isolation of those three points as the main principles. Indeed, to the extent that there might be said to be a single main principle of the Hennigian system, it would be none of those mentioned by Simpson but rather the idea that the taxa which we recognize in our classifications should be based on synapomorphies. And if contemporary cladistics had to be summarized through three main principles, they would certainly not deal with dichotomous speciation or geological age. They might run something like this: first, that nature is ordered in a single specifiable pattern which can be represented by a branching diagram or hierarchical classification; second, that the pattern can be estimated by sampling characters and finding replicated, interrelated sets of synapomorphies; and third, that our knowledge of evolutionary history, like our classifications, is derived from the hierarchic pattern thus hypothesized.

Now one might ask whether this tentative statement of principles does or does not represent a transformation of Hennig's position. If it does, it can presumably do so only in one rather limited sense, because Hennig's conclusions, that is, his methods for analyzing data and constructing classifications from them, remain essentially unchanged. At most, what has changed is the manner in which those conclusions are justified. Hennig presented his methods by referring to one particular model of the evolutionary process, whereas contemporary cladists recognize that neither the value nor the success of the methods is limited by the value or success of Hennig's particular evolutionary model.

Hull (1979) has pointed out that such transformations are by no means unusual in the history of science. As he puts it, "If a line of reasoning which led to a particular conclusion turns out to be somewhat less than cogent, it really does not

matter all that much, just so long as the conclusion depicts reality with greater fidelity than previous attempts." Further, "methodological rigor . . . is invariably a retrospective exercise." This paper is an attempt at precisely that kind of retrospective exercise, and will examine some of the differences between classical and contemporary cladistics in an effort to determine whether the changes are indicative of the kind of single, coherent perspective that we would expect of a methodologically rigorous system.

The first problem encountered is a large one concerning the justification of scientific methods in general. On what basis should we prefer some methods over others, in systematics or any other science? This question itself appears to be beyond the realm of science, in that we don't seem to have a general way to evaluate methods scientifically. It may seem paradoxical to suggest that systematics (or any science) must adopt methods without itself being able to attest to their efficacy. But the fact is that we use our methods in an attempt to solve problems. If we already knew the correct solutions to those problems, we could easily evaluate and choose among various competing methodologies: those methods which consistently provide the correct solutions would obviously be preferred. But of course, if we already knew the correct solutions, we would have no need of the methods.

Evaluations of scientific methodology, then, typically involve questions that are philosophical rather than scientific, from which we can conclude that one's general philosophy of science may greatly influence methodological discussions and decisions. In systematics, for example, some workers seem to adopt a philosophical position of extreme empiricism (or perhaps even logical positivism), and the result in phenetics (Griffiths, 1974). As Gaffney (1979) and others have indicated, cladistic methods fit well with the strategy of falsificationism, and it's from that perspective that the justification of cladistic methods will be examined here.

Unfortunately, the strategy of falsificationism provides us at most with only a very vague guide to evaluating methods. Popper's writings, for example, are primarily concerned with the justification of particular scientific theories, such as the taxonomic hypothesis that spiders are more closely related to whipspiders than they are to scorpions, or, expressed another way, that there is a group (*Labellata*) including spiders and whipspiders but excluding scorpions. With regard to methods, Popper's advice would seemingly be only to choose whichever methods allow us to test a hypothesis most severely. This, incidentally, may be relevant to the philosophical controversy between Popper and Kuhn, in that their different views of the scientific process may simply refer to different domains. Given a hypothesis about the relationships of spiders and a method by which to test it, the outcome is not likely to be decided by any of the sociological constraints with which Kuhn deals. That one method rather than another is chosen to try to answer a particular question, or that someone even got to the point of asking that particular question (rather than, for example, one about the similarity of spiders and scorpions) may well be influenced by all the factors that Kuhn formerly amalgamated in his concept of a paradigm.

