inability to deal with fossils, cladists seem particularly unable to bridge broad phyletic gaps. Parsimony is not reliable across such gaps and in broader gaps non-parsimony is inevitable. Cladistics is only really reliable when treating groups with many closely related surviving members and a closely related out-group.

10–16. Characters selected or omitted, polarizations, and selections of outgroups by cladists are often amazingly biased and subjective. An *a priori* assumption such as the non-vascular ancestry of bryophytes could fatally prejudice a study of the origin of land plants, especially when used to justify the exclusion of all fossil evidence from the study.

Cladists often avoid personal bias in the selection of characters by obtaining them secondarily from pre-existing studies. The latter practice, however, is even more unacceptable, perpetuating blindly the errors and bias of previous workers.

13a. Interpretation of homologies can be treacherous. Such structures as nodes and stipules in higher Angiosperms represent complex degrees of decurrency of leaf characters into the subtending stem and must be interpreted in this broader context.

14a. Occurrence of chemicals in plants is often totally dependent on the occurrence of the types of glands in which they are produced. Though many genes may be involved, a single gene often determines the presence or position of both features.

16a. Cladists seem particularly inclined to err on polarization. Perhaps the rejection of loss of characters as a synapomorphy causes many cladists to reject the idea that loss occurs. Also, cladists in their pursuit of objectivity presume to judge polarity of characters independently of evidence from other characters. However, many characters can only be polarized by considering interaction with other characters. Also, features such as paleae in asteraceous heads have commonly evolved from epaleaceous ancestors, a fact only evident after some knowledge of the relationships of the plants is obtained.

Notably absent from the key is reference to errors in parsimony. There is no theoretical fault in the idea of parsimony. When parsimony leads to contra-intuitive results, the fault is in the failure to analyze and incorporate the sources of the intuition into the properly tabulated and polarized characters.

There is a final problem with cladistics, the fact that it is a very cumbersome method. Any effort to resolve large and diverse groups would become excessively prolonged by its use.

The method should be learned widely by taxonomists, but should be used sparingly. By the nature and number of their characters, and in the frequency of reticulate evolution and reduction, plants are, on the average, poor subjects for cladistic study.

The primary accomplishment of cladistics, hopefully, will be to force taxonomists to give reasons for their phyletic conclusions. There is no question that use of cladistic methods would improve the work of many taxonomists, but it is also unfortunately true that those most likely to be helped are the same ones least likely to recognize when they have made an error in cladistics. Good taxonomy will continue to be primarily dependent on having good taxonomists, cladist or non-cladist.

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CLADISTICS—A REPLY

The two preceding articles are all, in some way, critical of cladistics. I am not going to respond to every point in them but I am going to correct some errors and clear up some misunderstandings. Rather than list all possible references I have simply included a list of suggested readings.

Every systematist who has chosen to use cladistics has asked himself three questions, and so should the reader. First, "What do I want to achieve with my taxonomy?" If the answer to this question is to simply define groups of individuals with some character or characters and to put these groups of individuals, called species, into larger groups that are in turn defined by some character or characters, then cladistics is not a method for you. If, on the other hand, you are striving to make groups (either of individuals or of species) that are natural, or reflect the pattern of relationship, or to produce a classification that reflects the phylogeny, then you should certainly be interested in cladistics because all it is attempting to accomplish is to identify and recognize the pattern of relationship among the organisms we study.

The second question is "Do you want to expose yourself and your classification to scrutiny?" Intuitive classifications are inherently non-criticizable and non-comparable in any useful way. You can say that two classifications are different but it is difficult or impossible to pinpoint what is responsible for the difference(s). A cladistic classification, on the other hand, has all of the characters on the diagram and you can easily see which characters are causing the groupings and you can ask and answer questions about what would happen to the classification if specific characters were changed or removed or added. Contrary to what has been said by one of the previous articles, I enjoy sitting down with three competing classifications of seed plants and examining the apomorphies and their placement and checking to see what characters are used and what is causing the different cladograms. When you produce a cladogram and a cladistic classification you are putting all of your expertise in a group on record for everyone to evaluate and it is my experience that many of my colleagues are unwilling to do this. It is much easier to say "I have been working on this group for years and A is related to B" than it is to say "A is more closely related to B than either taxon is to anything else because they alone share the following six apomorphies . . . ."

