



## Mayr on Cladism-and His Critics

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*Systematic Zoology*, Vol. 24, No. 2 (Jun., 1975), 257-262.

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### Mayr on Cladism—and His Critics

“It remains to be seen if systematists will respond to the challenge . . . by shedding their commitments to this or that ‘school’ of systematics, becoming sensitive to the areas of conflict, and sorting out for themselves what is useful and worth preserving.”

(G. Nelson, 1973)

A recent issue of *Systematic Zoology* featured two polemical reviews (Rosen, 1974; Nelson, 1974) of a recent comprehensive critique of cladistics by Mayr (1974). Since Mayr's article has thus been brought to the attention of the readership of this journal, a discussion of the various critical issues raised therein seems in order. Rosen (1974) states that “I have been able to identify only two central issues in the controversy as developed by Mayr, . . .”, and Nelson (1974) deals with only one issue raised by Mayr. Yet Mayr's paper clearly makes at least eight distinct points, several of them serious indictments of cladistic theory and practice. Some of Mayr's most telling arguments are not responded to by either Rosen or Nelson. This makes for good polemics but poor science. While Professor Mayr hardly needs my help in defending his views, I hope that I can make some contribution to the important issues raised in this controversy.

Had I known of the tempest in a teacup that this Point of View would engender I might have thought better than to submit it. The Editors sent my manuscript to numerous reviewers and I received no less than twenty-eight reviews of my remarks, an effort inordinately disproportionate to the importance of my contribution. Nevertheless, I cheerfully (?) worked my way through all of their comments. Clearly, it was impossible to satisfy all critics, but I have attempted to clarify passages found obscure and to remove erroneous or inappropriate statements. Some requests for changes by my many colleagues were unsuitable, not because they were without merit but because responding to them would have transformed my manuscript from a brief Point of View into an unin-

tended and unnecessary major discourse on cladism, evolutionary systematics, or phenetic classification. My views on these issues are well known and have been published in the pages of this journal and elsewhere.

It may be helpful to the reader if I briefly outline my purposes in writing this note so that my intentions will not be misunderstood. I felt that Ernst Mayr's views had been misrepresented and wanted to set the record straight. It seemed to me then, and still does now, that various points raised by Donn Rosen and Gareth Nelson were of questionable validity and value, and I attempted to bring these out. At the same time, I noted weaknesses in Mayr's arguments and felt that in fairness these should be listed as well. While writing, I decided to put down several paragraphs on the value of phylogenies as such. These are similar to remarks made by me at several recent conferences, but they have not appeared in print before. In no way was this article intended as an exposition of the phenetic school of taxonomy, although given my philosophical orientation, I do not doubt that my views can be inferred by the careful reader. More than the above I did not attempt to do, and I shall resist the temptation to be drawn deeper into a full blown critique of any school of taxonomy. It was suggested that I consider Hennig's (1974) reply to Mayr's paper. When I drafted this Point of View I had not yet seen Hennig's article. I have since read it and find its arguments unconvincing. I do not at this time intend to discuss Hennig's remarks, but if I were to undertake the task, I would publish my comments in the *Zeitschrift für Zoologische Systematik und Evolutionsforschung*. My remarks here relate to the Rosen-Nelson Points of View published in *Systematic Zoology*.

I would like to express my appreciation to the Editors for the plenitude of suggestions procured for me. To my many colleagues who produced them—many thanks. I shall not list those reviewers who signed

their comments, but single out only the twenty-ninth reviewer, my old friend Peter H. A. Sneath, who has the distinction of having his review solicited by me. *Honi soit qui mal y pense.*

#### CLADISTIC METHODOLOGY

Early on in his extensive paper, Mayr (1974, p. 97) distinguishes between (1) the estimation and reconstruction of cladistic sequences, and (2) the construction of classifications based on cladistic criteria. Concerning the first of these issues, the casual reader may be left with the impression that Mayr approves of Hennig's techniques for inferring cladogenies and Rosen (1974, p. 46) draws this inference in his article. Yet a careful reading of Mayr's paper will uncover five pages (p. 116–120) which make it patently obvious that Mayr is well aware of what in my judgment as well are at least four serious difficulties in the procedures employed by Hennigian cladists for finding evolutionary branching sequences: the difficulty of determining the direction of evolutionary sequences, the difficulty of discriminating between parallelism and convergence, the rejection of information on similarity in evaluating cladistic relationships, and the difficulties posed by mosaic evolution. These points and others have been repeatedly raised by critics of the Hennigian cladistics (e.g. Colless, 1967; Sneath and Sokal, 1973, Section 2.5). There seems little point in reiterating these issues here, except to note that recent contributions to the controversy especially from cladists have tended to give the impression that the reconstruction of cladograms was an established science and that the main issue at stake was whether cladograms alone should serve as bases for classification. It is, of course, perfectly legitimate to discuss whether the philosophic basis of a classification should be phenetic, cladistic, or a combination thereof—regardless of whether classifications can actually be constructed on these bases. Yet it is relevant to inquire whether cladograms that are sufficiently reliable in a statistical sense can in fact be

