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# THE USES OF CLADISTICS<sup>1</sup>

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The usefulness of cladistics derives from the fact that cladogenesis, the branching component of phylogeny, is a part of the theory of evolution. I am an evolutionary systematist, a member of the Simpson-Mayr school of systematics, which has profound objections, principally in the area of classification, to the cladistic or so-called phylogenetic school of Hennig (30). Nonetheless, I think cladists are quite right when they complain that their very real and important contributions to biogeography and to chronistics and coevolution have been ignored or seriously misunderstood. It is the purpose of this discussion to review and enlarge on these areas. Accepting the tenets of the cladistic school on biological classification is neither necessary nor desirable, but cladistic analysis is a prerequisite for an evolutionary classification.

## TERMINOLOGY

Simpson (46) characterized Hennig's terminology as idiosyncratic. The years since have demonstrated that this terminology is a mixture of valuable concepts and terms occasionally misapplied, badly defined, or not defined at all. The list below is meant to correct this situation and to provide a vocabulary for evolutionary systematics. Deviations from Hennig are identified and equivalent terms provided. Ashlock (1, 2) has discussed the terms related to monophyly, and Tuomikoski (47) has provided helpful discussion of some concepts.

*Cladistic*: Pertaining to the branching sequence in evolution.

*Anagenetic*: Pertaining to the accumulation of changes in ancestor-to-descendent lineages.

*Cladistic analysis*: Analysis of the characters of organisms to infer the evolutionary branching sequence of a group's phylogeny (*phylogenetic analysis* of Hennig).

*Cladistic classification*: Classification in which only holophyletic (q.v.) taxa are permitted and categorical rank is determined by the group's age.

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*Monophyly*: A monophyletic group is one whose most recent common ancestor is a cladistic member (q.v.) of that group.

*Holophyly*: A holophyletic group is a monophyletic group that contains all descendants of the most recent common ancestor of that group (*monophyly* of Hennig).

*Paraphyly*: A paraphyletic group is a monophyletic group that does not contain all descendants of the most recent common ancestor of that group.

*Polyphyly*: A polyphyletic group is one whose most recent common ancestor is not a cladistic member (q.v.) of that group.

*Cladistic member*: A cladistic member of a group is any recent member of a holophyletic group, as demonstrated by one or more synapomorphous characters, any fossil that shares these characters, and all inferred ancestors within the group.

*Apomorphous*: The relatively derived state of a sequence of homologous characters.

*Plesiomorphous*: The relatively primitive state of a sequence of homologous characters.

*Synapomorphous*: Uniquely derived apomorphous character that is found in two or more taxa under consideration. Such characters serve to demonstrate the holophyly of groups of taxa that possess them.

*Autapomorphous*: Apomorphous characters found in a single taxon not being considered for further subdivision.

*Sister-group*: In a dichotomous cladogram, the two holophyletic groups that are descendent from any inferred ancestor.

*Phylogeny*: The evolutionary history of organisms, to include both cladistic and anagenetic information (in Hennig's usage, the cladistic aspects of evolution).

## CLADISTIC ANALYSIS

A cladogram is a hypothesis, the best explanation of the distribution of characters, be they morphological, behavioral, or other, in the organisms under study, using all of the facts available. It cannot be proved, although it may be supported by external evidence.

Hennig and his followers employ for cladistic analysis what has come to be known as "Hennig's principle": Only synapomorphous characters delimit monophyletic taxa. For evolutionary systematists, the principle as stated presents some problems which are solved if it is restated: Only synapomorphous characters delimit holophyletic groups. The word monophyletic as used by Hennig (all the descendants of the most recent common ancestor) indicates a concept of very great theoretical importance and utility, but the concept is far from the traditional meaning of monophyletic and is unsuitable for evolutionary systematics. The term holophyletic was coined by Ashlock (1, 2) for Hennig's concept. The word *groups* is used instead of *taxa* since, unlike cladists who may proceed directly from cladistic analysis to classification, evolutionary systematists require additional anagenetic analysis before formal taxa can be delimited.

Hennig has never really defined *synapomorphous*, at least in English, nor has its complementary term *plesiomorphous* been defined. In reading the works of cladists, one quickly realizes that apomorphous characters must be derived characters, while

plesiomorphous characters are primitive. It is not so immediately apparent that not all derived characters are synapomorphous. While loss of wings in holometabolous insects is derived, and fewer than five toes in tetrapods is derived, use of such characters in cladistic analysis will result in preposterous groupings. (Generally one should be suspicious of "loss" characters.) Reliable synapomorphous characters (sometimes referred to as true synapomorphies) are unique and complex. For example, feathers and a horny bill on birds are excellent for making an inference that the common ancestor of modern birds had these characters as well. Other good examples are the tube feet of the Echinodermata, the halteres of Diptera, and retractible claws of cats.

It is also obvious that the systematist must arrange the characters of the group under study into primitive-to-derived sequences (transformation series of cladists; primitive-to-derived character states of numerical taxonomists), and that the parts of these sequences must be evolutionary homologues.

