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CLASSIFICATION: MORE THAN JUST BRANCHING PATTERNS OF EVOLUTION

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ABSTRACT

The past 35 years in biological systematics have been a time of remarkable philosophical and methodological developments. For nearly a century after Darwin's *Origin of Species*, systematists worked to understand the diversity of nature based on evolutionary relationships. Numerous concepts were presented and elaborated upon, such as homology, parallelism, divergence, primitiveness and advancedness, cladogenesis and anagenesis. Classifications were based solidly on phylogenetic concepts; they were avowedly monophyletic. Phenetics emphasized the immense challenges represented by phylogeny reconstruction and advised against basing classifications upon it. Pheneticists forced reevaluation of all previous classificatory efforts, and objectivity and repeatability in both grouping and ranking were stressed. The concept of character state was developed, and numerous debates focused on other concepts, such as unit character, homology, similarity, and distance. The simultaneous availability of computers allowed phenetics to explore new limits. Despite numerous positive aspects of phenetics, the near absence of evolutionary insights led eventually to cladistics. Drawing directly from phenetics and from the Hennigian philosophical school, cladistics evolved as an explicit means of deriving branching patterns of phylogeny and upon which classifications might be based. Two decades of cladistics have given us: refined arguments on homology and the evolutionary content of characters and states, views of classifications as testable hypotheses, and computer algorithms for constructing branching patterns of evolution. In contrast to the phenetic movement, which was noteworthy for seeking newer concepts and methods, even including determining evolutionary relationships (which led eventually to numerical cladistics), many cladists have solidified their approaches based on parsimony, outgroups, and holophyly. Instead of looking for newer ways to represent phylogeny, some cladists have attempted to use branching patterns: (1) as a strict basis for biological classification and nomenclature and (2) to explain the origin of biological diversity even down to the populational level. This paper argues that cladistics is inappropriate to both these goals due to: (1) inability of branching patterns to reveal all significant dimensions of phylogeny; (2) acknowledged patterns of reticulate evolution, especially in flowering plants; (3) documented nonparsimonious pathways of evolution; and (4) nondichotomous distribution of genetic variation within populations. New concepts and methods of reconstructing phylogeny and developing classifications must be sought. Most important is incorporation of genetic-based evolutionary divergence within lineages for purposes of grouping and ranking.

Key words: cladistics, classification, explicit phyletics, phenetics, phylogeny.

INTRODUCTION

The history of biological systematics is essentially as old as biology itself, going back to the Ancient Greeks (Mayr 1982). Early insights to plant classification were provided by Theophrastus around 300 B. C. (see Theophrastus 1916), although these largely stressed simple differences in habit. From these early beginnings flowed numerous efforts to organize the living world into increasingly predictive systems of information retrieval. Plant classification emphasized medicinal properties (The Age of the Herbalists, 1470–1670; Arber 1912), structural features (e.g., Cesalpino 1583), and even specific numbers of stamens and carpels (Linnaeus 1735). Slowly a more balanced system

appeared with the post-Linnaean “natural systems” of Jussieu (1789) and Candolle (1824–1838).

Darwin's (1859) *Origin of Species* provided a convincing rationale for why classifications had predictive value: similarity based on descent from a common ancestor. Although the theory of evolution by means of natural selection provided no new classifications directly, perspectives on classification changed dramatically. The newer, post-Darwinian classifications, such as that of Engler and Prantl (1887–1915) were based on evolutionary assumptions and ideas. The influential “dicta” of Bessey (1915) were a series of evolutionary assumptions that had major impact on classificatory perspectives. The importance of monophyletic groups (i.e., those that derive from a common ancestor) to classifications was recognized and search for them intensified. Numerous phylogenetic branching diagrams were produced, and it was accepted that monogra-

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phers, especially at the generic level, would provide evolutionary discussions and a phylogram as part of the expected syntheses. Evolutionary (phylogenetic) systematics thrived for a century and major systems of classification were produced, such as Hutchinson (1926, 1934), Thorne (1968, 1976, 1992), Takhtajan (1969, 1980), Dahlgren (1980), Cronquist (1981), and Dahlgren and Clifford (1982).

In the late 1950s, however, some workers began to question some of the methods of evolutionary classification. Perhaps due to the increasingly quantitative nature of other areas of biology and perhaps also a reaction to the century-old intuitive methods almost approximating apprenticeship, focus turned to how biological classifications might also be made more quantitative (Sneath 1957; Michener and Sokal 1957). This perspective led to the development of phenetics, which emphasized use of many equally weighted (or non-weighted) characters clustered to provide branching patterns (Sokal and Sneath 1963; Sneath and Sokal 1973). Such a quantitative approach to classification was made possible by the availability of computing machines, without which advances in phenetics in the 1960s and 1970s would have been severely hindered if not rendered impossible.

Phenetics taught us many things. It showed the importance of carefully examining characters for information content, and it gave us the useful concept of character state. It focused on the difficult problem of homology and it forced a total reevaluation of the philosophy, concepts and methods of classification. It also showed how different procedures often lead to different results. The main problem with phenetics was that in attempting to be totally quantitative and objective, it ignored evolutionary assumptions on the grounds that they were too subjective and complex. But this perspective proved ultimately frustrating to systematists who knew that taxa had derived from the process of evolution and who suspected this background should probably be reflected in a classification of high information content. Phenetics, then, proved not the final solution to the needs of biological classification.