produced from Recent material. Published criticisms of such procedures (all those mentioned by Mayr, plus the difficulty of deciding among the very large number of possible tree topologies, the added complication introduced by reticulate evolution and by branches that are now extinct and about which no information is available, and others) have never been satisfactorily answered. The rejoinder by Schlee (1969) notwithstanding, I have read nothing that would dissuade me from concurring with Colless (1967) "... that the 'Hennig System' is simply an intuitive, prototypical form of statistico-phenetic taxonomy, and that its advocates simply misunderstand the nature of the latter process." (See also Colless, 1969a, 1969b).

#### CLADISTIC CLASSIFICATION

Turning now to Mayr's critique of the theory of cladistic classification, his first objection is to the appropriation of long established terms in evolutionary biology and their redefinition with narrower meanings by Hennig's followers. Phylogeny, relationship and monophyletic are the three terms singled out by Mayr. I concur with him in deploring this development (Sneath and Sokal, 1973, p. 28, 30, 36–50). While the arrogation of commonly used and understood terms by a partisan group may irritate its opponents, the potential damage wrought by impeding learning among students and communication among groups with divergent views is more serious. Not that any of us are blameless. Mayr unabashedly uses "evolutionary systematics" for his philosophy, thereby implicitly relegating the rest of us disbelievers into the limbo of nonevolutionism. I have yet to meet a non-evolutionary taxonomist, although I have it on good authority that some do in fact exist. Phenetic taxonomists have on occasion used terms such as "natural classification" in a sense not recognized by taxonomists of other persuasions. Yet, in my experience rational discourse on controversial matters is facilitated by the use of commonly accepted, clearly defined, and nonemotive terms, such

as “natural classification *sensu* Gilmour,” or “phenetic relationship,” not plain “relationship” as Mayr (1974, p. 102) mistakenly claims. The more zealous among the cladists might well consider whether Cain and Harrison’s (1960) important conceptual distinction between phenetic and cladistic relationships, a major contribution to taxonomic theory, should be obfuscated, as it would be were they really to succeed in forcing the rest of us to synonymize the terms phylogeny and phylogenetic relationship with cladogeny and cladistic relationships.

Rosen criticizes most strongly Mayr’s argument that systematists should consider cladistic *as well as* patristic relationships when constructing classifications. According to Mayr, the preoccupation with branching sequences makes cladists ignore adaptive aspects of synapomorphy (derived patristic similarity—Sneath and Sokal, 1973) hence ignore one of the major features of evolution, the entry of lineages into new adaptive zones. Mayr clearly states that both evolutionary divergence (presumably expressed as phenetic dissimilarity) and branching sequences are needed and that these elements should be appropriately weighted. This “combined” point of view of Mayr’s is very close to the position held by various numerical taxonomists (Sokal and Camin, 1965; Sneath and Sokal, 1973, p. 53–60). I, for one, find it difficult to see how any reasonable person would construct a classification of a group in which unequal evolutionary divergence occurred without taking the general appearance of the organisms (phenetics) into consideration. To drag in the hoary example once more—most of us are not ready to abandon the class Reptilia as a natural taxon.

Yet this is also the section in which Mayr lays himself open to the most serious criticism voiced by Rosen. Repeatedly, Mayr refers to “careful,” “proper,” or “appropriate” weighting without ever providing explicit rules. For this he and others (Bock, 1969) have been faulted by the numerical taxonomists (Sneath and Sokal, 1973) as well (see also Bock, 1973, for a later expres-