Estabrook (22) has reviewed computer approaches to cladistic analysis. Methods are based on two principles: parsimony and compatibility. Parsimony (the cladogram with the fewest steps is the most probable one) makes the assumption that evolution usually takes the shortest route. Rogers, Fleming & Estabrook (43) have criticized the principle on mathematical grounds. I would add that while no law of evolutionary theory requires evolutionary parsimony, the principle is not without use. Compatibility (the largest collection of compatible characters is best evidence for the true cladogram) more accurately reflects evolutionary theory. The compatibility matrix of Camin & Sokal (14) and the successive approximations approach of Farris (23) are two such methods. Though both include parsimony in their calculations, the trees produced are not always the most parsimonious; rather, they reflect a high degree of compatibility.

Computer cladistic analysis can be helpful in producing cladograms when no cladistic hypotheses are clearly evident from the data, or in producing alternate hypotheses. Computer-produced cladograms, however, should always be checked for synapomorphy [using, for example, Wilson's (48) consistency test]. Other ways to check the validity of a cladogram are suggested elsewhere in this review. Strict operational methodologies are notably inappropriate (31) to cladistic analysis since cladogenesis is a theoretical, not an empirical, concept.

## BIOGEOGRAPHY

### *Direct and Indirect Biotic Connections*

To my mind the most important paper to appear in recent years on the subject of historical—as opposed to ecological—biogeography is Hennig (27), translated into English by Wygodzinsky under the title, "The Diptera fauna of New Zealand as a problem in systematics and zoogeography" (29). The paper is at once brilliant and badly conceived. Its title and organization are such that few but dipterists would be attracted, yet the principles covered are of use to all systematists and biogeographers.

In his introduction, Hennig writes (29)

Many a taxonomist who writes a monograph of his group leaves questions unanswered which he, and only he, could have answered and only because he had been unaware of the existence of these questions. Such questions consequently remain unanswered, because it is too difficult to obtain again for study the material (types, rare species, etc.) which the monographer had at his disposal.

The general questions that interest Hennig are: From which other areas has a given, relatively isolated land surface (large island or continent) received its faunal elements, and with which other areas has it therefore been connected? When, how long, and in what sequence have these connections existed?

To attack these questions, Hennig says that it is necessary to ask about each endemic species in the area concerned (here New Zealand): which is its sister-species and where does it occur. It is likely that the first sister-group, which may or may not be a single species, will also be found in New Zealand; but continuing cladistic analysis will yield a sister-group on another land mass and eventually in all biotic areas of the world. Hennig refers to this method of analysis as "search for the sister-group."

One would expect highly vagile organisms to be distributed in both New Zealand and Australia. The relative proximity of the land masses forms an adequate explanation for the distribution. A more exciting possibility is that the sister-group of a New Zealand or Australian group occurs in South America. Hennig refers to such groups as A-S (Australian-South American) groups.

In listing A-S genera of Diptera, Hennig notes that such highly derived and recent large groups as the Schizophora are poorly represented, while more primitive flies are well represented. He feels that this is no accident. Hennig suggests three possible routes between southern land masses of the eastern Old World (A) and the New World (S): (*a*) across the southern Pacific; (*b*) across the Antarctic continent; and (*c*) across northern hemisphere land masses. Routes *a* and *b* Hennig terms direct routes, while *c* is designated as indirect.

Before discussing how one establishes whether or not a given group followed a direct route of distribution, Hennig dismisses two superficially attractive indications that are, in fact, insufficient to distinguish between direct and indirect faunal connections. These are: (*a*) members of an A-S group that are more similar to one another than either is to any other group in the world; and (*b*) members of an A-S group that form a holophyletic group.

Neither case provides proof of direct distribution, since the A-S group might have had its origin in the northern hemisphere, migrated to different parts of the southern hemisphere, and later been replaced by more advanced groups in the northern hemisphere.

Hennig proposed three criteria that are adequate to show a direct connection between disjunct parts of A-S groups: the progression rule, the phylogenetic intermediate rule, and the multiple sister-group rule.

**THE PROGRESSION RULE** Hennig's well-named progression rule refers to a geographic sequence of taxa whose direction of progression is indicated by a series of

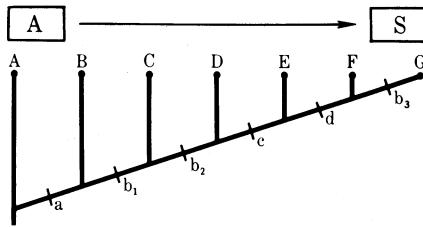


Figure 1 Hennig's progression rule.

increasingly derived synapomorphous characters. Figure 1 illustrates Hennig's hypothetical example, where taxon A is found in New Guinea, B in Queensland, C in Victoria, D in Tasmania, E in New Zealand, F in Tierra del Fuego, and G in Chile. If it is established that group A through G is holophyletic, and further, if cladistic analysis convincingly demonstrates a sequence of holophyletic groups BCDEFG, CDEFG, DEFG, EFG, and FG as established by a series of synapomorphous characters (either unrelated characters such as a, c, and d in Figure 1 or a sequence of progressively more derived homologous characters such as  $b_1$ ,  $b_2$ , and  $b_3$ ), then one would have to agree that the group A through G did indeed progress from New Guinea through Australia, Tasmania, New Zealand, and on directly to South America. To hypothesize an alternate route through the northern hemisphere, one would have to suppose a migration of the derived taxa (or their ancestors) through an area of more primitive species, without having left traces.

