

INVITED SPECIAL PAPER

INCONGRUENCE BETWEEN CLADISTIC AND
TAXONOMIC SYSTEMS¹

VERNE GRANT

Section of Integrative Biology, University of Texas, Austin, Texas 78712 USA

Cladistic and taxonomic treatments of the same plant group usually exhibit a mixture of congruences and incongruences. The question arises in the case of the incongruences as to which version is right and which is wrong. Many cladists believe that cladistics is a superior approach and gives the best results. There are several conceptual and methodological differences between cladistics and taxonomy that cause incongruence. One important conceptual difference is the use of different criteria for grouping: order of branching vs. similarity and difference (clades vs. taxa). Another is the policy regarding paraphyletic groups: to ban them in cladistics but ignore the ban in taxonomy. These two differences automatically lead to some incongruences. One approach is not right and the other wrong; each is operating by its own standards. However, when cladists apply the paraphyly rule to a taxonomic system and conclude that it needs revision to eliminate paraphyly, as cladists often do, they are judging the taxonomic system by a wrong standard. Several differences between the two schools in the use and handling of characters can also cause incongruence. First consider phenetic characters. Taxonomy uses a very wide range of these, whereas phenetic cladistics sets restrictions on the selection of characters, which deprive it of potentially useful evidence. Taxonomic systems generally rest on a broader empirical foundation than phenetic cladistic systems. Next, consider molecular cladistics, which is the leader in the use of DNA evidence. Two sources of incongruence between molecular cladistics and taxonomic systems can come into play here. First, the molecular evidence used in cladistics comes mainly from cytoplasmic organelles, whereas taxonomic systems are based on characters that are determined mainly by the chromosomal genome. More generally, the database in a molecular cladogram is, in itself, too narrow to serve as a foundation for an organismic classification. In cases of incongruence, the molecular evidence can be a reliable indicator of taxonomic relationships sometimes, misleading other times, and may afford no clear basis for a systematic decision. In this situation, it is helpful, indeed necessary, to integrate the molecular evidence with the phenetic evidence and bring more characters to bear on the question.

Key words: cladistics; molecular systematics; paraphyly; phylogenetics; systematics; taxonomy.

Research in plant systematics is currently being carried out by workers belonging to two main rival schools—cladistics (phylogenetics) and taxonomy—which have different conceptual frameworks and use different organizing principles, criteria, terminology, and types of evidence. Cladistic and taxonomic studies generally lead to partially different or incongruent results. Not surprisingly, cladists and taxonomists hold very different views regarding the value and role of their own field and that of the alternative school. The various differences between the schools will be discussed in this paper.

Systematic texts written by cladists present taxonomy as an old-fashioned field that has made valuable contributions in the past, but has a large subjective component, and is being replaced by the new cladistics with its set of objective formal procedures (e.g., Wiley et al., 1991; Moritz and Hillis, 1996; Judd et al., 1999, 2002). Some cladists even suggest that we abandon the Linnaean hierarchy (de Queiroz, 1997). In other words, cladistics is superior to taxonomy. We will examine this viewpoint.

A standard research protocol in plant cladistics is to pick a group with its existing classification system(s), subject it to a cladistic analysis, often a molecular cladistic one, plot the results on cladograms, compare these with the preexisting taxonomic system, note the incongruences, and conclude that the

system needs to be revised to conform to the cladograms. Examples are numerous in the current journal literature.

It will be shown that conclusions of this sort are unwarranted. Incongruences between cladograms and taxonomic systems of the same group are to be expected, especially in groups of large size. This is a result of the differences between cladistics and taxonomy in goals and methods. Cladistics produces cladifications, not taxonomic classifications, and the two differ in the way natural variation is grouped (Mayr, 1997; Mayr and Bock, 2002).

A division between cladistics and taxonomy is inevitable given the mutually exclusive criteria and methodology of the two fields. The division is reinforced by the promotional efforts of some strongly committed cladistics. Widespread misunderstanding of taxonomy among cladists is another contributing factor. However, although division cannot be eliminated entirely, it can be moderated. There is good reason for workers to combine the best results of the two approaches. Some cladists combine morphology-based taxonomy with cladistic results in the interpretation stage of the investigation; and some taxonomists, myself included, find molecular cladograms to be very interesting and valuable, and use them in their work. We will return to this aspect of the relationships between the fields in the discussion.