The stimulus of phenetics, combined with new philosophical and methodological perspectives from Hennig (1950, 1966) and especially workers at the American Museum of Natural History (e.g., Nelson 1971, 1972), led to cladistics. Hennig was following the German school of interest in phylogeny but reacting against the idealistic-morphological systems of classification in popular use (Mayr 1995). Examples of workers interested in cladistics who came from phenetics included Camin and Sokal (1965), Estabrook (1968) and Farris (1970). This cladistic approach emphasized explicit construction of branching diagrams of phylogeny and basing classifications upon them.

During the past two decades, cladistics has been

successful in many ways and for a variety of reasons. It certainly has provided explicit means for the reconstruction of branching patterns of phylogeny. It has also stressed that classifications are testable scientific hypotheses. It is superficially easy to do, especially with aid of computer programs such as PAUP (Swofford 1993). It has provided a convenient vehicle for analysis of DNA sequence and restriction site data that are accumulating in increasing quantities. And, other biologists, now more comfortable with molecular phylogenies that seemingly have higher levels of confidence through statistical evaluation, are seeking and using phylogenies as never before (e.g., Harvey et al. 1996). Study of phylogeny has returned to its rightful important role in comparative biology that it enjoyed from 1859 to the early decades of this century. This also helps emphasize the significant role that systematics has for other areas of biology. In fact, we have reached a point where the major innovations in techniques for tree construction and evaluation are being developed by workers who are not systematists! They are frequently molecular population geneticists with strong mathematical backgrounds who earlier showed little interest in phylogeny reconstruction because of lack of statistical rigor.

Despite all these positive contributions of cladistics, the impact on actual plant classification has been minimal. During the past 20 years, we have continued to refine our concepts and philosophy about interpreting relationships, but few new classifications have resulted from these analyses. Those that have appeared have been the subject of considerable discussion (e.g., Anderberg 1990, 1992; Orchard 1992).

Cladistics, then, is at a crossroads. It either will begin to have greater impact on actual plant classifications, or it will evolve into something else as occurred earlier with phenetics. It is the thesis of this paper that we should intensify our efforts to go beyond cladistics and achieve explicit evolutionary classification. In this fashion, we build upon the positive developments and experiences from both phenetics and cladistics to provide a quantitative approach to evolutionary classification that has been the principal method for nearly a century and is still the dominant method worldwide for practicing taxonomists.

The purposes of this paper, therefore, are to: (1) review some of the problems with cladistics; (2) comment briefly on the impact of DNA data in cladistic analysis; (3) discuss why cladistics finds itself now at a crossroads; and (4) review methods of explicit phyletic (= evolutionary) classifications as improvements over simple cladistic approaches, including a new quantitative method for determining apomorphic support for recognition of taxa.

PROBLEMS WITH CLADISTICS

As with previous approaches to classification, now after more than 20 years it is appropriate to reevaluate the efficacy of cladistics. There already have been numerous critiques (e.g., Mayr 1974; Cronquist 1987; Stuessy 1990), and much has been said on nearly every topic. However, the fact remains that new cladistic classifications have not replaced all previous ones based largely on phyletic (= evolutionary) approaches. We might ask, therefore, why is this so? The answer seems to lie with numerous problems with methods, concepts and philosophy, some unique to cladistics, and others also problematic for phyletics or phenetics (i.e., for any method of biological classification).

First are methodological problems. Studies of evolutionary groups require that they are well enough understood to include all known representatives. Such groups are believed to have come from a common ancestor and hence monophyletic. The difficulty is that many groups are simply not well known; hence cladistic analysis can yield only the most tentative of hypotheses, subject to drastic change as new relatives are encountered.

Selection of characters and states that have evolutionary import is a central area of cladistic analysis. Because fewer characters are usually employed, establishing the proper evolutionary significance of each character and its states is much more critical in cladistics than in phenetics, which stresses maximum character information. This is an area that has not yet received sufficient critical attention (see, however, a careful analysis of the problem by Stevens [1991]). What are the levels of confidence that tell us we have, in fact, captured the relevant evolutionary data? We have relied on the concept of "conservation" in many instances, and an attempt has been made to quantify this measure (Farris 1966), but this is not entirely satisfactory as a measure of evolutionary information content. The issue of weighting of cladistic characters is also of concern (e.g., Wheeler 1986). Allied to this is difficulty in establishing logical interconnectedness of character states to form a character-state network. Parsimony is invoked, usually because no data are available to the contrary. More and more workers are tending not to order completely their states evolutionarily, which has the effect of lessening evolutionary constraints in this part of the analysis, and in some ways more closely approximates weighted phenetics.