The progression rule can be used only when the distribution of the organisms is not seriously disturbed. However, that a group of organisms fits the progression rule is evidence that it has not been seriously disturbed. It is highly unlikely that a group of organisms would be disturbed in such a way as to give a false logical progression of synapomorphous characters.

*Examples* No published account has come to hand that employs the progression rule in establishing a direct A-S connection. However, such an account is currently in preparation for the mutillid wasps by D. J. Brothers. The progression rule may also be used to arrive at biogeographic conclusions not involving A-S routes. A routine revision of the ischnorhynchine lygaeid bug genus *Neocrompus* (3) made no mention of the progression rule, but it clearly applies. *Neocrompus* was originally described for a single species from Samoa distinguished partially by the widely flaring rear portion of the seventh abdominal segment, a character unique in the Lygaeidae. The 1966 revision added four species to the genus. One, from New Guinea, has the seventh segment unflared and similar to all others in the family. Two of the species, from Fiji and the Austral Islands, are flared like the Samoan species, and the last, from Tahiti and nearby islands, has the flared seventh segment with an additional lobe shaped somewhat like a protruding thumb. Clearly, the New Guinea species is the most primitive of the five, and the Tahiti species the most derived, indicating an eastward progression of the genus across the South Pacific.

**THE PHYLOGENETIC INTERMEDIATE RULE** Hennig did not provide a name for this rule, but he headed the discussion "Demonstration of phylogenetically intermediate forms on islands situated on the direct line of connection between South America and Australia-New Zealand."

Evidence of a former direct connection between two continents (such as Australia and South America) would be provided if forms more primitive than Old World and New World representatives were found on islands on or near the shortest direct route between the continental areas concerned (Figure 2). The phylogenetic intermediate rule is really a special case of the progression rule in which members of a group proceed in two directions from an origin that is no longer inhabitable (Antarctica). The same strictures apply to acceptance of the phylogenetic intermediate rule hypothesis as to acceptance of a progressive rule hypothesis.

No examples of use of the phylogenetic intermediate rule have come to hand.

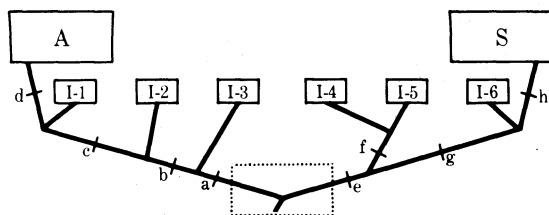


Figure 2 Hennig's phylogenetic intermediate rule.

**THE MULTIPLE SISTER-GROUP RULE** Again, Hennig provided no short name for this model. The rule may be stated: If a monophyletic (i.e. either holophyletic or paraphyletic) group can be demonstrated to have multiple sister-group relationships between the areas under discussion, then a direct connection between these areas has been established (Figure 3). With an A-S multiple sister-group relationship, one must give serious consideration to Antarctica as the home of the group's common ancestor, although either Australia or South America remain as possibilities.

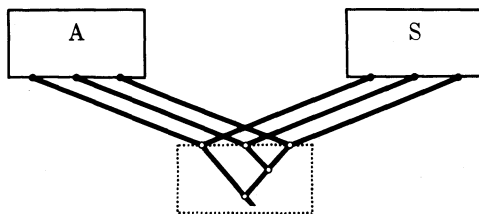


Figure 3 Hennig's multiple sister-group rule.

Figure 3 demonstrates three or six transoceanic crossings of the monophyletic group, depending upon possible involvement of Antarctica. Hennig feels, as was pointed out earlier, that a single sister-group relationship between taxa in Australia and South America is not sufficient evidence for a direct connection. However, as the number of A-S sister-group relationships within a single monophyletic group increases, the credibility of a northern origin decreases. If their origin were northern, the distribution of the organisms in Figure 3 would require six southern migrations and subsequent loss of all trace of the origin.

*Examples* It is with applications of the multiple sister-group rule that the most successful uses of cladistics have come. Notable is Brundin's work with chironomid midges, for it was the first cladistic analysis that dealt with the concepts of continental drift. The major work was published in 1966 (10) but the earliest discussion was in 1963 (8), and he provided summaries in 1965 (9) and 1967 (11). The major work and the two summaries carry Brundin's cladogram that, if accurate, demonstrates twenty transantarctic relationships. Such massive demonstration of the multiple sister-group rule clearly establishes direct southern faunal connections. These were not merely A-S relationships, but included Africa as well. Especially striking in Brundin's cladogram is the sequence of sister-group relationships. The sister-group of an Australian organism is found in South America, not New Zealand as one might expect from the proximity of the land masses. New Zealand midges are the sister-group of Australian and South American midges together. Brundin (9) does not hesitate to conclude that he is on the track of the real nature of transantarctic relationships. He states:

The conclusion is inescapable that the transantarctic relationships developed during a period when the southern lands were directly connected with each other. There is no reason to speculate on island stepping-stones or chance dispersal over wide stretches of ocean. We have to accept as a fact that the transantarctic relationships and the distribution patterns of the chironomid midges are orderly. And they show very clearly that the connections between the southern lands were broken according to a certain sequence which started with the separation of southern Africa. The next event was the break of the links between Antarctica and New Zealand, which obviously never had any direct connections with Australia. Later separation between Antarctica and Australia occurred. The last connections between Antarctica and Patagonia were cut still later, probably not very long ago. We have indeed the right to be confident, since this sequence of events, as indicated by the chironomid midges, is in good accordance with modern opinions among the geologists concerning the disruption of Gondwanaland.