Attention is called here to some previous critiques of cladistics by taxonomists: Cronquist (1987); Stuessy (1990, 1997); Mayr and Ashlock (1991); Mayr (1995, 1997); Mayr and Bock (2002); Brummitt (1997, 2002); Turner (1998); Grant (1998, 2001a); Diggs et al. (1999) (Appendix 6); Diggs and Lipscomb (2002).

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TAXA VS. CLADES

Taxonomy throughout its long history has grouped natural variation or biodiversity according to similarity and difference. As Whewell put it (1859, book 16, p. 357): botanical classification depends on "the ideas of Likeness and Differences." The basic units, taxa, are similarity groups that differ from other similarity groups; and taxonomic classifications are groupings of lower-level taxa within higher-level taxa. Before Darwin, the similarity within low-level taxa was attributed to an Act of Creation and the hierarchy of taxa to the Plan of Creation. Since Darwin, of course, this pattern has been understood to be a result of branching phylogeny.

Darwinism brought about modifications of the similarity criterion. The goal is to block out monophyletic similarity groups. Similarities resulting from convergence are to be segregated into different taxa. It is recognized that microscopic or biochemical similarities may sometimes be more reliable guides to monophyletic relationships than gross morphological characters.

The systematic units of cladists are putative ancestor-descendant lineages or clades; and these are grouped into a hierarchical pattern of branching according to the order of branching. Thus, cladistics groups a different aspect of natural variation than the one used in taxonomy.

In some cases, there may be little or no difference between a cladification and a classification. Incongruences between the two modes of grouping are likely to appear in systems of units at middle or higher rank. Consider a midsize or large group containing an extant ancestral genus (A) and several different derived genera ($D_1, D_2 \dots$). Cladists will group these all in the same major clade, whereas a taxonomist will consider the character differences between the A and D genera and put them in different groups.

Brown (1938) found a nectary character that, with other characters, distinguishes an extensive line of evolution in the hypogynous dicots. In some members of the primitive family Theaceae (*Eurya*) and the more advanced family Clethraceae (*Clethra*), the basal part of the superior ovary is glandular and secretes nectar, but there is no disk-shaped nectary. In the hypogynous members of the Ericaceae, the basal nectary is a defined disk, and such a disk is present in the more advanced families Primulaceae and Polemoniaceae. These families range through a series of grades in other floral characters: free petals and numerous stamens (Theaceae); free petals and 10 stamens (Clethraceae); sympetalous with 10 stamens (Ericaceae); sympetalous with five stamens (Polemoniaceae, Primulaceae) (see Cronquist [1981] for details).

Cladists have restudied the group, using new and old evidence, and have confirmed the phyletic relationships of the core group, while making transfers of some peripheral families (Angiosperm Phylogeny Group, 1998; Judd et al., 1999, 2002; Anderberg et al., 2002). To emphasize phylogeny, they include the entire phylad in a single large order Ericales.

Accuracy or inaccuracy is not the issue in this case or in scores of other cases like it. The difference in treatment stems from the criteria used. If monophyly is the primary criterion, we get the cladistic order Ericales, which is very heterogeneous. For taxonomists, the objective is to group the Ericaceae and other similar families (Clethraceae, Monotropaceae, Epacridaceae, etc.) together in a relatively homogeneous, and thus more useful, order Ericales.

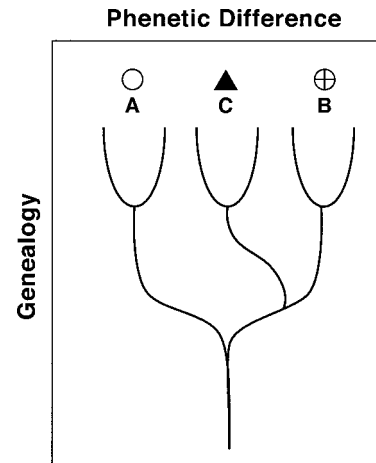


Fig. 1. Phylogenetic tree of three species groups, A, B, and C. Degree of phenetic difference between them is symbolized by circles and triangles. A and B are moderately different; C is very different from A and B. A, B, and C will be grouped in different ways by cladistics and taxonomy. Further explanation in text.