One of the greatest difficulties with cladistics, as also with phyletics, has been the determination of evolutionary polarity (i.e., which character states are primitive and which are derived). Difficulty with this point was one of the main stimuli for the development of phenetics. As we often have little direct evidence that bears on the issue, we must rely on a series of as-

sumptions and indirect evidence, all of which have problems (Crisci and Stuessy 1980; Stuessy and Crisci 1984). Many cladistic practitioners have focused entirely on outgroup comparison, often restricted to sister groups (e.g., Watrous and Wheeler 1981). Other workers have stressed a broader outgroup vision (e.g., Donoghue and Cantino 1984; this criticized as "relaxed parsimony" by Nixon and Carpenter 1993) as well as allowing ontogenetical perspectives (e.g., Forey et al. 1992). The problem here is that the further one goes from the study group, the higher goes the probability that similar character states are nonhomologous. The greatest problem with outgroup analysis, long used in phyletic classification, is not the concept—but its uncritical use. As pointed out by Stuessy and Crisci (1984), strict sister-taxon (or close relative) outgroup can fail in certain instances. Disney (1993) stresses problems with outgroup and mosaic evolution. The solution to the problem is not abandonment of the concept, but a reminder of caution and a plea for maximum biological information before final polarities are determined. Developmental data and ecological correlations are among the other insights that should be sought. Stressing outgroup alone narrows our ability to make the most informed evolutionary decisions regarding one of the most critical aspects of cladistic analysis.

As happened with phenetics, several algorithms for branching pattern reconstruction within cladistics have evolved, the most prominent being parsimony, character compatibility, and maximum likelihood (e.g., Felsenstein 1984). For DNA, numerous additional algorithms exist due to simplicity of the characters and states, their differential rates of permutation, and their large numbers of data points. For morphological data, in recent years the parsimony method, especially using PAUP, has reigned supreme. However, increased interest on weighting of character states and lowering of homoplasy of trees has led to convergence of parsimony toward character compatibility. Morphologically based cladistics, therefore, has tended to solidify on outgroup comparison (especially with reference to sister taxa), unordered character state networks, and parsimony algorithms as found in PAUP.

The second set of problems with cladistics is conceptual. That evolution is not always parsimonious has been demonstrated on several occasions (e.g., Gastony 1986; Sang et al. 1995; Schilling and Panero 1996). The numerous documented cases of reticulate evolution in vascular plants (see Grant, 1981, for many examples) as well as many progenitor-derivative species pairs (e.g., Gottlieb 1973; Crawford and Smith 1982; Crawford et al. 1985; Kadereit et al. 1995) remind us that simple dichotomous branching diagrams cannot do justice to the real world of higher plant phylogeny. Lamboy (1994) has recently demonstrated this point

convincingly. We must remember that cladograms are models (or hypotheses) of relationships that discard unwanted information ("noise"; Gauch 1993) and represent, therefore, different degrees of reflections of reality.

Another serious conceptual problem with cladistics is its reliance on few characters. Obviously with gene sequence data this point is obviated, but with morphological data it is serious. Frequently, branch points on cladograms are supported by only single synapomorphies. If and when such units are accepted formally in the classification, it represents a return to single-character taxonomy that was discarded during the 19th century for lack of predictive quality of resultant groups. Further, this type of minimal support for branch points makes the phylogeny (and any resultant classification) unstable, changing dramatically with a change in characters and states or the addition of new evolutionary units in the analysis (Stuessy 1990). Cladistics need not be so narrow in selection of characters and states, however, as emphasized by Thiele (1993). The impact of extinction in cladistic analysis has rarely been addressed. Because of the low stability of cladograms due to use of few characters, the degree of missing taxa due to extinction could markedly impact tree topology. Olson and James (1982a, b) have determined, based on fossil evidence, that many of the birds of Hawaii have become extinct, up to 75% of known species on Oahu. This sort of error can lead to drastic alteration of tree structure, depending on the nature of variation lost. The important point is that we should be seeking new ways to infer extinction events such as by the insertion of hypothetically extinct taxa and evaluating the robustness of branch points in the analysis (similar to jackknifing, e.g., Lanyon, 1987, but adding, rather than subtracting, taxa).

The most serious problem for cladistics, and in my opinion a fatal one as it relates to classification, is use of only branching information in phylogeny. Phylogeny has many dimensions, including cladistics, chronistics, patristics, character-state divergence, rate of evolutionary change, and others. Traditional evolutionary classification attempted successfully to interpret all aspects of phylogeny and to incorporate these data into a highly informative classification. The problems here lay not with the information content, but rather with the lack of explicit approaches. Cladistics has lost much to gain confidence of explicit methods.

Another problem with cladistics is its sole reliance on synapomorphies as a criterion for determining relationships. The stress on synapomorphy vs. symplesiomorphy is in part semantic: the former becomes the latter if looked at from above a node. I believe that shared primitive character states can indeed be helpful in defining taxa, especially in the context of polythetic rather than monothetic groups (for definition, see So-

kal and Sneath 1963). Who would argue against the primitive character states of laminar placentation, essential oils, undifferentiated stamens, etc. as helping to define Magnoliales? More importantly, other dimensions of relationships are ignored, such as crossing (cytogenetic) data. These biologically informative data such as degree of stainability of pollen in artificially generated interspecific hybrids, derive from interactions *between* taxa and therefore are more akin to coefficients of association rather than synapomorphic data. Nonetheless, they are extremely valuable, especially as they relate to biological bases of species. Recent macromolecular studies of the tarweeds (Compositae, Madiinae) by B. Baldwin (1996, 1997) show remarkable congruence with cytogenetic data by Clausen et al. (1945) and Carr and Kyhos (1981, 1986; see also summaries by Clausen, 1951, and Kyhos et al. 1990). Some cladists have criticized cytogenetic data (i.e., crossability) on the grounds that they are plesiomorphic data of no value to phylogenetic reconstruction (Funk 1985). This is simply not true. As species diverge from a common ancestor via diploid allopatric means (a simple example), they accrue genetic and reproductive differences from the common ancestor and this occurs in parallel (this is also one of the reasons why cladistics can also be regarded as parallel anagenesis; Stuessy et al. 1990). Crossing of distinct species, therefore, measures the degree of difference from the ancestor: the less they cross, the more they have diverged and the less related they are judged to be.