Another such study was done by Edmunds (21) in the mayflies, and he in a similar manner summarized his results:

From the total evidence from Ephemeroptera plus minimal geological evidence as noted, the suggested sequence of the breakup of Gondwanaland is as follows. 1. India drifted to the north (evidence largely geological). 2. South Africa plus Madagascar drifted to the north with the continent pivoting so that the break with South America widened most rapidly at the south leaving Africa and Brazil attached or close together in the



tropics. The presence of many African groups in Madagascar suggests that the split of Madagascar from Africa was one of the last breaks. 3. New Zealand plus New Caledonia drifted to the north. 4. New Caledonia separated from New Zealand. 5. Australia drifted north and Antarctica drifted south. (The direction and sequence of 5 in relation to 6 are based on geological evidence.) 6. South America drifted northwest in relation to Antarctica.

Edmunds' study confirms the results of Brundin's study. Both are in the best tradition of the scientific method: both use one kind of evidence (synapomorphic characters) to arrive at an hypothesis (their respective cladograms) and then find their hypotheses to be confirmed not only by each other but also by external evidence (the sequence of the breakup of Gondwanaland as postulated from geological evidence).

Hennig's (29) discussion of the multiple sister-group rule does not include continental drift, but continental drift provides the best theoretical explanation for the multiple sister-group rule. In Figure 3, the land mass with the dotted outline may be considered to be a pre-drift supercontinent upon which a holophyletic group has evolved three widely distributed lineages. If the supercontinent split into two daughter continents (A and S in Figure 3), both would carry the three lineages. The continental splitting may continue. If the three lineages on daughter continent A were each to develop into two lineages, and continent A split in two, each fragment (call them A-1 and A-2) would carry all six lineages. The sister-group of a lineage found on fragment A-1 would be found on fragment A-2. The sister-group of a lineage on continent S, however, would be found on both A-1 and A-2, not on one fragment only. The sequence of the splitting of continents from Gondwanaland explains the orderly splitting that Brundin and Edmunds found.

**THE DRIFT SEQUENCE RULE** The Brundin and Edmunds studies have introduced what amounts to a fourth biogeographic rule which can be applied to the problem of direct versus indirect connections between various land masses. The rule may be stated: If the sister-group relations of a monophyletic group conform to the sequence of continental drift of at least three continents, then direct biotic connections between the continents have been established. At least three continents are specified because sister-group relations between two only are, as Hennig has pointed out, inconclusive. As stated, the multiple sister-group rule need not be a part of the evidence for direct connections. For example, if three holophyletic groups were each confined to New Zealand, Australia, and South America, and the sister-group of the New Zealand group was found to be in Australia and South America together, conforming to the last few splits from Gondwanaland, then requirements of the drift sequence rule would have been met. Requirements of the multiple sister-group rule, however, would not. The Brundin and Edmunds studies are, of course, all the stronger for having met both of these rules.

It is possible that the drift sequence demonstrated from geological evidence may not be matched by the cladistic branching of a particular group of organisms, even though they were on a supercontinent before breakup. Such discrepancies may be caused by uneven distribution of the organisms over the supercontinent, by such

barriers as mountains, epicontinental seas, or ice, or by extinction on one or more of the fragments of the supercontinent. It is hoped that someone will prepare an atlas of continental drift to show not only the positions of the land masses through geological time but also what is known of climatic and other possible barriers.

Several authors have discussed the sequence and timing of the breakup of Pangea. The broad movements have been clearly established, but changes in the interpretation of details must be expected for several years to come. Literature on the subject should be watched carefully as it appears, but the following papers will serve as a starting point (4, 5, 16, 20, 24, 42).

An obvious criticism of all of these biogeographical models is that the models themselves (such as the Gondwanaland breakup sequence) were used to "discover" the characters used in the study and thereby compromise the validity of the conclusion. There is no denying that the best demonstration of a biogeographic model would come from a study in which the investigator assembled a convincing array of strong synapomorphous characters without reference to the distribution of the organisms under study. Such an ideal is too much to ask, however. Good synapomorphous characters are very difficult to find, and a systematist welcomes anything that aids him in looking for them. The validity of such studies must be judged by assessing the quality of the characters establishing the groups and the possibility of alternate hypotheses based on the same or additional data.

#### *Other Biogeographic Uses*

**PLACE OF ORIGIN** Darlington (19) and Brundin (12) have exchanged opinions on various points, including the validity of Hennig's biogeographic rules and of Brundin's application of them. Part of the exchange dealt with whether the more primitive or more derived members are likely to be found at the center of origin of groups. Brundin, in the more perceptive of the discussions, noted that Darlington's arguments are based on single, arbitrarily selected characters, when such questions as the center of origin of a group should be answered by means of sister-group or cladistic analysis of the group. Nelson's (38) discussion of the subject provides some specifics of the methodology.