MONOPHYLY AND PARAPHYLY

Monophyly is defined differently in evolutionary biology and cladistics. In evolutionary biology, the term monophyletic refers to a group of organisms that is descended from its most recent known or inferred common ancestor (Haeckel, 1866; Mayr and Ashlock, 1991). A monophyletic group in the traditional sense of the word may include all or only a part of the descendants of the common ancestor, and the ancestor may be a taxon of various ranks. In cladistics, by contrast, a monophyletic group is a group consisting of *all* the inferred descendants of an ancestral *species* (Hennig, 1950, 1966; Mayr and Ashlock, 1991; Judd et al., 1999, 2002).

In cladistics, a group that includes only some of the descendants of the ancestral species is not monophyletic but paraphyletic. The objective of cladistics is to block out monophyletic clades. Therefore the elements of a paraphyletic group must be rearranged so that they do form one or several clades. Degree of phenotypic differentiation is not a criterion in the grouping of the organisms into clades.

Visualize a simple phylogenetic tree consisting of two primary branches, A and B, derived from a common stem species (Fig. 1). A and B are similar but well-differentiated species groups. A third branch C consisting of species that are phenotypically very different from A and B arises from the base of branch B. Taxonomists, applying the criterion of degree of difference, and unconcerned about paraphyly, may treat A and B as sections of one polymorphous but monophyletic genus and C as a distinct monophyletic genus. Cladists, on the other hand, may group A, B, and C into one all-inclusive clade or split the group into some smaller clades.

Thus a taxonomic system can be putatively monophyletic for taxonomists but paraphyletic and in need of revision for cladists. The terminological source of misunderstanding could be prevented if we used the qualifiers, monophyletic *sensu* taxonomy and monophyletic *sensu* cladistics, but we don't do this. Instead we have numerous instances of cladists declaring an existing taxonomic treatment to be nonmonophyletic when it is quite monophyletic by taxonomic standards.

Hileman et al. (2001) carried out a molecular cladistic analysis of *Arbutus* and related genera in the tribe Arbutae. *Arbutus* is a well-defined genus, well differentiated from related genera such as *Comarostaphylis*, *Arctostaphylos*, and several small genera (Wells, 2000). In the molecular cladogram, however, the western North American species of *Arbutus* are widely separated from the Mediterranean species of *Arbutus*. *Comarostaphylis* and *Arctostaphylos* lie between the two clades of *Arbutus*. Hileman et al. (2001) conclude that *Arbutus* is not monophyletic.

An alternative and more plausible interpretation of the cladogram of Hileman et al. (2001) should be considered. The genus *Arbutus*, consisting of relatively mesic trees, is basal in the tribe Arbutae and has diverged into two branches, a western North American branch and a Mediterranean branch, differing in inflorescence and leaf characters. The xerophytic shrubby genera *Comarostaphylis*, *Arctostaphylos*, and related small genera (see Wells [2000] for details) are derivatives of *Arbutus* in the western United States and Mexico. This plausible phylogeny would account for the nested position of the shrubby genera in the cladogram.

New genera originate from preexisting genera. The ancestral genus has often radiated into two or more sections in its particular adaptive zone. A new divergent species may arise from a species in a section of the ancestral genus, occupy a new adaptive zone, and, in time, radiate in its zone and become a new genus. When a cladogram is plotted for a group like this, it will show the pattern just described: primary clades (A and B) for sections of the basal genus and a nested clade (C) for the derived genus (Fig. 1).

The ban on paraphyletic groups is a source of much unnecessary confusion in systematics. The paraphyly concept belongs to cladistics, not taxonomy, and when it is applied to taxonomic classifications, as it commonly is, it conflicts with the similarity/difference criterion. The solution is to simply ignore or reject the paraphyly rule in taxonomy.

The paraphyly concept has been criticized by numerous authors: Cronquist (1987); Mayr and Ashlock (1991); Mayr (1995, 1997); Mayr and Bock (2002); Rieseberg and Brouillet (1994); Sosef (1997); Brummitt (1997, 2002); Grant (2001a); Diggs et al. (1999) (Appendix 6); Diggs and Lipscomb (2002). I have not seen any response to these criticisms.