The three specific areas of cladistic theory that will be examined here are (1) the use of dichotomies, (2) views of species delimitation, and (3) the units of analysis. After that, an attempt will be made to sum up the change in perspective indicated by these three cases and to inquire about any general relevance or significance that the transformation may have.

As seen in Simpson's remarks, it has been common for Hennig's critics to attribute to him the belief that the process of speciation is always dichotomous, that an ancestral species always divides into two descendant species. However, Hennig maintained no such belief, arguing only that "If phylogenetic systematics

starts out from a dichotomous differentiation of the phylogenetic tree, this is primarily no more than a methodological principle" (1966:210). Hennig presented two arguments in favor of the use of dichotomy as a methodological tool. His first argument (strictly methodological) was that we cannot distinguish between cases of multiple speciation and cases of dichotomous speciation for which the relevant characters have not yet been detected. His second argument (not primarily methodological) was that "it is very improbable that a stem species actually disintegrates into several daughter species at once" (1966:211); however, Hennig acknowledged that this second argument is weak because of the indeterminacy of the concept of simultaneity in evolutionary time.

Both of these arguments reflect a concern with the mechanism of speciation, as if the purpose of taxonomy were to investigate the process of speciation (be it dichotomous or otherwise), come to some conclusions about it, and then construct classifications in such a way as to insure their compatibility with those particular conclusions about how the evolutionary process has functioned (Wiley, 1979, argues in favor of this position). Without intending any disrespect toward ideas about the mechanisms of evolution, it is obvious that any such ideas are only hypotheses, and that to be adequate, they should make some predictions about what kinds of patterns are and are not possible results of the mechanisms they envision. So if classifications (that is, our knowledge of patterns) are ever to provide an adequate test of theories of evolutionary process, their construction must be independent of any particular theory of process. The question with regard to the methodological preference for dichotomous hypotheses, therefore, is whether the preference can be justified by arguments that do not depend on any particular view of the mechanism of speciation. This does indeed seem possible, by simply looking at the information content of cladistic hypotheses.

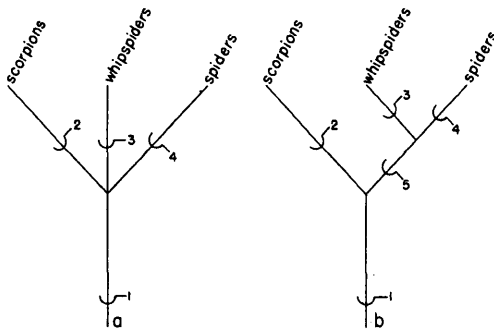


FIG. 1.—Information content of a trichotomous (a) and dichotomous (b) cladogram. See text for explanation.

A trichotomous cladogram for scorpions, whipspiders, and spiders is shown in Fig. 1a. We might ask what information is conveyed by the cladogram, that is, what predictions or hypotheses it makes. There seem to be four. There is one which says that if we sample the characters of these organisms, we will discover some characters (synapomorphies, if you prefer) that are shared uniquely by scorpions, whipspiders, and spiders; a second hypothesis predicts that we will find some characters (or synapomorphies) unique to scorpions; a third, that we will find some synapomorphies in whipspiders only; and a fourth, that we will find some characters true only for spiders.

These are all very nice predictions, but if any of these hypotheses are to be testable, they must also tell us what we will not find; that is, they must prohibit something, so that if we find these prohibited features in the real world our hypothesis is placed in jeopardy. Here again, there seem to be four correlated prohibitions; look first at hypothesis 1. This statement does not prohibit the existence of synapomorphies found in these three groups plus any other organisms; indeed, we expect to find some such characters in the sister group(s) of these animals. Nor does the hypothesis prohibit the existence of synapomorphies that might be found in only two of the three groups; there might well be synapomorphies unique to scor-

pions and whipspiders, for example, without this hypothesis, of a group including all three, being false. However, hypothesis 1 does prohibit the existence of any synapomorphies that are found both outside of this entire group *and* in only *some* of the members of this group. For example, it prohibits the existence of any synapomorphies shared uniquely by spiders plus ticks, or spiders plus elephants. Hypotheses 2 through 4 makes similar prohibitions; number 3, for instance, prohibits the existence of synapomorphies found in only some whipspiders plus any other organisms.