The first place to look for the probable origin of a group, i.e. the original distribution of its common ancestor, is within the area of distribution of the monophyletic group to which the common ancestor belongs (including geographically holophyletic and paraphyletic groups). There are limitations, however. Too many of the species may have a wide distribution. Extinction can cause very serious errors. If members of a group migrate more than once from area A to area B, and the group then becomes extinct in area A, then the distribution of living forms will be misleading. A suitable fossil found in area A must be taken into account. If, on the other hand, a single species from a group that had its origin in area A migrated to area B, speciated, and became the founder of a new large group of organisms, while all members of the group remaining in area A became extinct, then, in terms of living species, area B is the place of origin of the group. Where a monophyletic group has been found, as by Brundin and Edmunds, to occupy several southern continents, the area of origin is the sum of these continents, or Gondwanaland. Confirmation

that such a southern distribution is actually a Gondwanaland distribution would have to come from at least one of the four rules previously discussed.

**NUMBER OF INTRODUCTIONS** The determination of how many times a particular taxonomic group has crossed geographic barriers to account for its present distribution is a problem whose solution requires application of some obvious principles, and some that are not so obvious as well.

One example can be found in the Hawaiian birds of the endemic family Drepaniidae (the honeycreepers), well known for their bizarre beak modifications. Each species of Hawaiian honeycreeper has as its closest relative another Hawaiian honeycreeper, and only collectively are they related, more distantly, to a mainland group. The consensus of those who have discussed the group is that the honeycreepers resulted from a single introduction to the Islands. The various species, or some intermediate ancestors, certainly could have evolved elsewhere, migrated to the Islands, and left no trace of their origin, but there is no evidence of it. Thus the simplest inference, that there was one introduction to the Islands, stands.

The Drepaniidae is probably a monophyletic (and holophyletic) group. If so, the example can be stated cladistically: A holophyletic group that is distributed only in a limited geographic area probably had its place of origin within that area. As there is no evidence that the most recent common ancestor lived elsewhere, the group is not only holophyletic but also geographically holophyletic, and represents a single introduction.

Geographic holophyly is illustrated in Figure 4a where the taxa labeled O are found at the place of origin and those labeled X represent the geographically holophyletic group. The migration from the place of origin must have taken place during the time period indicated by internode 2-4 on the cladogram, as shown by the arrow.

If another related group of Hawaiian land birds such as the honeyeaters (*Moho* and *Chaetoptila*, another holophyletic group with mainland relatives thought to represent a single introduction to the Islands) is added to the Drepaniidae, then the assemblage becomes geographically polyphyletic: that is, the most recent common ancestor could not have lived in the Islands. Thus, in a geographically polyphyletic

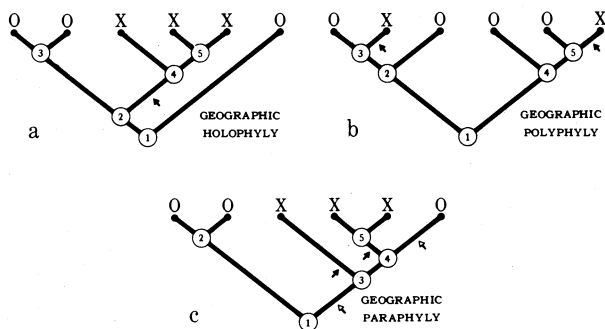


Figure 4 Cladograms illustrating number-of-introduction principles.

group, the minimum number of introductions is equal to the number of geographically holophyletic subgroups that make up the larger geographically polyphyletic group. Geographic polyphyly is illustrated in Figure 4*b*. Arrows again indicate the internodes where migrations must have taken place.

An additional possibility, geographic paraphyly, requiring involvement of at least three groups, is illustrated in Figure 4*c*. This group had its origin and development in one area and has a descendent group in a second area. If a third group descendent from the second is found in a third area, one has an example of the progression rule. If this third group is found in the same region as the original ancestral group, conditions for geographic paraphyly have been met.

Geographic paraphyly involves an element of ambiguity. If in Figure 4*c*, the O's are found in Siberia, the X's in North America, and the ancestor of 1 is firmly established as having an Old World origin (descendent of a complex of Old World forms), it is obvious that the group migrated from the Old World to the New across the Bering Straits and that two migrations have taken place. The question is, in which direction? The group may have migrated from the Old World to the New twice, as indicated by the black arrows. It is equally possible that the group migrated to the New World and later evolved a group that migrated back to the Old World, as indicated by the white arrows.

Additional information is needed to remove the ambiguity of geographic paraphyly. For example, if the group represented in Figure 4*c* had the taxa labeled O in the Americas and those labeled X in the Hawaiian Islands, then one would postulate that two migrations had taken place from the Americas to the Islands, based on the assumption that an insular form would have a difficult time competing with continental forms.

The minimum number of migrations a group has made to island archipelagos is very important to MacArthur & Wilson's *Theory of Island Biogeography* (34) and to Leston's "Spread potential and the colonization of islands" (33).

## CHRONISTICS

Chronistics, the study of the age of biological groups, is most often left to paleontologists. As Hennig (30) has said, the paleontological method has the reputation of being the most reliable, if not the only, method of determining the age of groups. But, like most methods, it has limitations. Spottiness in the fossil record limits the method to giving only minimal ages of groups, not absolute ages. Moreover, fossils show fewer characters than recent organisms, making them more difficult to use for cladistic analysis.

However, properly dated fossils can be more significantly assessed with cladistic analysis than without. Hennig (30) demonstrated this with three groups of Diptera, and a generalized example is illustrated in Figure 5. The figure shows three groups of recent organisms, X, Y, and Z, whose cladistic analysis was based upon characters (or groups of characters) a, b, and c, demonstrating that X, Y, and Z are progressively more derived.