PARAPHYLY VS. MONOPHYLY IN *GILIA*

Gilia (Polemoniaceae) is a large, multi-section, and taxonomically difficult genus. It was an artificial catchall genus in the nineteenth century but became progressively more natural in the twentieth century as disparate blocks of species were segregated out of it (see Grant [1999]). By the time of the Grant (1959) treatment, the more obvious disparate elements were gone and the genus was thought to be natural. But later work revealed some previously undetected disparate species.

The first of these was the *Gilia leptalea* group, which was segregated into a special section for holding purposes (Day, 1993a, b) and later transferred to *Allophyllum* (Grant and Day, 1999). Several other disparate species were also segregated out of *Gilia* at this time (Grant, 1999; Grant and Day, 1999). The core genus *Gilia* as presently constituted (in Grant and Day [1999]; Grant [1999, 2001a]) remains large and polymorphous, with two subgenera and six sections, but has enough common characteristics to justify the conclusion that it is monophyletic.

Johnson et al. (1996) and Porter (1997) made molecular cladistic analyses of the Polemoniaceae, using a chloroplast gene in the 1996 study and a ribosomal DNA segment in the 1997 study. The species of *Gilia* do not form a single clade in the molecular cladograms, but are dispersed among other temperate genera of the family. Johnson et al. (1996) concluded that the *Gilia* of Grant (1959) and Day (1993a, b) is extremely polyphyletic. They use the term "extreme polyphyly" as a conclusion based on their molecular cladograms. However, the incongruent part in the cladogram is a mixture of polyphyly and paraphyly (see Grant [1998, 2001a]).

Porter and Johnson (2000) expanded the molecular evidence into a cladification of the family. In this they segregate the *Gilia leptalea* group and *G. tenerrima* out of *Gilia*, as Grant and Day had also done (Grant, 1999; Grant and Day, 1999). In their system they go on to split the core genus *Gilia* (of Grant [1999] and Grant and Day [1999]) into six genera: a shrunken *Gilia* sensu stricto, three former sections elevated in rank (*Aliciella*, *Giliastrum*, *Saltugilia*), and two new small genera (*Dayia*, *Bryantiella*) (Porter and Johnson, 2000).

Some incongruences between the taxonomic and cladistic treatments are the result of making a new cladistic study of an old system and finding flaws in it, which have also been found and corrected by the taxonomists. These incongruences will be set aside for this discussion.

There remains the enormous difference between the taxonomic and cladistic treatments of the core genus *Gilia*: as a single multisection genus or as six smaller genera. This part of the overall incongruence is due to the difference between taxonomic and molecular cladistic concepts and methods. One treatment cannot be said to be right or wrong. However, there is an open question concerning the relative merits of the taxonomic and cladistic approaches. Furthermore, it is inappropriate to apply the term "polyphyletic" in its cladistic sense to a competent taxonomic treatment that differs from a molecular cladistic treatment.

The core genus *Gilia* (with usually $x = 9$ but also $x = 8$) is basal within the tribe Gilieae and is putatively ancestral to a group of genera with $x = 7$ (*Eriastrum*, *Ipomopsis*, and *Langloisia*) (Grant, 1959, 2001a). In the molecular cladogram of Johnson et al. (1996) the latter three genera are nested between the two subgenera of the core genus *Gilia*. For Johnson et al. (1996), this pattern means that *Gilia* sensu lato is "polyphyletic," or more correctly nonmonophyletic or paraphyletic. As I see it, the observed pattern is in agreement with the phylogenetic hypothesis outlined earlier of a polymorphous ancestral genus *Gilia* and a derived group of genera with $x = 7$ (Grant, 2001a).

PHENETIC CHARACTERS

External morphological features are always, of necessity, the first type of character to be used in the macrotaxonomic exploration of a plant group above the species level. Some of these morphological characters are discrete, but others are quantitative and hard to define. Micromorphological, cytological, physiological, and chemical characters have all found a place in the pantheon.

A broad database consisting of information about diverse characters and types of characters is essential for taxonomy. One line of evidence frequently conflicts with another line in a broad database, and then the question as to how to handle the discordant variation arises. Picking one prominent char-

acter and using it consistently will not do; long experience shows that this leads to artificial classifications. The opposite extreme is to use all available characters, pool them, and treat them by some morphometrical or biometrical method, so as to derive a quantitative measure of difference. This treatment has its place, but it also has a big disadvantage. Some characters are really more valuable markers than others, and the valuable characters can be swamped out by the trivial ones in computing a multicharacter index value.