Once again, at the conceptual level there are many cladistic algorithms from which to choose. In fact, there are so many different techniques available, especially statistical evaluations, that they far outstrip the veracity of the data themselves. We need to reinvigorate efforts on understanding characters and states rather than seeking the shortest tree which probably is a gross simplification of the real phylogeny. One might argue that we should be seeking trees deliberately longer than the shortest one, perhaps by adding biological constraints such as hypothetical extinction, progenitor-derivative and reticulate relationships, and developing statistical evaluations of the results. Most impressive are the existing measures for evaluating robustness of tree topologies. These have proliferated due to input from mathematically inclined population geneticists who have new confidence in phylogenetic reconstruction. Methods are available for evaluation of the data relative to the tree topology in the form of Consistency Index (Kluge and Farris 1969), Distortion Coefficient (Farris 1973), Retention Index (Farris 1989a, b), Rescaled Consistency Index (Farris 1989 a), and Decisiveness (Goloboff 1991). Other measures deal with evaluation of the tree topology by resampled data or taxa such as the Bootstrap (Felsenstein 1985; Sander-

son 1989), Clade Stability by character removal (Davis 1993), Jackknife (Miller 1974), Homoplasy Excess Ratio (Archie, 1989*a, b*), Permutation Tail Probability (Faith and Cranston 1991), Homoplasy Slope Ratio (Meier et al., 1991), and Topiary Pruning (Wills 1996). Still other measures include the Decay Index (= branch support; Bremer 1988, 1994), generation of and comparison with random trees (Penny and Hendy 1985), and through assessing distribution of apomorphies within cladograms, e.g., by Successive Approximations Character Weighting (Carpenter 1988, after Farris 1969), and the Homoplasy Distribution Ratio (Sang 1995).

The third set of problems with cladistics is philosophical. Although there is nothing inherent in cladistic methods that requires employment at all levels of the taxonomic hierarchy, some practitioners have so extended its use even down to the populational level (e.g., Davis and Nixon 1992). Such zeal has led to renewed debates on the nature of species focusing on how they should be defined in a cladistic context (e.g., Davis 1995). This has reached such exaggerated levels that most species must now be regarded as "meta-species" (Donoghue 1985; de Quieroz and Donoghue 1988) because they are clearly paraphyletic (Riesberg and Brouillet 1994; Crisp and Chandler 1996). This zest to extend cladistic analysis pervasively throughout the living world seems based on the idea that having a uniform and comprehensive mode of classification would once and for all insure a "scientific" and philosophically supportable classification of all life forms. While laudable, such a perspective naively assumes that the processes of evolution have been sufficiently similar in all groups so that the generated diversity can be dealt with in equal fashion. With so many types of genetic variation partitioned in so many different types of organisms, with vastly differing reproductive regimes, this effort would seem futile (for agreement, see Doyle 1995). A number of these problems have been pointed out, and alternative algorithms based on population genetic data suggested, by Crandall et al. (1994).

Perhaps the most serious philosophical problem with cladistics is the belief that only holophyletic taxa can be accepted in classification. The original definition of monophyletic, derived from Darwin (1859), Haeckel (1866) and others of the last half of the 19th century, stressed groups that have a common ancestor. Hennig (1966) modified this century-old definition to apply to groups that have a common ancestor *and* that contain *all* the descendants of that ancestor. Groups that are monophyletic but do not contain all the descendants were called paraphyletic (Hennig 1966). Such paraphyletic groups are not accepted in strict cladistic classification. By definition, these perspectives exclude paraphyly as being a nonevolutionary, and

therefore inappropriate, basis for classification, simply because for more than 150 years nearly all workers have agreed that classification should be based on monophyletic groups. Ashlock (1971, 1984), seeing the problem clearly, suggested the term holophyletic for the narrower definition of monophyly. Under this perspective, monophyly consists of both holophyly (the only evolutionary unit accepted by cladists) and paraphyly, both being accepted by evolutionary systematists. This voluntary loss of evolutionary information in classification is the most serious problem with strict cladistic approaches.