If a properly dated fossil relative of group X-Y-Z is discovered showing only the characters symbolized by a, little can be said about the age of the group. The fossil

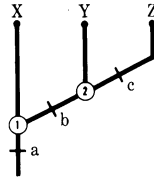


Figure 5 Cladogram illustrating chronistic principles.

might have come from the internode ancestral to node 1, the internode between 1 and X, somewhere along internode 1–2 before characters b evolved, or from a side branch leading to an extinct taxon from any of the three mentioned internodes. At best, all this fossil can do is to establish a date after which the characters a could not have evolved.

If a dated fossil bearing characters b is found, however, then the investigator has a date after which the inferred ancestor at node 1 could not have originated. Such a fossil, then, would help determine the age of the primitive branch to X. Similarly, a fossil bearing characters b and c must have evolved subsequent to node 2, and provides a date after which ancestors at both nodes 1 and 2 could not have originated. Favorable fossils, then, can help to date various parts of a cladogram, even lineages for which no fossils are available.

Barriers to migration can be used to date parts of cladograms, just as fossils are used. For example, both Brundin on chironomid flies and Edmunds on mayflies have much to say about the ages of their organisms. Both of these groups, by the multiple sister-group rule and the drift sequence rule, have been established as present on Gondwanaland at the latest before Africa drifted away. The date when Africa separated from Gondwanaland, then, is the latest possible time for the origin of the groups. Similarly, the New Zealand break establishes a date of origin for the New Zealand elements of the groups and for their sister-groups.

Thus, if a group of organisms can be established to have crossed what is now a barrier to their migration, and a date is known for the initiation of that barrier, then the latest possible date of origin, not only for the group that crossed the barrier but for its sister-group as well, is the date of the barrier. Barriers may be of many sorts: epicontinental seas, deserts, mountains, forests, gaps in strings of islands preventing island-hopping; effectiveness of all barriers depends on the vagility of the organisms involved.

## CO-EVOLUTION

Hennig (30) discussed what he called the parasitological method, dependent upon Fahrenholz's Rule: "In the case of permanent parasites, the relationship of the host can usually be inferred directly from the systematics of the parasites." The assumption is that the evolution of the hosts is directly paralleled by that of the parasites (Figure 6a). Hennig points out a number of reasons why this assumption can lead to false conclusions. The parasite group may have joined its host group well after

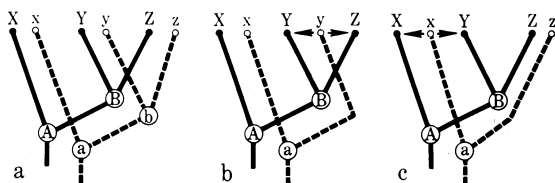


Figure 6 Cladograms illustrating problems possibly encountered in the study of host-parasite or symbiont lineages.

the host group began to evolve. Even if the two evolved together, some host lineages may have escaped from their parasites, or a parasite may have transferred from one host lineage to another. Unequal rates of evolution in various lineages of host and parasite may also cause problems if similarity rather than cladistics is used as a criterion for relationship.

Even without these problems, and with a proper cladistic analysis of the parasites, some less obvious difficulties can be created by incomplete parallelism of speciation in the host and parasite lines. In Figure 6b, a speciation of the host at B is not paralleled by a speciation of the parasite, and the same parasite *y* is found on both hosts Y and Z. One would here, on the basis of the parasite, correctly conclude that the hosts Y and Z form a holophyletic group. In Figure 6c, however, the parasite again has not speciated in a parallel manner with the host at A, but the presence of parasite *x* on both hosts X and Y here leads to an incorrect assumption that X and Y form a holophyletic group.

Perhaps a better way to look at Fahrenholz's Rule is to treat it as a question rather than a rule. If a cladistic analysis is made on both the host and parasite (or other symbiotic system) groups, then one could ask: Did the parasite evolve with the host? If not, was there a partial co-evolution of the host and parasite? The degree of co-evolution would be shown by the degree that the cladogram of the host matches the cladogram of the parasite. A study by W. Ramírez (in preparation) on *Ficus* (to subgeneric level) and the fig-wasp pollinator (Agaonidae) demonstrates a nearly complete congruence between cladograms of the figs and of the wasp pollinators, indicating a nearly complete parallelism of the evolution of the two groups. Ramírez can even demonstrate to some degree how the figs and wasps adapted to one another by comparing the characters that appear on equivalent internodes of the congruent cladograms.

Another possible co-evolutionary use of cladistics is in the study of hard-to-associate morphotypes within the species of a single group: immatures versus adults in groups with a pronounced metamorphosis, and males versus females where these differ grossly. If sets of morphotypes are complete, cladistic analysis in each set within the group should yield identical cladograms. It would be especially interesting to apply cladistic analysis to those cases where the original association was made on biological grounds, for then differing rates of evolution, if any, could be studied in the morphotypes.

## CLASSIFICATION

Probably the most important and controversial use of cladistics is in classification. The phenetic school of taxonomy does not concern itself with cladistic analysis, feeling that phylogeny is inherently unknowable. There are, of course, numerical taxonomists interested in computer methods of cladistic analysis, and such persons should not be confused with pure pheneticists. Another nameless group, whose best spokesman is Blackwelder (6, 7), and which is not concerned with cladistic analysis, feels that taxonomy is something one does, not something one thinks about. Cladistic analysis, then, is of concern to the cladistic and evolutionary schools of systematics.