A third way, which many taxonomists have adopted, sometimes intuitively, is to look for one or a few diagnostic characters that are supported by various other characters and that hold up throughout a group. We never know beforehand where in the exo- or endophenotype we will find the diagnostic character; it can be anywhere. And there is no formal recipe for finding it. The favorable conditions for discovery are a wide array of characters, an exploratory state of mind, and a trial-and-error approach.

There is a subjective element in the third approach. Two taxonomists working on the same group can emphasize different primary characters and obtain different results. The problem usually becomes resolved eventually with the search for and finding of additional characters. New characters often strengthen the case for one of the older classifications.

The third approach has a basis in evolution. Organismic groups are products of adaptive radiation. The ancestral species in an adaptive radiation has some pivotal character that enables it to occupy and diversify in a new adaptive zone. Taxonomists can use the pivotal character or some character associated with it as a key character. The key character may have an obvious adaptive value, as for instance seed pods and beans with stored nutrients in the Leguminosae, or its adaptive value may be unknown to us, or it may be simply a marker of the unseen true pivotal character. In any case, such a key character defines a natural group.

A cladistic analysis usually starts with an existing taxonomic system and uses the taxonomic characters employed in it. However, cladistics uses a selected subsample of the taxonomic characters. First, it uses the derived characters, but not the putatively ancestral ones. Second, it uses phenotypic characters that segregate into two or three discrete character states and rejects quantitative characters that exhibit continuous variation. Cladistics then processes the characters according to set formal protocol. Finally, cladistics analyzes the phenotypic variation so as to portray clades, not taxa.

The differences between cladistics and taxonomy in methodology can be expected to produce different results, and they do. I mentioned earlier the differences between the two schools in the way they circumscribe the order Ericales. These differences extend to the other orders of angiosperms as treated taxonomically by Cronquist (1981) and cladistically by the Angiosperm Phylogeny Group (1998) and Judd et al. (1999, 2002).

MOLECULAR CHARACTERS

DNA sequence data have often resolved systematic questions where phenotypic evidence was inconclusive and have revealed relationships that were not suspected on the basis of traditional characters. DNA evidence is intrinsically powerful. Many molecular cladists appear by their actions to regard it as a panacea for deciding systematic questions. Papers bearing titles like the following are common in the literature: "Phy-

logenetic relationships in the Crassulaceae inferred from chloroplast DNA restriction-site variation" (van Ham and Hart [1998], example taken at random).

The DNA that is currently being used in plant molecular systematic studies comes mainly from chloroplasts, mitochondria, and ribosomes. These are all organelles, and the first two are part of the cytoplasmic genome. Ribosomes are nuclear in origin, but are atypical in that category, being encoded in a special site on the nucleolus-organizing chromosome pair. The chromosomal genome, with the exception of this special site, is not represented in the sample of DNA being used in plant systematics and phylogenetics.

The chromosomal genome (exclusive of the nucleolus-organizing region) contains the Mendelian genes that determine the vast majority of phenotypic character differences that are used in plant taxonomy and morphological cladistics, as shown by numerous studies (see Grant [1975] for review). Molecular cladistics and morphology-based systematics are dealing with different parts of the overall genome.

Furthermore, a molecular cladistic study generally utilizes one or only a few genes, whereas the phenotypic characters used in morphological systematics are expressions of scores or hundreds of genes. The molecular database is good as far as it goes but is very narrow.

Molecular cladograms are being compared with phenotype-based classifications in one plant group after another in the current literature. In any given group, one frequently finds congruence between cladogram and classification for some characters and incongruence for others. This is as expected on the considerations presented previously.

Reed and Frankham (2001) assembled 71 cases in plant and animal groups in which data are available for both molecular variation and quantitative phenotypic variation. They computed the correlation coefficients between the molecular and phenotypic variation in the 71 datasets. The correlation is generally weak, with a wide range ($r = -0.88$ to $+0.90$) and a mean value of $r = 0.217$. These results show that molecular characters usually do not reflect accurately the quantitative phenotypic variation in a group (Reed and Frankham, 2001).