Looking now at a dichotomous cladogram for the same three taxa (Fig. 1b), it's obvious that all four of the hypotheses expressed by the first cladogram are also expressed in the second, but that there is an additional one, no. 5, predicting that we will find some synapomorphies true only for whipspiders and spiders, and that we will not find any synapomorphies unique to any other organisms plus only some members of the group Labellata (whipspiders plus spiders). In short, the dichotomous cladogram contains 25 percent more information than does the trichotomous one (five hypotheses instead of four), and this additional information content is in itself justification enough for a preference for dichotomous hypotheses, without recourse to any knowledge claims about the mechanisms of speciation. What Lakatos (1970) calls "Popper's supreme heuristic rule: 'devise conjectures which have more empirical content than their predecessors'" leads us to replace polytomous cladograms with dichotomous ones whenever characters are available by which to test the additional hypotheses that the replacement involves.

A second problem area closely related to that of dichotomy is that of species delimitation. Hennig (1966:66) maintained that "the temporal duration of a species is determined by two processes of speciation: the one to which it owes its origin as an independent reproductive community, and the one that divides it into

two or more reproductive communities"; in other words, species originate and terminate only through branching. This concept of the species has two corollaries: first, that phyletic speciation (without branching) is impossible, and second, that species always become extinct at branching points. Both of these corollaries are seemingly statements about the nature of the evolutionary process, so here again, if we are to have a consistent methodology, the points must either be supported by arguments that do not refer to evolutionary mechanisms, or be abandoned. Contemporary cladists can take the latter approach; as it turns out, Hennig's views on limiting species at branch points are irrelevant to cladistic practice.

For example, Fig. 2 shows segments of a phylogenetic tree, with time on the ordinate, divergence on the abscissa, and samples taken at three intervals. The cladogram that would result from an examination of these samples does not depend on the question of whether the phylogenetic tree did or did not branch between the times sampled, but only on the question of whether detectable changes occurred in any observed characters. In other words, in Fig. 2a, where the vertical orientation of the tree indicates that no such change occurred, the taxonomist will not be able to distinguish the three samples and will have only one species. In Fig. 2b, where detectable change did occur between times 2 and 3, the taxonomist will be able to distinguish only two species, one including samples 1 and 2 and one (with at least one additional apomorphic character) including sample 3; the result would be a two-taxon cladogram. The same two-taxon cladogram would result from another possible phylogenetic tree, shown in Fig. 2c, in which branching did occur but no detectable change took place in one of the populations (as would be the case in the favorite model of speciation in small peripheral populations). The idea that the species sampled at time 1 became extinct at the time of the branching is irrelevant to the cladogram, for one can only inves-

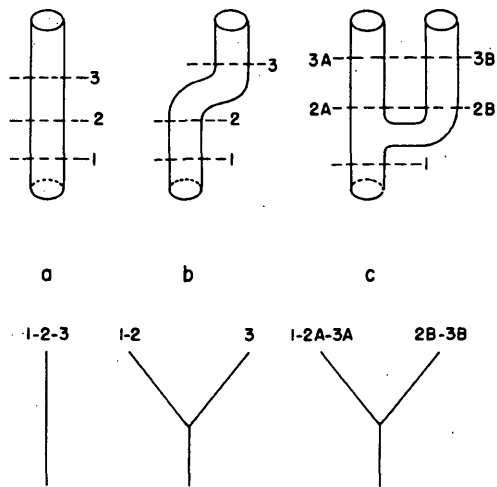


FIG. 2.—Possible phylogenetic trees (top) and their resulting cladograms (bottom). See text for explanation.

tigate the interrelationships of taxa that one can first distinguish, that is, of taxa which have unique sets of apomorphic characters. From the resulting cladogram, one cannot determine which tree (if either) is the cause of the cladogram.