The cladistic school of Hennig will allow only holophyletic groups of organisms in its classifications and rejects both polyphyletic and paraphyletic groups. Sister-groups are to be given the same categorical rank, and rank is determined by the age, i.e. date of origin, of the group. The age criterion is apparently less stringent than others, for Hennig (30) has suggested that vertebrate zoologists need not be held to the age-rank system he suggests for insects, and Nelson (40) suggests some measure of relative difference be incorporated while maintaining the other precepts. Resulting classifications are most often grossly different from those produced by other schools of systematics.

Evolutionary systematics, in contrast, will allow both holophyletic groups and paraphyletic groups, both of which have traditionally been considered to be monophyletic units. Polyphyletic groups, or those based upon convergence, are excluded, as they are not genealogical groups. Formal taxa are recognized as genealogical groups of relative internal homogeneity that are separated from phylogenetically related groups by decided gaps. Categorical rank is based upon tradition, with changes made conservatively. In general, the precise definitions of categorical ranks must remain unsolved problems. Classifications in evolutionary systematics will be similar to those of the pheneticists and to traditional classifications, but will be based upon an estimate of genetic similarity rather than phenetic similarity.

The most important work supporting the cladist's view on classification, of course, is Hennig (30). Some other discussions that, together with Hennig (30), give most of the arguments in favor of cladistic classification and against evolutionary classification are (10, 13, 15, 17, 18, 26, 28, 39-41, 44, 45). Evolutionary systematists have been less vocal than cladists. The principal works of the Simpson-Mayr school are Simpson (46) and Mayr (37). Other discussions that support evolutionary systematics and argue against cladistic classification are (1, 2, 19, 32, 35, 36, 47). Darlington's (19) discussion is unfortunate, since he did not have an adequate understanding of the cladist's viewpoint, but I can agree with some of his statements. Hull (32) agrees with the philosophical position of evolutionary systematics, but he criticizes its weak methodologies. Pheneticists have also entered the discussion, giving arguments against both the cladistic and evolutionary schools, often confusing them.

Cladists have developed a number of arguments defending their system against evolutionary and other schools of systematics. For example, speciation is the only decisive process in evolution, and as cladistic branching is a direct result of past

speciation events, classifications that depend only on cladistic analysis of evolution are the most precise possible and will reflect nature's own hierarchy. Only with cladistic classifications can the phylogeny of higher taxa be read directly from the formal classification, and only with a cladistic classification can the mysteries of historical biogeography be understood and studied. Cladistic classifications, furthermore, have historical precedence, because Darwin was the first cladist.

The cladists go on to say that classification systems dependent upon anagenesis are just as typological as those of the phenetic school. Mayr's "genetic similarity" is indistinguishable from "taxonomic distance" of the numerical taxonomists, and similarity itself is a composite based upon plesiomorphous, apomorphous, convergent, parallel, and reversed characters. The measurement of similarity depends upon atomization or unit treatment of characters, which is unrealistic. Any of the proven benefits (e.g. biogeographic) of phylogenetic systematics (cladistics) are impossible under other systems, and any compromise system (phenetic plus cladistic) is bound to lead to confusion. Higher taxon names of the noncladist do not give you the characters of the group or seem to serve any other purpose.

Finally, evolutionary systematics involves a great deal of "art" in its methodology, and evolutionary classifications can only be inferred. Since there is no real method involved, the Simpson-Mayr school deserves no further consideration.

It should be emphasized that these arguments are a composite of those advanced by cladists. No one cladist would use all of them, and many could probably think of more.

As a theoretical and practical science, systematics has many tasks. Some are discussed in this review, and it is to the credit of the cladists and especially of Hennig's admirable logic that new depths have been added to the science of systematics. Other tasks are the traditional ones of describing and explaining groups of similar organisms, and of providing an information retrieval system for all concerned with these organisms. All science is, as Hull (32) has so well demonstrated, most productive when it is based in well-formulated theory. Systematics in the fulfillment of its tasks is most productive when it uses evolutionary theory to its fullest, and it is with evolutionary theory that systematics makes its ultimate explanations, with classification providing the framework for these explanations. Omissions of major parts of evolutionary theory from the systematic process can lead only to loss of information in resultant classifications.

All schools (evolutionary, cladistic, and phenetic) are complex bodies of theory and methodology. All, within their own contexts, can stand improvement. It has often been repeated that evolutionary systematics contains too much art, and Hull (32) has called for a reduction of this art. Evolutionary systematists are indebted to both pheneticists and cladists for forcing a reexamination of evolutionary systematics and pointing to better ways of approaching problems.

For example, it has been the practice of evolutionary systematists to treat the phylogenetic dendrogram as merely a summary of an already completed classification. The phenetic and cladistic schools, on the other hand, treat dendrograms or other graphic displays as necessary steps in the process of formulating a classification. In fact, the dendrogram has become an integral part of their classification. The lesson for evolutionary systematics, if it is to achieve its stated goal of maximal use



of evolutionary theory, is that in forming a classification, one must first approach the problem of classification with cladistic analysis to establish the branching patterns of phylogeny and then establish relative amounts of evolution on each internode of the cladogram. The cladogram is thus preserved in its entirety, and the major anagenetic gaps on the tree are established, providing a means to delimit the holophyletic and paraphyletic groups that become formal taxa. The benefits of such a methodology, I believe, will be very great.