Chloroplast genes have been used extensively in plant cladistic studies. Chloroplasts are semi-independent organelles that can become disassociated from their normal nuclear genome (Rieseberg and Soltis, 1991). Consequently, a particular chloroplast gene may or may not be a reliable indicator of the overall genome of the species in which it is found, depending on its history.

Cronn et al. (2002) analyzed molecular characters in diploid species of *Gossypium* belonging to the various chromosomal genome groups (A, B, D, etc.). They used three types of DNA and one or more genes in each type: ribosomal DNA (one gene), other chromosome segments (11 loci), and cpDNA (four genes). The cladograms for the 12 loci in the two types of nuclear DNA are in agreement with the other evidence concerning phylogeny of *Gossypium*. But the cladograms for the four chloroplast genes are incongruent with this evidence and give incorrect phylogenetic indications.

Chloroplast gene trees differ from nuclear ribosomal DNA trees, not only in *Gossypium* as just noted, but also in Triticeae (Gramineae) (Kellogg et al., 1996), *Ceanothus* (Rhamnaceae) (Hardig et al., 2000), *Osmorhiza* (Umbelliferae) (Yoo et al., 2002), and *Phlox* (Polemoniaceae) (Ferguson and Jansen, 2002).

The species of *Eucalyptus* subgen. *Monocalyptus* in south-

eastern Australia and Tasmania are grouped into several taxonomic series. The cpDNA haplotypes are incongruent with the taxonomic subdivisions, but correlate with geographical areas. The species are known to hybridize when they coexist. In this group the cpDNA variation appears to reflect chloroplast sharing resulting from hybridization and not the primary divergence of the species (McKinnon et al., 1999).

A causal connection between hybridization and the spreading of chloroplast genes has been reported or suggested by a number of authors (see Rieseberg and Soltis [1991] for review). Examples in addition to *Eucalyptus* occur in *Zea*, *Triticaceae*, *Osmorhiza*, and *Phlox* (Doebley, 1989; Kellogg et al., 1996; Ferguson and Jansen, 2002; Yoo et al., 2002).

Some authors have held that the DNA sites assayed in molecular systematic studies are better indicators of phylogeny than morphological characters because the former are more or less isolated from environmental selection, whereas the latter are exposed to selection (e.g., Sytsma et al., 1990). There was never much empirical evidence to support this assumption; in fact there is some recent evidence against it. Populations of *Triticum dicoccoides* and *Hordeum spontaneum* living in ecologically different sites in Israel have different forms of ribosomal DNA that are correlated with the environmental variables. This finding suggests that at least some of the rDNA variation is determined by selection (Gupta et al., 2002; Nevo et al., 2002).

Assume, plausibly, that the organellar DNA sites used in molecular systematics often have a selective value. Then consider this assumption in the context of mosaic evolution, the evolution of different characters or genes at different rates in the same group. The combination of the two factors can explain discordance between molecular and phenetic indicators of systematic relationships. Genes in cytoplasmic organelles can change at a slow rate in a group while the chromosomal genome determining many phenetic traits evolves rapidly (or vice versa). Then the molecular evidence derived from organelles will indicate close relationships among lineages in the group, while phenetic characters indicate more distant relationships between the same lineages (or vice versa).

ARTIFICIAL SYSTEMS

The way in which characters are chosen determines the nature of the resulting classification. One way is to select a character in advance and use it to sort out the variant forms into classes. This is a recipe for producing an artificial system of classification. Some of the classes may be natural or monophyletic, but it is very unlikely that all of them will be so. The approach that has worked for building natural classifications is different. All available characters are considered, with no preconceived favorites; and sets of characters that define general similarities and differences are used. Often one or two of these are useful as key characters, but these are discovered, not selected beforehand.

A classical example of an artificial classification is the sexual system of Linnaeus (1753, 1759). Linnaeus used stamen number, other stamen characters, and carpel number to group angiosperms into 23 "classes." The system puts unrelated genera in the same class (e.g., Pentandria), puts related genera in different classes in some cases, and has some natural or nearly natural classes (e.g., Tetradyamia, equivalent to the Cruciferae). A 24th class, Cryptogamia, was set up for non-

flowering plants. Linnaeus realized that the sexual system was artificial and regarded it as a precursor to a natural system yet to be constructed.