The import of this is only that the construction of cladograms is not the same thing as reconstructing phylogenetic trees, because cladograms are not trees but sets of them, such that a particular cladogram might be the result of any of a large number of possible phylogenetic trees. Since no known species, Recent or fossil, would ever be placed between the nodes of a cladogram (i.e., in anything other than a terminal position), the question of whether more than one such species can occur between a given pair of nodes, or of whether a given species can extend beyond a node, never arises. Strangely enough, Simpson (1978a:221) has actually criticized Løvtrup's non-canonical cladograms on the grounds that they "are not really phylograms and not meant to be," when that is actually true of all cladograms. Simpson goes to argue that because of this "classification based on them is not even consistent with, let alone expressive of, phylogeny," which is false, since for any phylogenetic tree

there is one and only one corresponding cladogram. If the cladogram that follows from the true phylogeny (assuming that the true phylogeny could be known) is the same as the cladogram expressed by a classification, then the classification is clearly consistent with phylogeny.

Simpson merely compounds his error when he objects (1978a:220) to Hennig's insistence that the ancestral species (stem species) of an order must belong to that order. Simpson states that "In *classification* that would mean that the ancestral species . . . would belong to the same genus as its 'sister species' but to a different family and order." Simpson's interpretation is again false; if we actually had representatives of the stem species of an order, and could distinguish them from the other members of the order, they would be represented in a cladogram as the sister group of all the other members of the order, and included in a classification as a separate suborder (and, of course, a separate family and genus). The actual sister species of that stem species, if known as such, would be included in a separate order, family, and genus. Simpson contends that his objection alone "is enough to show that . . . the canonical Hennigian system is not only illogical; it is absurd," but the only thing actually shown to be absurd is Simpson's own misunderstanding.

In short, it matters not to cladistics whether phyletic speciation (Fig. 2b) either could or could not, or did or did not, take place in evolutionary history. Such questions occur only on the level of phylogenetic trees, not cladograms, and the message of cladistics is that cladograms, and not trees, are the necessary and sufficient basis of classification.

The third of the three areas of cladistic theory to be examined here is the matter of units of analysis, that is, of characters or character states. Hennig, of course, maintained that one must distinguish between plesiomorphic and apomorphic character states, defined by reference to actual evolutionary transformations, though naturally not also recognized in

that way. And taxonomists of all persuasions seem to agree that they wish to be able to predict from their classifications the maximum possible number of unknown characters. But what exactly is a taxonomic character? The conventional analysis indicates that a character consists of two or more different attributes (character states) found in two or more specimens that, despite their differences, can be considered alternate forms of the same thing (the character). A character is thus a theory, a theory that two attributes which appear different in some way are nonetheless the same (or homologous). As such, a character is not empirically observable; hence any (misguided) hope to reduce taxonomy to mere empirical observation seems futile. But if alternate character states are in some sense the same, how can they be different? There seem to be only two possibilities: either one state is a modified form of the other, or both are modified forms of a third state. In either case, the "sameness" that constitutes the character is thus the *unmodified* state, which all the organisms that show the character share, either in its original or in some modified form.

What, then, are the possibilities for prediction? Suppose that we have recognized a group (spiders) on the basis of two character states believed unique to spiders. In other words, each character has one state found in at least some non-spiders and a second state found only in spiders:

Character X, Y: State 1 (non-spiders)
State 2 (spiders).

Now suppose that we find a new specimen about which we know only that it has state 2 of character X. Can we predict that the new specimen will have state 2 of character Y as well? No, clearly not; the new specimen might well have a different state of the second character:

Character Y: State 1 (non-spiders)
State 2 (most spiders)
State 3 (some spiders)

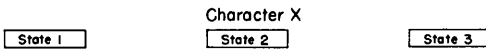
if that new character state represents a

modified form of state 2, found in all other spiders:

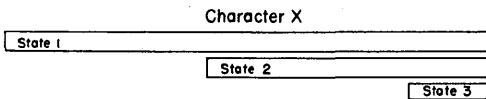
Character Y: State 1 (non-spiders)
 State 2 (spiders)
 Substate a (most spiders)
 Substate b (some modified spiders).