Finally, because of the recommended dictum of cladistic classification that sister-taxa should be classified at the same rank in the Linnaean hierarchy (e.g., Hennig 1966), serious difficulties arise. The main problem is the proliferation of categories needed to reflect the numerous units resulting from such a rigid perspective, as shown clearly in other papers in this Symposium, and has led some workers to suggest abandonment of the Linnaean hierarchy (e.g., de Quieroz [1997]). The overwhelming practical taxonomic and nomenclatural problems aside, after more than 200 years of organismic classification using the Linnaean hierarchy as the point of reference, one must ask what the achievement would be? For cladists the success of having a complete correspondence between cladogram and classification might be reward enough. In my opinion, this narrowed perspective with reduced evolutionary information content is no gain at all and certainly not desirable. Even if theoretically desirable, it would still be suspiciously viewed in the face of enormous practical difficulties. I would add that in this urgent climate of seeking to inventory the world's biota (Anonymous 1994), and requesting funds from the rest of society to do so, it would be highly counterproductive to simultaneously recommend whole-scale change of names of organisms for any reason.

DNA DATA AND CLADISTICS

DNA sequence and restriction site data analyzed with cladistic methods have already had a marked impact on interpreting relationships among plants (e.g., Crawford 1990), particularly in reconstruction of phylogeny. A spectacular example is the work of Jansen and colleagues (e.g., Jansen and Palmer 1987; Jansen et al. 1990, 1991, 1992) on higher-level relationships in Compositae, a family so natural and cohesive that it has defied understanding of close relatives and intrafamilial classification (i.e., subfamilies and tribes). Restriction site (Jansen and Palmer 1987) and sequence data (Jansen et al. 1992) from cpDNA pointed to subtribe Barnadesiinae of Mutisieae as basal for the family. This was an unexpected result. Members of this subfamily form a complex of nine genera and

some 90 species distributed in southern and Andean South America. These initial DNA phylogenies allowed new perspectives to be developed on the origin and early biogeography of the family (e.g., DeVore and Stuessy 1995; Stuessy et al. 1996).

The spectacular success of many new DNA phylogenies in complex groups that had previously proved nearly intractable suggests that any serious future efforts to reconstruct phylogeny must take DNA relationships into account. These successes and the robust statistical evaluations that the large amounts of data allow, have made molecular phylogenies sought after by all manner of evolutionary biologists (Avice 1994; Harvey et al. 1996). Although morphologically derived phylogenies (cladograms) have been produced for more than two decades, it has been molecular data that have caused the great interest due to higher levels of confidence in the results. Other biologists need to know the phylogenetic constraints of their organisms as they investigate comparative morphology, anatomy, cytology, phytochemistry, behavior and ecology. This has also helped position systematics in its rightful central role in all of biology.

But despite all these positive dimensions of DNA data in phylogeny reconstruction, there are also problems, again methodological, conceptual and philosophical. The methodological problems deal with several issues, including which portion of the genome to sample, how to properly align the sequences obtained, and how to analyze massive amounts of data. In plant systematics, the initial data for macromolecular phylogenies came mostly from cpDNA restriction site data (e.g., Palmer 1987) and then moved quickly to sequences from the chloroplast genome and now to nuclear genes. New regions are constantly being explored for taxonomic potential. Some regions are so conservative as to be useful only at higher levels of the hierarchy (e.g., *rbcL* [cpDNA]) whereas others seem better suited for revealing relationships at lower levels (e.g., ITS [nrDNA]). We can only guess at the hundreds and thousands of new gene sites that will be evaluated for systematic potential in the years ahead. The practical matter of alignment of sequences is also problematic if considerable variation exists in the data sample, but statistical techniques are available to offer at least the best judgement possible (e.g., the computer programs CLUSTAL, Higgins et al. 1992; ALIGN, Wheeler and Gladstein 1994). Dealing with vast quantities of data has also been problematic, requiring faster and faster computers to yield parsimonious solutions.

Conceptual problems are also encountered with DNA data in phylogeny reconstruction. Homology, strangely enough, has been reduced in DNA to a comparison of four base pairs (= positional homology; Hillis 1994). One would think that we have finally

reached a point of dealing simply and directly with the slippery homology issue, but this is clearly not the case (see recent discussions in Hall 1994). The issue has moved to another and more subtle plane: the identity of base pairs is not alone sufficient because we do not always know *how* they became identical. We must now employ concepts of orthology, paralogy and xenology (for definitions, see Hillis 1994). That is, depending upon the evolutionary history of the group, similar base pairs may be judged homologous in different ways; the statistical evaluation of related base pairs in the sequence being important to determine. A further problem for homology is the knowledge of transposable elements (e.g., Mazodier and Davies 1991; MacRae 1995) that complicates simple analyses of sequences. Usually such events affect a substantial section of DNA and hence are detectable, but we will doubtless learn much about the limits and occurrences of transposable elements in the years ahead and surprises are to be expected.

Unequal rates of sequence evolution are also a problem for cladistic analysis with DNA data. We already assume that transitions are more likely than transversions, but what of other sequence alterations, rates of mutation, etc.? We also know about unequal rates of evolution throughout the genome (e.g., Wilson et al. 1987; Li 1993), which interfere with application of the molecular clock hypothesis, and which also complicate interpretation of cladistic results. Much will be revealed in the years ahead: caution must be exercised at this time in basing classification solely on these data.