The third question is whether or not one is willing to spend the time to read and study and learn to use cladistic methodology effectively.

Taxonomists who are not interested in natural groups and who are unwilling to state explicitly what characters they are using to group are justified in not being interested in cladistics; all others, however, should be very interested because it offers a means to accomplish both. That brings up a point mentioned in one of the articles, that traditional systematists are not conducting experiments and therefore they are not interested in repeatability. What are we doing if we say that A is more closely related to B than it is to C? We are stating a conclusion based on the data we have gathered from our research. If our conclusion is not supported by any given set of characters then it is not reconstructable and it is indeed just an opinion that cannot be evaluated. However, if one supplies a list of six apomorphies to support this conclusion then it can be reconstructed or repeated and it has a greater value. To say a classification is repeatable means that it can be reconstructed from the data given. To not be in favor of being able to reconstruct the classification seems to me to be asking the reader to take one's classification on faith, something most scientists are not willing to do.

Many times the argument of parsimony has been discussed and I am not going to go into detail on this subject. Suffice it to say that no cladist has ever said evolution is parsimonious. The principle of parsimony says that given all of the data, one chooses the simplest solution to a relationship question. One makes the fewest assumptions of reversal and parallelism as possible. If all the data are used in the analysis, then the criticism must be that there are some things one knows without data. Well, it is possible to turn a cladogram into a phylogenetic tree using such unknown data but it is convenient to have the cladogram published also so that the supportable groups are obvious. Certainly, proposing a taxonomy based on "unknown data" is questionable no matter what system of classification is used.

Concerning paraphylesis, again; paraphyletic groups create problems in a classification because they are undefinable and they do not reflect an evolutionary unit. The members have no common evolutionary history. If we examine the example of the angiosperms, the monocots are monophyletic and the dicots are paraphyletic because the monocots represent a clade that comes out of the dicots. Thus, while we can speak of the evolution of the monocots we cannot speak of the evolution of the dicots because they have no common history except when you include the monocots. Rather than refer to the evolution of the dicots we should speak of the evolution of the Rosideae + Asterideae or of the Hamamelideae, etc. One further point concerning paraphylesis, never has any cladist that I know of said that ancestors of all living species are extinct. What they have said is that we never know for sure if taxa without autapomorphies are ancestors. This is very different because it allows for the possibility that an extant taxon (or even a fossil) on a cladogram may be an ancestor but it does not require it. Taxa without autapomorphies have been shown to be parents of hybrids, hybrids, or merely poorly understood taxa. Certainly there is nothing in cladistics to stop one from guessing as to whether or not a taxon without autapomorphies, be it extant or only known from fossils, is an ancestor.

Referring to cladistics as a computer method is not valid since the vast majority of cladograms are produced manually. Also, comparing cladistics and phenics is no longer valid as numerous studies have shown. The goal of phenetics is to show overall similarity, not to build phylogenies. The goal of cladistics is to show patterns of relationship or phylogenies. Pheneticists use, or should use, data from individuals and usually it is largely quantitative. Cladists tend to use groups of individuals as their terminal taxa and so use characters that do not vary among individuals, more often than not these are qualitative. It is not impossible to use the same data in both types of programs but it is only valid with certain types of data.

It has been said many times that the quality of a cladistic study is only as good as the characters used. It is apparent that the most important part of a cladistic study and the part that takes most of the effort is the selection and analysis of characters. Hastily selected characters, using other people's data without understanding them, failing to understand characters, will all give poor results. These are not problems with the method and such accusations should not be used to fault the method. The fault lies with the individual(s) who are conducting the studies. I must emphasize that such mistakes are more easily recognized in a cladistic study than an intuitive one because the data are obvious.

Hybridization occurs in many plant groups. When it has been carefully studied it usually does not present insurmountable problems in a cladistic study. When it is rampant within a group or when the group has not been the subject of a thorough modern revision then there are definite problems with attempting a cladistic analysis. This situation has never been denied by cladists.

Fossil data are often used in cladistic studies and there are numerous cladistic studies by paleobiologists that illustrate this. When only a few characters are missing, an analysis can be done with all taxa. When some of the fossils have a large amount of missing data then they can be added after the cladogram is finished. This method may result in polytomies, but contrary to a commonly heard criticism, polytomies are not only allowed but frequent in cladistic studies.