In this situation, of course, state 2 is functioning as a character (a unit of "sameness"), not a character state; just like character X, it is divided into an original and a modified form. If we agree that for the character (the "sameness") to exist, the character states must be modifications, it is apparent that predictions cannot really function at the level of character states. Because of the ever-present possibility of further modifications, predictions will hold only for characters (i.e., for sets of original plus modified character states).

In this sense, then, the concept of a character state is potentially misleading. To view some character X as being composed of three states:



implies that the character states are alternatives, when they are actually additions:



In this case, character X is actually equivalent to state 1 (i.e., it defines a group, all the members of which have state 1, either in its original or some modified form). States 2 and 3 are best regarded as new characters (Y and Z), for which the same provisions hold. Further, state 1 itself is a modification of some other character (state) and represents a restricted subset of some other, more general character. Thus, all characters can be seen as modifications (or restrictions) of other characters, and the grouping of character states within a character can be seen as just arbitrarily delimiting clusters of separate characters that are increasingly

more restricted in generality (i.e., that form nested sets of increasingly modified versions of other characters). One might envision a great chain of characters (or synapomorphies, or homologies) stretching from those of complete generality, which are true for all life, on to those true for only a single species.

The implications of this for prediction can be readily seen in a simple example involving tetrapod and non-tetrapod vertebrates. Systematists have long been in agreement that the limbs of tetrapods are homologous with the fins of non-tetrapod vertebrates ("fishes"). If we regard fins and limbs as alternative states of a character (paired pectoral and pelvic appendages), we might thereby sort out vertebrates into two groups, Pisces (for those with fins) and Tetrapoda (for those with limbs), and vertebrates were indeed classified in that way for many years. However, one of these groups (Pisces) proved not to be maximally predictive, in that many characters were found that are shared uniquely by tetrapods and some (but not all) fishes. If, however, the limbs of tetrapods are not only homologous with fins, but are also modifications of fins, the problem disappears. We can recognize that we have two characters; one, fins, or paired appendages, is found in all vertebrates in one form or another; a second, limbs, is found in all tetrapods (including snakes!) in one form or another.

What, then, are the implications of this for the distinction between plesiomorphic and apomorphic character states? Hennig accepted four tests of apomorphy, two of which (stratigraphic and geographic position) are not generally accepted by contemporary cladists, while the other two, ontogeny and outgroup comparison (called by Hennig the criterion of the correlation of characters) are used heavily. In the latter kinds of tests, a preliminary hypothesis of the homology of two character states is made, and the test discriminates one of the states as being plesiomorphic. But does either kind of test actually demonstrate one character state to be more primitive in real

evolutionary history? Of course not; as Nelson (1978) has shown succinctly, the results of either test merely show one character state, the "plesiomorphic" one, to be more general than the other (i.e., to occur in more groups). The fact that neither stratigraphy nor geography can provide information on the relative generality of characters may account for their lack of usefulness in character analysis.

From these results, we can readily see why so-called "plesiomorphic" character states cannot be used to form groups. If we form a group Pisces, we have based it not on a character, but on the absence of a character. The group Pisces includes those organisms with fins that also happen to lack modified fins (limbs). Such use of the absence of a character is one of the best hallmarks of an artificial group. Given that every natural group may have one or more characters unique to it, it is possible, by using the absence of features as characters, to define any conceivable combination of species as a group. For example, one could define a group consisting only of the platypus and man by simply listing the synapomorphies of mammals together with the absence of the autapomorphic features of all other groups of mammals. Admittedly, this is an extreme example, but it is what gradistic ("evolutionary") taxonomists advocate every time they argue in favor of paraphyletic groups, which can be defined only by the presence of some characters together with the absence of others. It should be obvious that any theory of systematics under which any conceivable grouping is allowable on the basis of a given set of character distributions is no theory of systematics at all.