And philosophically, the problem exists as to whether we are looking at the proper parts of the genome for our comparisons. We usually examine genes that workers in other areas of biology have already discovered with their techniques. What portion of the genome contains the most significant evolutionary information? This is not unlike attempting to select the most evolutionarily significant morphological characteristics. Decades will pass before we will understand the limits of much of the genome for systematic purposes. It is not inconceivable that after learning much more about gene interactions, especially developmental constraints, we might decide that DNA sequences by themselves are not the data of choice for reconstructing phylogeny, at least not in isolation. Perhaps "supercharacters" will be used that combine DNA sequences with developmental interactions and anatomical and morphological data. This would be slightly similar to the concept of "total evidence" for phylogeny reconstruction (e.g., Chavarr'a and Carpenter 1994), but obviously at a more sophisticated and integrative level.

CLADISTICS AT THE CROSSROADS

These numerous problems with both morphological and DNA data in cladistics raise concerns about its present status and future directions. In my opinion, cladistics is at a crossroads. It must either go the road of totally replacing existing classifications (such as recommended by Christoffersen, 1995, and others in this Symposium), or it must take the path of being modified into an improved system. After nearly 20 years of stimulating activities, cladistics has yet to make a major impact on plant classification. Most of the results so far have confirmed taxa established previously on phyletic bases, but some have not. In these cases, the all-too-frequent conclusion is that further study is needed before a final answer can be reached. Occasionally, direct taxonomic and nomenclatural action has been taken, sometimes meeting with strong opposition from phyletic workers (e.g., Anderberg 1990, 1992; Orchard 1992). Methods of analysis have now far outstripped veracity of character data, especially morphological. Workers have been hesitant to act on cladistic results in the past due to: numerous problems discussed above; unclear correspondence of cladistic units to the Linnaean hierarchy; and failure of cladistics to deal effectively with autapomorphic data. A good example can be taken from Baldwin's (1996) excellent work on the *Madiinae*. Molecular data (ITS) reveal all the Hawaiian tarweeds, including *Argyroxiphium* and *Wilkesia*, to tie cladistically within the *Madia-Raillardiopsis* complex on the California mainland. Because the result renders the mainland taxa paraphyletic, cladistic rules rejecting paraphyly would recommend combining the extremely morphologically divergent island taxa into *Madia* or *Raillardiopsis*. Such a suggestion has been met less than enthusiastically by island taxonomists (B. Baldwin, pers. comm.) perhaps due to failure of cladistics to take into account the large amount of anagenetic (or patristic) genetic and evolutionary character-state divergence from mainland to island relatives.

The time has come, I believe, for cladistics to mature into a more lastingly effective system of classification that will be evolutionarily based and information rich. This will then serve the real needs of society as a general-purpose evolutionary classification in the context of the Linnaean (or other) hierarchy. Such a maturation involves change into quantitative phyletics or explicit evolutionary classification (Stuessy 1990).

METHODS OF EXPLICIT PHYLETIC CLASSIFICATION

General purpose classification of high evolutionary information content must be sought by a modification of cladistics into explicit phyletics. Evolutionary classifications have not been rejected in recent years on theoretical or conceptual grounds—they have simply

been ignored on the grounds that because they are intuitively generated, direct comparisons with cladistics and phenetics have not been possible.

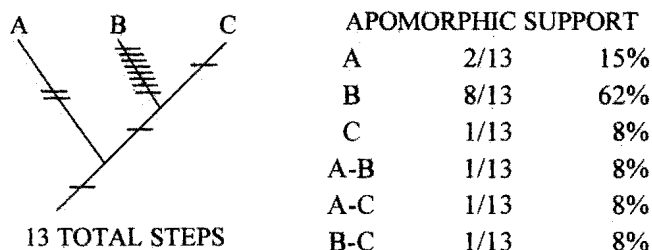
Several methods for explicit phyletics already exist. Estabrook (1986) recommended "convex phenetics" (and his new program CONPHEN) as the method of choice. Here the basic analysis is phenetic clustering, but the phenogram is constrained to only allow convex (i.e., monophyletic s.l.; Meacham and Duncan 1987) groups. This has been used effectively by Carpenter (1993) in classification of Caesionid fishes.

Stuessy (1987, 1990) recommended several extensions of cladistic analysis to yield different types of phylograms of increased information content. The simplest are cladograms but with branch lengths proportional to the degree of character-state divergence. This was also clearly demonstrated in the Wagner Groundplan Divergence graphic method (Wagner 1980) and is available in PAUP. Consensus techniques blending cladograms, patrograms (a dendrogram based on patristic distance) and/or phenograms were also recommended, as were resemblance matrix additions. For this latter method, quantitative values for patristic relationships were added to cladistic distances all derived from cladistic analysis and reclustered to yield a phylogram. A two-dimensional graphic technique was also recommended, vector analysis, whereby points in phenetic space were separated outward from each other based on their cladistic (and/or patristic) quantitative relationships.

Hall (1988, 1991, 1995) has offered a series of complex perspectives involving self-graded deweighting of homogeneity and agglomerative clustering and dilation. His computer program UNITER was developed to handle the calculations. Despite the positive direction of these efforts and his proper emphasis on polythetic classification, the unavailability of the computer program (it requires a FORTRAN compiler) and the complexity of the concepts make them difficult to evaluate critically.

Ashlock (1991) has developed a method called "anagenetic analysis" that uses character weighting, anagenetic distance between nodes and taxa, subtended taxa values, and precise phylogram construction. This has the advantage of being done manually so that the relationships can be easily recognized.