Modern revisions and treatments based on molecular cladograms for one or a few genes have the attributes of the old artificial systems. A molecular character is selected in advance by the worker(s); its variant forms are recorded throughout a group; and the group is subdivided according to the molecular character.

Johnson et al. (1996) surveyed the chloroplast gene *matK* throughout the family Polemoniaceae, drew the cladograms, and blocked out a series of subgroups designated by informal names. Porter and Johnson (2000) then used the *matK* gene and several other organelle genes as a database for a formal system of named taxa. The arrangement of the taxa parallels the clades in the molecular cladograms. The primary clades become subfamilies, the secondary clades become tribes, and the third-order clades are genera or small sets of genera. The classification lacks phenotypic diagnosis of the taxa, but has good descriptions (see Grant [2001a] for analysis).

This cladification can be compared with broad-based taxonomic systems of the family: the old one (Grant, 1959), which was out of date in some respects when molecular studies were started in the 1990s, and more recent revisions, which took the molecular evidence into consideration (Grant, 1998, 1999, 2001a; Grant and Day, 1999). The chloroplast gene *matK* is a pretty good marker, and there is much congruence between the taxonomic and molecular systems. But there are also many incongruences. The molecular system has many unnecessary small genera. Some molecular groups are polyphyletic from failure to use characters of pollen morphology (see Grant [2001a]).

Molecular cladograms are very valuable. How useful they are depends on how they are handled at the stage of interpretation. A molecular cladogram that is translated directly into a cladification or classification is likely to yield a partly artificial system. The traditional taxonomic approach of integrating new evidence with other lines of evidence and making informed judgement decisions will generally produce better results.

BACKGROUND KNOWLEDGE

Taxonomists working on a revision or monograph routinely study their plants in the field and garden, where feasible, as well as in the herbarium. These contacts build up a body of background knowledge and perceptions about the plants, which is hard to quantify but which contributes to sound taxonomic decisions.

Some individual cladists do likewise, but some do not. In either case, familiarity with the plants in the field and garden is not a requirement in the protocol for a cladistic analysis. Furthermore, there is no place in the cladogram to put subtle but significant impressions about plant affinities. Cladifications have to make do with a narrower information base than that in taxonomic classifications.

This difference in approach has a bearing on the problem of identification of plant materials used in a revisional study. A taxonomist or cladist who has studied a group in the field and herbarium can make correct identifications. But what is the source of the identifications in a molecular cladistic study by a strictly laboratory worker? Is it the name on herbarium sheets that provide tissue samples? This could

be very misleading. Identification is no small problem, but is rarely addressed in the materials and methods section of cladistic papers. The potential for error in published results is very real.

DISCUSSION

Incongruences are ubiquitous in comparisons of cladograms with taxonomic classifications. How do we handle them? Advocates of cladistics claim that it has a more repeatable and objective method than taxonomy and is the preferred approach (e.g., Wiley et al., 1991; Moritz and Hillis, 1996; Judd et al., 1999, 2002). In cases of incongruence, the cladogram can be presumed to be correct. Let us examine this assumption. We will compare the cladistic and taxonomic approaches with respect to six indicators of effectiveness in reaching their respective goals.

(1) Cladistics is based on inferred phylogenies, which makes for an uncertain foundation. Phylogenies of groups above the species level are, with rare exceptions, unverifiable hypotheses. Taxonomic systems are based on observable characters and do not rest on phylogenetic hypotheses.

(2) Cladograms can be tested for accuracy in special cases in which we have a known pedigree, as in cultivated plants and long-term selection experiments. Such tests have been carried out in species of *Avena*, *Hordeum*, *Gilia*, and *Helianthus*. In each case the cladogram differed significantly from the known pedigree. Both reticulate and dichotomous pedigrees were represented in the set of cases (Grant, 2001b). It is well known that cladograms do not pick up reticulate evolutionary patterns; we find that they do not always get dichotomous branching patterns right either.

(3) Taxonomic methods are designed to organize natural variation into similarity groups (taxa) and hierarchies of such groups (classification systems). Cladistics does not do this; it identifies clades and produces cladograms. Some incongruences between classifications and cladograms of the same group develop as a result of the differences in the units used, taxa or clades. In such cases, both systems may be correct by their own standards.