At any rate, cladistic methods obviously do not depend on the recognition of historically primitive or historically derived character states (i.e., they do not depend on the actual reconstruction of evolutionary history). The methods merely attempt to discriminate more general from less general characters and to discover a hierarchic system in nature by, as Hennig (1966:122) put it, "trying to

bring the relationships indicated by . . . several series of characters into congruence." Herein may well lie the primary difference between cladistic and phenetic methods: whereas phenetic methods are willing to accept incongruence between characters as a feature of the real world, cladistic methods regard the discovery of apparent incongruence as an indication that the taxonomist has made a mistake. He might have underestimated the generality of a character, by overlooking one of its modified forms (the kind of mistake called plesiomorphy). He may have overestimated the generality of a character, by confusing it with what is in actuality a different character (the kind of mistake called convergence or parallelism). Or he may even have regarded something as a character when it isn't, for example, when it's only the absence of a character. The refusal to accept incongruence (i.e., randomness) as a feature of the real world leads us back to what was suggested as the first principle of cladistics: that nature is ordered in a single specifiable pattern. Admittedly, that's not a scientific theory; it can't be tested, since any failure to find order in nature doesn't necessarily mean that the order isn't there. But Popper (1968:61) has argued that such a metaphysical statement, when translated into a methodological rule, is a necessary underpinning of all science. The rule is not that we must believe nature to be completely orderly, but that we must refuse to ever give up the search for that order. If we give up the search for regularities, we also give up the game of science.

What general statement can be made about the three particular aspects of cladistics that have been examined here? It would appear that, as Nelson (1979) has indicated, cladistic methods are just attempts to discover a real order in nature, the "natural system," if you prefer. But of course, that's been the desire of taxonomists since long before Darwin. So what about evolution, and its role in taxonomy? Presumably, its role is exactly as early evolutionists perceived it, namely,

as an explanation for the existence of a natural hierarchic system. Does that mean, as Simpson has suggested, that the taxonomist must first construct a phylogenetic tree, and then somehow arbitrarily chop it up to form a classification? No, it means only that systematists must analyze characters in an attempt to find order in nature, and that once order has been found, we may, if we wish, assume that it's the result of evolution, after which natural groups may be viewed as monophyletic, apomorphic characters may be viewed as evolutionary novelties, and degrees of relationship may be viewed as reflecting relative recency of common ancestry. The implication is that cladistic methods are not the methods of phylogenetics *per se*, but the methods of taxonomy in general, and that our knowledge of phylogeny stems from our knowledge of taxonomy (Platnick and Nelson, in press).

But the question is: does all this represent a transformation of Hennig's position, or have these ideas been part and parcel of cladistics all along, even if they were perhaps not very carefully or clearly enunciated (or indeed, even if they were perhaps very carefully *not* clearly enunciated)? Rather than attempt to provide an answer, I'll merely present two quotations from Hennig, from which an answer might conceivably be forthcoming:

But the task of the phylogenetic system is not to present the result of evolution, but only to present the phylogenetic relationships of species and species groups (1966:194).

In comprehensive accounts of the theory of descent a great number of "proofs" of its correctness are generally given (paleontological, embryological, zoogeographic, and others). All these proofs are undoubtedly significant, but it must be pointed out that they gain this significance only through their relation to the hierarchic system The fact that . . . [taxa] included in the same group, may prove to be connected by other entirely different relationships (zoogeographic, for example) that were not taken into account in the original compilation [of the group] calls for an explanation. *The explanation is then provided by assuming common descent* (1966:14, emphasis added).

What, then, might be the general sig-

nificance of Hennig's point of view? At the time he wrote, the ruling tradition within evolutionary biology was seemingly the synthetic theory and related doctrines that developed along with it in the 1930s and 1940s. If the view of the relationship between systematics and evolution discussed above is the logical outcome of his ideas, then Hennig might be said to have diminished or even demolished that portion of the synthetic position concerned with systematics, at least as represented by Simpson, his trees, and his arbitrarily applied axe.