There already exist sufficient methods of explicit phyletics to begin to evaluate the results of such classification in comparison with cladistics. Carpenter (1993), to my knowledge, is the only person actually to provide such direct comparison (in Caesionid fishes). Working with CONPHEN and cladistic parsimony analysis to construct branching diagrams, he used conventional cladistic sequencing methods for taxa recognition (Wiley 1981) and invented a new means for delimiting taxa directly from the phylogram. Using an



TOTAL APOMORPHIC DIFFERENCE (MEAN %) BETWEEN OTHER CLADES AND TERMINI

	A	B	C	A-B	A-C	B-C
A	—					
B	47	—				
C	7	54	—			
A-B	7	54	0	—		
A-C	7	54	0	0	—	
B-C	7	54	0	0	0	—
\bar{X}	15	53	12	12	12	12

Fig. 1. Hypothetical example of a cladogram of three taxa (A-C) showing apomorphies, and calculations of apomorphic support for all possible taxonomic units (as percent of total steps in the tree) and total apomorphic difference between other clades and termini (mean percent, given at bottom by \bar{X}).

information optimality model as yardstick (Duncan and Estabrook 1976), he judged phyletic classification superior to that from cladistics. Many more studies of this nature need to be executed.

All these methods attempt to modify cladistic analysis by adding anagenetic information. The central issue is: how to form taxonomic groups from enhanced evolutionary phylograms. It may be impossible or undesirable to have *absolute* rules for such efforts. Certainly, phenetics failed with its attempt at absolute phenon lines for ranking (for original concepts, see Sokal and Sheath 1963). Cladistics has still not been successful with its various sequencing and/or ranking conventions (Wiley 1981), due largely to the problem of resultant "cornucopia of categories" (Colless 1977). I would now agree that general-purpose biological classification should be a combination of cladistic and patristic data, with phenetic data (i.e., numerous unweighted characters and states selected without any concern for evolutionary information content) being profitably used for studies with complex character trends and associations, especially at the populational level, and not employed solely to develop general-purpose classifications of high predictive value.

To help in better understanding the value of autapomorphic and anagenetic data in phyletic classification, a new approach is offered here. The issue is to evaluate these data for their import in recognizing tax-

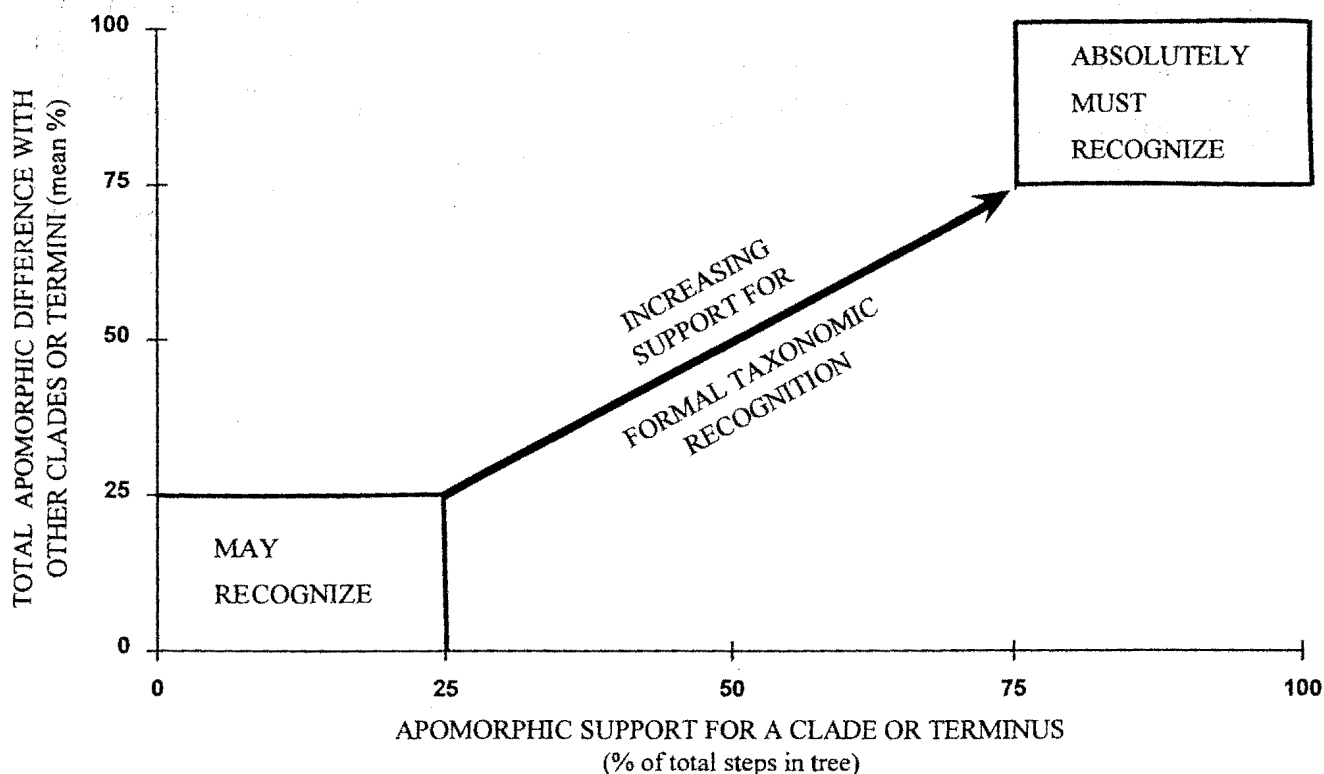


Fig. 2. Relationship between degree of apomorphic support for a group and degree of total apomorphic differences between it and other clades or termini, showing increasing support for formal taxonomic recognition.