(4) Cladistics places an arbitrary ban on paraphyletic groups, whereas paraphyly is a nonissue in taxonomy. Application or nonapplication of the paraphyly rule can make a large difference in a system. The system can have one arrangement of groups in a taxonomic classification and a different arrangement in its cladistic version because of the paraphyly rule alone. Where paraphyly is a source of incongruence, the incongruence should be regarded as an artifact of the cladistic method and is not a sufficient reason to revise the taxonomic system.

(5) One of the big differences between taxonomic classifications and cladograms is the breadth of the information base. This base is very broad in taxonomy in which no class of characters is excluded from consideration. It is narrower in morphological cladistics because of the exclusion of certain types of potentially valuable characters, and it is extremely narrow in molecular cladistics. Taxonomy has a more inclusive empirical foundation than cladistics.

(6) One area in which cladistics is superior to traditional taxonomy is the use of DNA evidence. Molecular cladograms often show some incongruences with existing classifications. The conflict between molecular and traditional characters presents a problem and should be handled on a case-by-case

basis. Some molecular evidence may point to desirable changes in the classification. Or the phenotypic evidence may be strong enough to override a molecular character in another case and may warrant retention of the status quo pending further study.

The comparisons just made do not support the presumption of a superiority of cladistics. The two schools are about equally effective, each in its own way, in two indicators (nos. 3 and 4). Cladistics is superior in one way (no. 6). Taxonomy is the better approach in three indicators (nos. 1, 2, and 5). The relative merits of the two schools are not as simple as the advocates of cladistics make them out to be.

We can also compare the two schools with respect to the usefulness of their products for society. There is a long-standing social need for similarity/difference classifications. This is why they have existed since prehistoric times (see Whewell, [1859], book 16, p. 357). First, there were the folk classifications, then the herbals of medicinal plants in the European Middle Ages, then the pre-Darwinian taxonomists, then evolutionary taxonomy. In modern societies, taxonomic classifications are used for identification and information retrieval by the general public, by people in technological fields, and in biological research (including cladistics).

Cladistics has no such general constituency. Phylogeny is of only secondary interest to most people including most kinds of biologists. Who needs a crocodile-bird clade when we already have a bird taxon and a crocodile taxon?

Some cladists see systematics going in the direction of cladistics in the future (e.g., Wiley et al., 1991; Moritz and Hillis, 1996; de Quieroz, 1997; Judd et al., 1999, 2002). This prediction doesn't take into account the special merits and general usefulness to society of taxonomy. It is more likely that, for the present and immediate future, we will have a dual presence of both taxonomy and cladistics (Brummitt, 1997, 2002). It is also likely and desirable that the two schools will interact synergistically with one another.

Sorting organismic variation into natural groups is not an exact science. The variation is multifaceted, the evolutionary processes involved are multifarious, and the true phylogeny is usually unknown. Taxonomy accepts these realities and recognizes the need for some subjective judgements in building classifications. Cladistics was invented for the purpose of improving on taxonomy (Hennig, 1950, 1966). Classification was to be based on phylogeny, and phylogeny was to be reconstructed by an explicit objective protocol. How well does this plan work in practice? It works sometimes, but it is not good enough. In cases in which classifications can be compared with up-to-date taxonomic classifications, the former are not consistently better, and sometimes the classifications are better, as we have seen.

In this situation, the best results can be obtained by combining the strong points of the two approaches. For example: (1) The taxonomic order *Ericales sensu stricto* of older authors (Cronquist [1981] and others) is more generally useful than the cladistic order *Ericales sensu lato* (s.l.) of Judd et al. (1999, 2002). Preserve the *Ericales sensu stricto* for general use (and retain *Ericales* s.l. in cladistics.) (2) Let's not attempt to apply the paraphyly rule to taxonomic classifications where it does not fit and only causes distortions in the system.

(3) The greatest strength of cladistics lies in its use of molecular evidence. The molecular cladograms can be and are translated directly into sets of molecular clades. However, it is

highly desirable to incorporate the molecular evidence in taxonomic classifications. To do this effectively, the molecular evidence should be handled in the taxonomic way; that is, weigh molecular characters in the balance with other types of characters, and exercise taxonomic judgement to resolve conflicts in the evidence.

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