sion of his point of view). Mayr provides a reference to rules for weighting (Mayr, 1969, p. 220–228). Yet an examination of the properties of characters that supposedly provide a priori taxonomic weight finds the rules wanting. Complexity of characters automatically gives them greater weight since they are composed of many unit characters. Consistency, lack of obvious adaptive value, lack of response to ecological shifts, or character correlation, all cannot be found unless taxa have been defined initially. It is circular to argue that character *i* is very important in taxon A because it varies little in that taxon, since the properties of character *i* are required to define the limits of A in the first place. These points have been made repeatedly (most recently in Sneath and Sokal, 1973, pp. 109–113), and we have yet to be shown an operational and biologically meaningful system of weighting. The weighting of character complexes for adaptive zones is even more difficult and, though possibly justified biologically, it is not really helpful for Mayr (1974, p. 106) to fault cladists: “that some events in adaptive evolution are far more important than others is completely ignored.” Rosen (1974) asks how much synapomorphy (derived patristic similarity) is necessary for a new adaptive zone, and points out that Mayr’s concept of weighting phenetics *vis-à-vis* cladistics is not operational. He also maintains that the relation between shared genotypes and phenetic resemblance is unknown, especially in higher taxa. Yet, we are beginning to obtain estimates of aspects of genetic distance at various taxonomic levels in organisms and comparisons of these estimates with phenetic similarities (cf. Hudson et al., 1966, with Mainardi, 1963; Arnheim et al., 1969; Ayala et al., 1974; King and Wilson, 1975) and saying that it cannot be done now is quite different from maintaining that it should not be done. By restricting their classifications to cladograms, cladists are removing from their classifications a potentially interesting and crucial aspect of macroevolution—the invasion of new adaptive zones. Rosen further weakens his own critique by con-

founding the problem of evolutionary phylogenetic analysis with classification. Referring again to the bird-reptile problem, he states "facile genetic interpretations of phenetic resemblance at the higher taxonomic levels may well have had a multi-fying influence on phylogenetic investigation by suggesting that precise answers to fundamental evolutionary questions are possible with a casual phenetic analysis. Knowing that crocodiles may have a more recent common ancestor with birds than with lizards should, instead, prompt an investigation of crocodile scales to learn if the scale morphology and development is consistent with, or refutes an alignment of birds and crocodiles based on other kinds of evidence." This is a laudable goal, but it is not classification. It is character analysis.

#### TAXONOMY—HOW MUCH AND HOW?

In connection with this argument, the question must be asked: Is it possible, and if so, is it worth while to carry out a comprehensive taxonomy of all organisms in nature following the methods and philosophies of any of the three schools being advocated today? As regards feasibility, phenetic taxonomy has been done successfully by traditional taxonomists since the days of Linnaeus. Numerical pheneticists have increased its precision, ability to handle many characters, and speed of execution. So called evolutionary taxonomy is currently not operational, although I do not doubt that some (even many) of the phylogenies described by the Mayr-Simpson school are not far off the mark. Hennigians claim that they can reconstruct cladograms, although this claim is being disputed. Even though numerical cladists are making progress, reliable cladograms still remain a goal rather than a reality.

But let us for the moment suppose that cladograms were possible of achievement (and if this came to pass it would in my opinion follow from the work of numerical cladists, such as Fitch or Farris, rather than from the techniques of Hennig, Schlee, Brundin, Rosen, or Nelson). What would it

profit us? Suppose a cladogram based on all Recent organisms were constructed. We might be handed a vast tree with more than 2,000,000 terminal branches and, on the simplest assumptions, a total in excess of 3,800,000 nodes, not counting any known fossils. Without clothing this topological scaffolding with phenetic information, none of the important evolutionary relationships could possibly be uncovered. And by the time the phenetic dimensions are added to the cladogram, we are again considering phylogenetic systematics in the traditional, non-Hennigian, sense of the word. For the study of rates of evolution, the nature of and changes in adaptive zones, character correlations, macroevolution, and the like, cladism alone is a dead end.

But what if developing methods of analysis made a "complete" systematics (phenetics *cum* cladistics) feasible? Even were this aim of the evolutionary taxonomists attainable, one would still wish to reconstruct phylogenies only for selected groups, either those of special interest to man, or others that seemed promising for the investigation of particular evolutionary phenomena or principles. A total phylogenetic tree of Recent organisms would be overwhelming in the information upon which it would be based, redundant in the lessons to be learned from it (who needs to demonstrate the gas laws for yet another gas, or test the universality of the Mendelian mechanism in yet another organism?) and unmanageable. Yet we must have a description of organized nature in view of the many needs of applied biology, the threat of disappearance of significant portions of the earth's biota, and the rapid accumulation of all kinds of new systematic information (Anonymous, 1974). It is for this reason that most numerical taxonomists have advocated phenetic classifications for general purposes, leaving phylogenetic classifications—when these become attainable—for specialists in evolutionary theory.