As for all of the complaints about our inability to determine homology or to pick outgroups or to deal with character loss, etc., I can only say that while certainly these are not simple problems they exist for traditional taxonomists as well. Further, cladistics has a definite advantage over traditional taxonomy in handling these problems. If the reader does not like the outgroup (or outgroups) he can change it and easily see what effect it will have on the cladogram. Many recent cladistic studies have used more than one outgroup. If the reader disagrees with the polarity or analysis of a character he can change it and see if a change occurs in the cladogram. Surely by now it is obvious that while many of the same problems exist in cladistics and traditional taxonomy the difference is that one can examine the results of a cladistic study and—especially if they are familiar with the groups involved—understand what the author has done and see if they agree or disagree and know the reason why. The other advantage is that the monophyletic groups produced in a cladistic study are statements about the evolutionary history of the groups. All of the members of a monophyletic group share a common history and because of that we can use the groups for studies in biogeography, coevolution, speciation, etc. So, my advice to the reader is to ask yourself the three questions presented above and if the answer is yes to all three then you might wish to start by reading the references listed below.

Suggested Readings

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COMMENT ON THE BIBLIOGRAPHY OF *FLORA HAWAIIENSIS* BY MILL ET AL.

The excellent article by Mill et al. (1985) provides an invaluable service in straightening out the bibliographic details for Otto and Isa Degener's *Flora Hawaiiensis.* However, it may be hazardous to simply accept the author notations at the bottom of each page of this work as representative of the true authorship, which is what Mill et al. (1985) apparently did. The following detailed example makes this clear:

Léon Croizat (1894–1982) contributed several accounts to *Flora Hawaiiensis,* all on Euphorbiaceae: Croizat and Degener (1936–37), Degener and Croizat (1937, 1946), and Degener et al. (1960). Mill et al. (1985: 232, 244) give Croizat and Degener (1936–37) as "Degener and Croizat," and indeed this is the inscription on the bottom of each recto of the leaves (each verso bears merely "Degener"—Croizat and Degener, 1936–37: Cham. 3, have these inscriptions reversed in the three copies seen). However, "Croizat and Degener" is the proper form of citation for several reasons: (1) In Croizat and Degener (1936–37: Cham. 1) it is noted that "the amended definition and the critical notes [for *Chamaesyce*] contributed *solely* by Dr. Leon Croizat are accepted in the *Flora Hawaiiensis* at considerable length because of their great importance" [my emphasis]. These notes are clearly in Croizat's distinctive style of writing, which, however, is tame here compared to that in his later, post-1951 works (see Schmid, 1985). (2) Two footnotes in Croizat and Degener (1936–37: Cham. 1) indicate "the writer," i.e., singular form. (3) The first point is later confirmed (Croizat and Degener, 1936–37: Cham. 4), to wit, "Degener, simply editor of this article and junior author for most of the following combinations." Thus, of the 20 new nomenclatural combinations in Croizat and Degener (1936–37), 13 are by Croizat and Degener, six are by Croizat alone, and only one is by Degener and Croizat. (4) Similarly, "*Chamaesyce* S. F. Gray descr. emend. Croiz." begins the account of the genus in Croizat and Degener (1936–37). (5) "Croizat and Degener" rather than "Degener and Croizat" is the citation form used for the 1936–37 publications in Degener and Croizat (1946), Degener et al. (1960), and in other works on *Chamaesyce* by Otto Degener or by Otto and Isa Degener (see Mill et al., 1985), although Degener and Degener (1959) give "sensu Degener & Croizat." (6) Finally, "Croizat and Degener" is the citation form usually seen in the literature on Euphorbiaceae, for example, Herbst (1971) and Webster (1967), and works cited in the latter and in Schmid (in prep.).

On the other hand, analysis of the pages for Degener and Croizat (1937, 1946) and Degener et al. (1960) suggests these are the proper forms of citation, as also indicated by Mill et al. (1985). Degener and Croizat (1946), in fact, contains a new varietal combination by "Degener & Croizat."

In conclusion, critical reading of the contents of *Flora Hawaiiensis* seems necessary to determine the proper authorship of the individual contributions. This amendation of Mill et al. (1985) is not meant to denigrate their tremendous bibliographic accomplishment as all such endeavors by definition cannot achieve the holy grail of perfection (e.g., see Langman, 1964: 9 on "random thoughts on bibliographies").

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