Because the new evolutionary dendrogram will have a cladogram at its core, it can be put to all the uses of the cladogram discussed in this review as well as any that might be thought of in the future. When cladists claim that only cladistic classifications allow understanding of biogeography, and that such studies are forever lost to the Simpson-Mayr school of evolutionary systematics, they are only partially correct. Evolutionary systematics without cladistic analysis cannot do these things. On the other hand, it is not the list of formal taxonomic names that is the result of cladistic classification which permits cladistic conclusions, it is the cladogram that does so.

Since in any dichotomous dendrogram there is one less branching point than there are terminal points, the number of names needed for a complete description of the cladogram is one less than the number of species contained in the group, in addition to the names needed for the species themselves. Any time a cladistic classification contains a group with three or more immediately subordinate taxa, the classification is ambiguous in its ability to reflect the cladogram. A trifurcation can represent a true evolutionary trifurcation or, more probably, any of three possible unresolved dichotomously branched systems. Four subordinate taxa could imply any of 17 possible interpretations. I don't believe that the cladists want to burden systematics with the number of names needed to make formal cladistic classifications completely describe cladograms. Thus formal cladistic classifications, like evolutionary ones, are not without ambiguity in their ability to describe cladograms. Both systems need to refer to cladograms for the benefits of cladistic analysis, which both have available. It is the cladistic analysis, not the cladistic classification, that provides the potential uses of cladistics.

The inclusion of relative anagenetic information in the dendrogram leads to a more complete understanding of taxa. In a cladistic analysis, only those characters with a high cladistic information content (synapomorphies) are needed or wanted. Schlee (44) reports that he used only 33 of some 500 characters studied in a classification of the sternorrhynchous Homoptera. Such a drastic paring of characters is right and proper for cladistic analysis, but also represents a huge information loss in the final dendritic or formal classification. As the cladogram was established on the basis of those relatively few characters, anagenetic analysis would attempt to place as many more characters on the dendrogram as possible. The basic cladogram would be available to help with decisions regarding the ancestral or derived nature of cladistically weaker characters. This methodology will require unitization of characters, which should not cause serious difficulty. It must be assumed that one's ability to discover characters is proportional to the actual amounts of evolution that have taken place throughout the history of the group. Such methods, which will require appropriate character weighting, will not only establish major gaps in

the phylogenetic dendrogram useful in delimiting formal taxa, but also will demonstrate most fully the evolutionary history of taxa and their attributes.

Mayr (37) has emphasized that evolutionary systematics classifies organisms on the basis of genetic rather than phenetic similarity. The cladists are quite right when they say that the concept of similarity is a composite one, but it is only with cladistic plus anagenetic analysis that the various kinds of similarity can be sorted out. Such analysis will count convergent, parallel, and reversed similarities as the genetic differences they really represent. Phenetic studies treat these genetic differences as similarities. Apomorphous and plesiomorphous similarities are the source of most genetic and phenetic similarities. This fact explains why an evolutionary classification as outlined will resemble phenetic and traditional classifications to a large degree. Since cladistic classifications are concerned only with apomorphous similarity, they are often drastically unlike those produced by any other method.

For the dubious advantage of being able to read off "phylogeny" from a formal listing of taxa, cladists are willing to pay, as Hull (32) has said, a price too high for many biologists. Species that split off in the Precambrian but gave rise to no other species would have to be classed as phyla. Such classifications would be highly monotypic and highly asymmetrical. In Nelson's (39) classification of the vertebrates, jawless fishes are treated at the same hierarchical rank as all other vertebrates put together, and birds are included in a group with crocodilians, well below their customary ranking in the taxonomic hierarchy. Such classifications, which group highly dissimilar taxa and separate similar ones, seriously restrict generalizations that may be made about the members of formal taxa and greatly interfere with nonspecialists' recognition of taxonomic groups. Cladistic classifications are inherently unstable; the discovery of a single character can establish that a group formerly thought to be holophyletic is paraphyletic, making it invalid in spite of a high degree of homogeneity.

I fail to see that a classification employing both cladistic and anagenetic information is confusing. Far from being a compromise between cladistic and phenetic systems, it incorporates the best of both. Because the methods are based upon theoretical rather than empirical considerations, it can do a far better job of explaining similarity than a pure phenetic approach can do.

Ghiselin & Jaffe (25) have shown that Darwin in his classification of barnacles knowingly accepted paraphyletic groups, and so the claim that Darwin was the first cladist is incorrect. Such arguments are trivial at best. Presumably, present workers know more about the subjects of phylogeny and classification than Darwin did. His major contributions to biology are widely recognized while his mistakes (such as his ideas about inheritance) are unimportant.

To say that the higher category names of noncladists are worthless because they do not give you the phylogeny or characters or anything else is really an attack on human language. The word *chair* meant nothing, either, until there was human consensus about what it would mean. The valid criticism that no good methodology exists for evolutionary systematics will become invalid as soon as such a method is published. I would suggest that it is inevitable that such methods will appear within the next few years.

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