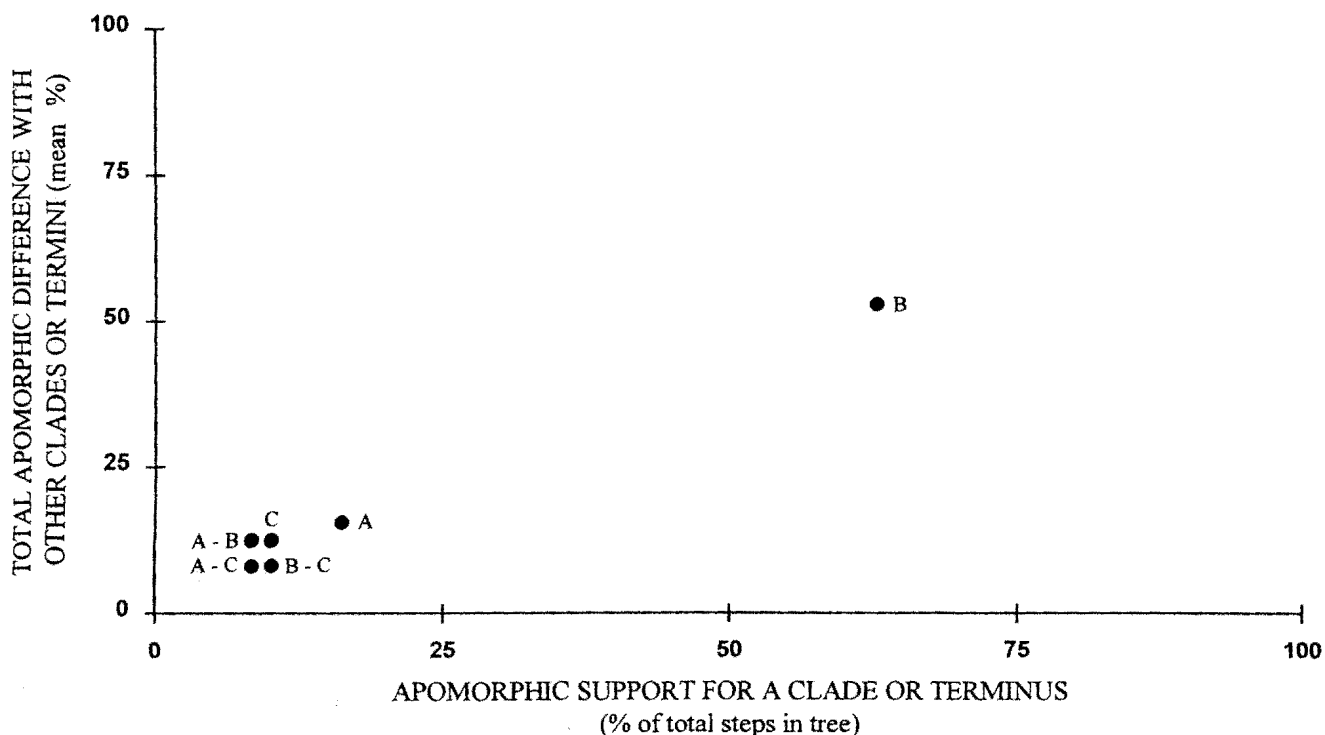


Fig. 3. Plot of hypothetical taxa (from Fig. 1) evaluated for apomorphic support for formal taxonomic recognition. Taxon B has a high level of support for treatment as a distinct taxon.

onomic groups. It is proposed to evaluate these data as follows. First, complete a cladistic analysis (see example in Fig. 1). Second, determine the degree of apomorphic support for a clade or terminus as a percent of the total steps on the tree (Fig. 1). The higher the percent of support of apomorphic character information, the greater the level of confidence for treating the unit as a formal taxon in the classification. Because this only stresses the total amount of apomorphic support, it is also necessary to compare these values with the total apomorphic difference between clades and termini with each other (Fig. 1). Any unit that is high in apomorphic support and also high in total mean apomorphic difference from other units must be treated as a distinct taxon in the classification (Fig. 2). Units scoring toward the lower levels of the spectrum of apomorphic support would not be recommended for taxonomic recognition based on apomorphic evidence alone (Fig. 2). Cladistic structure in these cases should be sufficient to reveal evolutionary information content of the group and result in predictive classification. Figure 3 gives the graphic results of the hypothetical example presented in Fig. 1, revealing strong support for taxonomic recognition for Taxon B. Some workers might wish absolute quantitative values for group recognition (obviously easily devised, if so desired), but I would caution against this. The point is not to have absolute values upon which taxonomic decisions are mandated, but rather to have a clear and explicit rep-

resentation of data that communicates how and why such decisions can and have been made.

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