What about other areas of evolutionary biology? In another subdiscipline concerned with evolutionary patterns, biogeography, Hennig also attacked the synthetic position that a biota is made up of elements with unique histories of dispersal, and that the purpose of biogeography is to reconstruct those unique histories. As he said (1966:169):

It is important that similar disjunctions may be found among very different animal groups, and this raises the question of whether they arose in the same or a similar way in all animal groups. If so, this might mean that the same age . . . would have to be attributed to all groups showing the same or a very similar picture of disjunctive distribution

and (1966:199):

if it is found further that the most closely related units [sister groups] usually vicariate whereas more distantly related units do not then a causal relationship is indicated—we may infer a causal relationship between the differentiation of space and the origin of differentiation in one of the groups occupying this space.

In arguing that there is a causal relationship between distribution and taxonomic pattern, Hennig began to tread on the home ground of syntheticist dogma, the notion that changes in gene frequency within populations caused by natural selection provide a sufficient explanation of evolution, and that the syntheticists have therefore solved the major problems of evolutionary biology. Here again, Hennig obviously realized that all the selection in the world hasn't changed the fact that what were two morphs of *Biston*

betularia are still (only) two morphs of *Biston betularia*, and he would probably have agreed with Sewall Wright's (1978:378) characterization of much of the 'synthesis' as "merely rhetorical pronouncements on such matters as 'gene interaction,' 'integrated coadapted complexes,' 'cohesion of the gene pool,' 'founder effects' and 'genetic revolution.'" As Hennig said (1966:199), "we must emphasize strongly that this [microevolution] does not provide a complete understanding of the evolutionary process and its laws."

So what Hennig may well have done in general (and may perhaps even have set out to do) is to demonstrate the inadequacy of the syntheticist paradigm, by showing us that we are hardly likely to achieve any understanding of the evolutionary process until we have achieved an understanding of the patterns produced by that process, and that even today we have hardly begun to understand the patterns.

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REFERENCES

- GAFFNEY, E. S. 1979. An introduction to the logic of phylogenetic reconstruction. In Cracraft, J., and N. Eldredge (eds.), *Phylogenetic analysis and paleontology*. Columbia University Press, New York, pp. 79-111.
- GRIFFITHS, G. C. D. 1974. On the foundations of biological systematics. *Acta Biotheoretica* 23:85-131.
- HENNIG, W. 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana.
- HULL, D. L. 1979. The limits of cladism. *Syst. Zool.* 28:416-440.
- LAKATOS, I. 1970. Methodology of scientific research programmes. In Lakatos, I., and A. Musgrave (eds.), *Criticism and the growth of scientific knowledge*. Cambridge University Press, pp. 91-196.
- NELSON, G. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. *Syst. Zool.* 27:324-345.
- NELSON, G. 1979. Cladistic analysis and synthesis: Principles and definitions, with a historical note on Adanson's *Familles des plantes* (1763-1764). *Syst. Zool.* 28:1-21.
- PLATNICK, N. I., AND G. NELSON. In press. The purposes of biological classification. In Asquith, P. D., and I. Hacking (eds.), *PSA 1978, Proc. 1978 Biennial Meeting, Philosophy of Science Association*, Vol. 2.
- POPPER, K. R. 1968. *The logic of scientific discovery*, second English edition. Harper and Row, New York.
- SIMPSON, G. G. 1978a. Variation and details of macroevolution. *Paleobiol.* 4:217-221.
- SIMPSON, G. G. 1978b. *Concession to the improbable*. Yale University Press, New Haven.
- WILEY, E. O. 1979. Cladograms and phylogenetic trees. *Syst. Zool.* 28:88-92.
- WRIGHT, S. 1978. [Review of] *Modes of speciation*, by Michael J. D. White. *Paleobiol.* 4:373-379.