#### FURTHER CRITICISMS

Mayr's critique continues by pointing out the formal and almost axiomatic definition

of species and of speciation required by Hennigian cladistics. This is shown by the supposed changes to two descendant species after a bifurcation in a species clade and the retention of the same species appellation despite gross phenetic change within one line in the absence of a branch. Our current ideas of species and speciation are undergoing renewed inquiry and possible change. It would therefore seem a dubious practice to rest a classificatory philosophy so heavily on a preconceived model of speciation. Related to the origin of species is the mode of origin of higher taxa in cladistics. Mayr stresses that higher taxa never really split but that often several members of a super-species simultaneously acquire new features. In fact, some speciation may proceed similarly with parallel shifts into new adaptive modes in different local populations of one species population (Sokal, 1973). The study of phylogeny is often simplified by the extinction of all but one of these parallel clades, yet a taxonomic theory cannot be built on this expectation.

Rosen blames "evolutionary taxonomists" for stating that "it is not enough, for example, to represent the direction and extent of evolutionary change in a given character graphically—the whole of historical change must somehow be reckoned with and translated into angles and linear dimensions in a branching sequence. It is the belief that this can be done in some reasonable way that leads to the next step—of translating the mixture of cladistic information, overall genetic similarity, and adaptational divergence into a classification. Such a classification, they feel, has a greater information content than a purely cladistic one. But in my opinion such classifications obfuscate phylogeny by defining groups with symplesiomorphies and subjectively elevating autapomorphies (unique derived features) in the formulation of taxa, and carry a heavy burden, not of information, but of highly individualized conclusions." This statement epitomizes the lack of agreement among cladists and "evolutionary taxonomists" and reveals a lack of understanding

of the nature of the information content of taxa (Sneath and Sokal, 1973, pp. 25–27) and the proper representation of evolutionary change. As early as 1965, Sokal and Camin stated that the maximum amount of information would be contained in a natural classification *sensu* Gilmour (i.e. a phenetic classification) to which a cladistic dimension had been added. Attempts at such representations have been numerous and date back to Sneath (1961). Yet it is true that neither Mayr nor his followers have shown us how to construct or analyze such structures. Phenetic relationships can already be represented objectively and with sufficient precision, while the cladistic sequences are still problematical, the claims of the Hennigians notwithstanding.

Mayr next points out the problems and inherent contradictions that develop from determining categorical rank of a taxon on the basis of absolute geological time or position in the branching sequence. The numerous connected problems have been discussed by other authors as well (e.g. Crowson, 1970). In fact, Hennig (1966, p. 183) himself has pointed out these difficulties.

#### WAS DARWIN A CLADIST?

The next controversial issue treated by Mayr is whether the interpretation of phylogeny given by evolutionary taxonomists or that offered by cladists corresponds more closely to Darwin's ideas on the subject. It is to this point that Nelson (1974) addresses himself especially. This question should be of primary interest to historians of science, but as Nelson correctly points out, appeals to tradition are often advocated in defense of orthodoxy. I find the entire argument beside the point. If ideas cannot stand on their own merits, they will not long survive, however illustrious the name with which they are legitimately or falsely associated.

#### CONCLUSION

Mayr summarizes the cladists' objection to evolutionary taxonomy (called "combined taxonomy" by Griffiths, 1972) as

failure to provide simple criteria for making decisions in classification. Mayr considers that "the nature of the material precludes a simplistic approach. The nature of variables that must be considered in the construction of the classification is so large that simple methods will not work. This is the reason why the evolutionary taxonomist carefully weights the evidence and uses his judgment in arriving at conclusions." It is on this point that numerical taxonomists join cladists in criticizing evolutionary taxonomy. We believe that methods must and will be developed for dealing with these problems. Whether these methods will be simple is difficult to say. What may not be simple today, may be considered thus a few years from now. When I was a student, principal components analysis was understood by no more than a handful of biologists in the country. Today hundreds of biologists—taxonomists, ecologists, and others—are using it, and far more sophisticated techniques, on a daily basis. I have no doubt that combined methods of phenetics and cladistics will be the backbone of systematics in the years to come. Yet for general purpose classifications, taxonomists may prefer to use phenetic classifications, as they largely do today. Until it becomes operational and quantitative, "evolutionary taxonomy" will continue to be subject to criticism. Cladistics, however, is more seriously flawed. Without a phenetic dimension, it remains a topological exercise.

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